Wild Birds in Urban Gardens: Opportunity or Constraint?

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Summary

This thesis examines whether urban residential areas, where small private gardens are the main wildlife resource, offer wild birds ecological opportunities as habitat or impose ecological constraints on them. Ecological opportunities should facilitate the establishment of an avifauna that does not depend on immigration, is similar in composition and structure to those in less-urbanised gardens and comprises individuals within normal ranges of biometrics, behaviour and condition. Ecological constraints may compromise the sustainability of this avifauna and restrict successful exploitation of the habitat to birds of particular characteristics.

The analyses presented first investigate which bird species urbanise and why, and secondly which species use gardens and how. Patterns and trends in the use of gardens by British birds are examined, in general and in urban areas. A case study builds on these two themes, linking urban and garden ornithology by investigating an avifauna that uses gardens as its primary habitat but within a highly-urbanised context. Field studies of the breeding avifauna and some aspects of its ecology are presented, together with data from a ringing study on the use of feeding stations and the mobility and persistence of individual birds.

More bird species urbanise than might be expected and urbanisation is not restricted to species with high behavioural flexibility. Gardens are an extension of natural habitat for many species, but in urban gardens utilisation rates are declining more than in gardens elsewhere, raising concerns for urban conservation policy. Small gardens in a highly-urbanised area support a breeding avifauna that is of low density but appears sustainable and of stable composition with individual birds maintaining normal territoriality and persisting over time. The spatial distribution of breeding territories is related to all-year artificial feeding but not to cat activity, and the mechanisms of birds' adaptation to urban life show interesting variation between species.

Contents

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Dedication

Sue Lincoln .... who sacrificed much more for this thesis than I did. Love and thanks ♥

Declaration

Chapter 4 of this thesis was previously published as Cannon, A. R., Chamberlain, D. E., Toms, M. P., Hatchwell, B. J. & Gaston, K. J. 2005, Trends in the use of Private Gardens by Wild Birds in Great Britain 1995 - 2002. *Journal of Applied Ecology* **42**, 659-671. I originated the calculation of Garden BirdWatch reporting rates and managed the data collection while employed by the BTO between 1997 and 2001; it was previously managed by D. K. Toomer and subsequently by M. P. Toms. I performed all analyses and drafted the ms; DEC suggested the trigonometric regression technique.

Chapter 5 is based on a manuscript submitted to *Biological Conservation* under the same authorship; I performed all analyses, drafted the ms and substantially re-wrote it for this thesis based on re-analysis and referees' comments.

1. Introduction and review of literature

1.1. Introduction

It is an everyday observation that despite the antipathy of urbanisation to biodiversity in general, cities and towns nonetheless support wild birds. Not only are urban avifaunas of ecological interest *per se*, their persistence despite habitat fragmentation and distortion, competition from commensal species, abiotic peculiarities and extreme disturbance may provide insights into how wildlife in modified habitats elsewhere can be helped. Furthermore, as global urbanisation continues, urban avifaunas are becoming of greater relative importance. Habitats associated with human habitation already support more than 20% of the British populations of Blackbird and the red listed Starling and Song Thrush (Eaton et al. 2004; Gregory & Baillie 1998). Although only 10% of British landcover, urban habitats hold between 17 and 62% of the populations of a number of other species (Noble et al. in press) including an estimated 54% of Starlings and 62% of House Sparrows (Crick et al. 2001), the latter now also red listed. Hence, they are increasingly appropriate targets for research and conservation efforts, the collateral benefits of improved awareness and quality of life maximised among dense populations. According to UN criteria around 47% of the world population and 90% of the U.K. population lived in urban areas by 2000. Worldwide, about 160,000 people move from rural areas to cities every day (United Nations Population Fund 2002).

This thesis reports a programme of work undertaken to improve understanding of some of the ecological opportunities and constraints applicable to wild birds in urban habitats. In particular, whereas most urban bird studies to date have focused on parks or other ecologically anomalous green spaces, this research considered the birds using a little-studied but important urban habitat: private gardens. In this introductory chapter, the general characteristics of the urban environment as wild bird habitat are outlined. The specific issues examined in subsequent chapters are then introduced and relevant literature reviewed. Finally, an outline is presented of the various approaches taken in subsequent chapters to increase understanding of these issues.

General treatments of urban ecology have long been available in professional and popular literatures (e.g. Adams 1994b; Baines 1986) but recently research interest has increased (Jensen 1998; Nilon et al. 1999; Pickett et al. 2001; Walbridge 1998). Urban ornithology has grown in parallel; several summaries of urban bird ecology are now available (e.g. Bowman & Marzluff 2001; Marzluff et al. 1996; Savard et al. 2000).

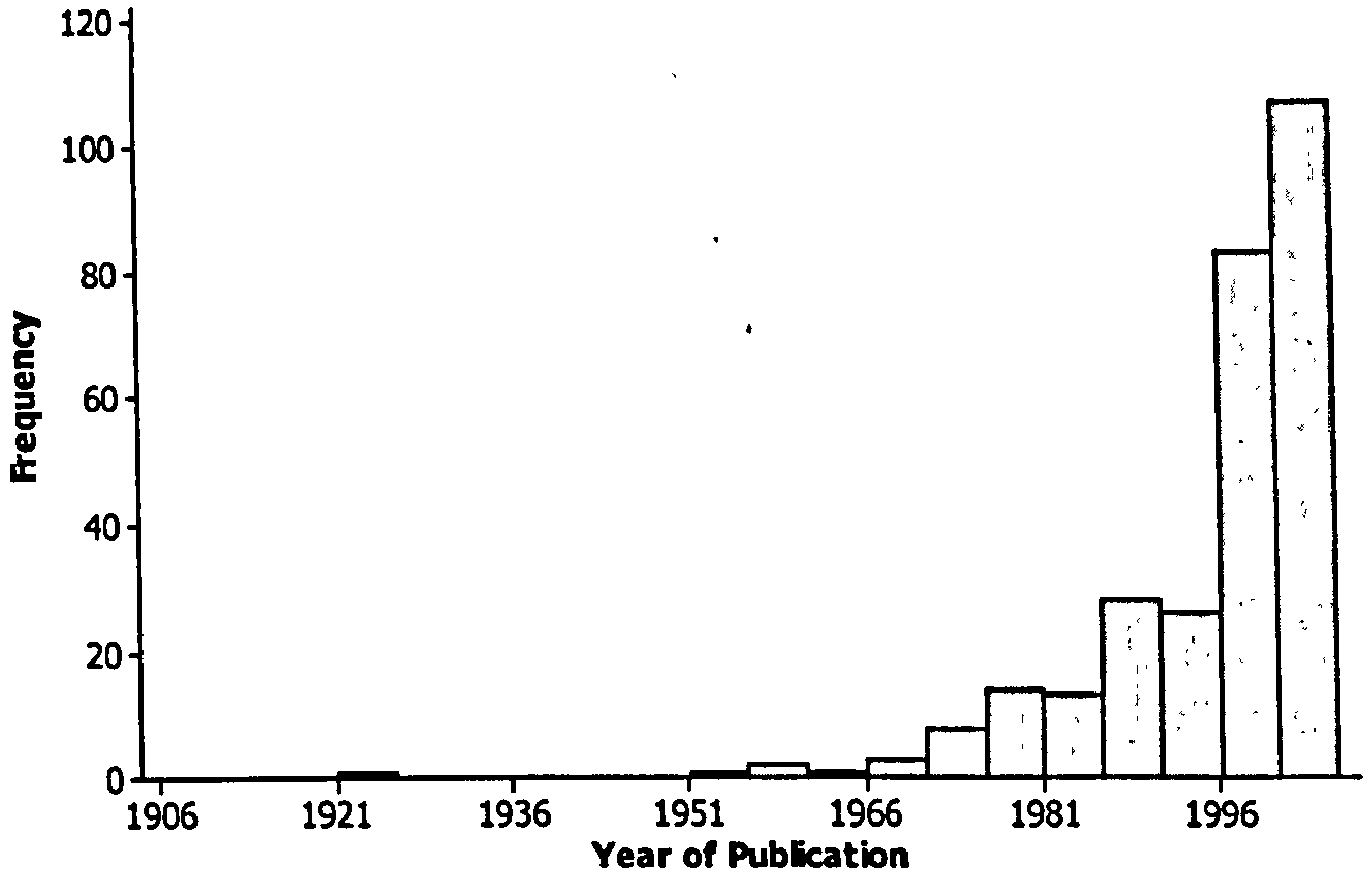

Figure 1.1. Frequency distribution of years of publication of 287 urban ornithology references consulted for this thesis. After Marzluff, Bowman et al. (2001b)

Around 75% of studies located by Marzluff, Bowman et al. (2001b) were from the last 20 years and figure 1.1 illustrates a similar bias in literature reviewed for this thesis. The European literature, however, does include some older work (e.g. Batten 1972; Erz 1964; Gladkov 1958, 1960 in Konstantinov 1996; Pitelka 1942; Simms 1962; Snow 1958) and the invaluable legacy of a generation of east European ornithologists constrained from wider travel (L.Tomialojc 2002 pers. comm).

Adams (1994) acknowledges Dasmann's (1966 in Adams 1994b) exhortation to "get out of the woods and into the cities" as a turning point in conservation biology. Urban biodiversity conservation and science now enrich people's lives in their home environment (Harrison et al. 1987); urban birds are particularly important in this context, being diurnal, visible, and often regarded sympathetically (Clergeau et al. 2001b) as well as being environmental indicators (Furness & Greenwood 1993). Even apparently pristine habitats are unlikely to have escaped human influence (Grayson 2001; Vitousek et al. 1997) so the faunas of modified habitats are relevant to almost all ecology. Understanding the dramatic ongoing changes in urban habitats may help predict more widespread future changes (Pickett et al. 2001) and characteristic features of urban ecosystems exemplify key themes in modern ecology, notably the prevalence of invasive alien species (Niemela 1999) and biotic homogenization (McKinney &

Lockwood 1999). Bird urbanisation can be seen as an 'ecological experiment' (Erz 1966), imposing "unprecedented and intense manipulations" (McDonnell & Pickett 1990) and offering accessible insights into processes and patterns, although research in habitats where biodiversity preservation and human exploitation interact is always challenging (May 1999). Mobile and subsidised, urban birds may not be appropriate 'umbrella' (Fleishman et al. 2000), 'focal' (Lindenmayer & Fischer 2003) or 'keystone' (Mills et al. 1993) species in any ecological sense, but they are 'touchstone' species for humans; visible and charismatic totems of wildlife and its conservation that perform "a strategic socio-economic role" (Walpole & Leader-Williams 2002), contributing to urban sustainability by engaging human supporters (Nilon et al. 1999). Inevitably incorporating human influences and socio-economics, urban ornithology is an ecology *of* urban habitats rather than ecology *in* urban habitats (Grimm et al. 2000).

Classifying habitats as more or less urban seems simple, but repeatable, standardised classification has become more complex as urbanisation rates outstrip urban population growth (Pickett et al. 2001). Possible metrics include position within spatial structure of conurbations, human population density and landscape characteristics. Spatial structures of cities are increasingly variable, with development clusters (Makse et al. 1995). Sometimes 'urban sprawl' has clear urbanization gradients that correlate with bird data (Crosby & Blair 2001). Elsewhere, 'exurban' or 'edge city' humans interface with non-urban birds (Greene 1997). Meanwhile, urban centres are redeveloped; such distortion of traditional concentric urban morphologies and linear urbanisation gradients complicates habitat characterisation (Alberti et al. 2001), as in Naples where bird diversity correlated with an urbanization gradient but presence/absence data did not (Mirabella et al. 1996). Nonetheless, both simple (Clergeau et al. 1998; Odell & Knight 2001) and complex (1996; 2001a; Melles et al. 2003; 2000) urbanisation gradients have successfully been identified but they remain "difficult places to carry out ecological research" (Matson 1990).

A figure of 620 people km^{-2} is cited as the US Census definition of 'urban' by McDonnell and Pickett (1990), more recently the US Census adopted thresholds such as population of 2,500 with density of 386 people km^{-2} (Gibson 1998); both seem low, the case study area for this thesis has over 2000 households km^{-2} and Singapore has >5800 humans km^{-2} (Soh et al. 2002). Simple metrics may be culturally biased but combined population and landscape measures have proved useful (Gorski 1997; Marzluff et al.

2001b). Opdam & Wiens (2002) identified dissection, perforation, fragmentation, shrinkage and attrition as five stages of natural habitat loss for a typology of relative urbanisation. Simpler metrics can mislead; 60-80% of typical temperate cities meets a conventional definition of 'forest' (Rowntree 1984 in Adams 1994). Comprehensively classifying urban land cover is time-consuming (Freeman & Buck 2003) but quantitative categorisations are essential, with landscape, vegetation and land use metrics (Marzluff et al. 2001a), which require standardization (McIntyre et al. 2000). Even in parks within the same biogeographic area, variations in origin, vegetation, management and surrounding land use differentiate their avifaunas (Tomialojc & Profus 1977), and even when age, location and host culture are known, simple habitat metrics such as proportion of green space are highly variable (e.g. Gorski 1997).

In 41 of 101 urban bird studies reviewed by Marzluff, Bowman et al. (2001b) the urban setting was not quantified at all; at the very least, authors should record study area size, estimated proportion of green space and human population. Furthermore, human activities, such as provision of quasi-natural habitat and supplementary food in private gardens, may subsidise bird populations such that simple relationships between relative urbanisation metrics and bird communities break down. The case study habitat in this thesis scores highly on quantitative urbanisation metrics, yet supports bird species that are not primarily urban. 'Top down' habitat metrics are essential, but arguably 'bottom up' observations of species occurrence and persistence are also meaningful in terms of assessing relative urbanisation of a habitat from the birds' point of view.

Basic ecological parameters of urban environments are more repeatably measurable. Differentiating abiotic factors include the urban heat island effect (Adams 1994b) that promotes winter roosting (Feare 1984) and range expansion (Williamson 1975), although in low latitudes cities may be cooled by watering of plants (Pickett et al. 2001). High abstraction and runoff lowers water tables despite higher precipitation (Adams 1994b); waterbirds face variable levels, summer drying, turbidity, channelisation and higher water temperatures, though the latter can augment habitat, the banks of the river Don in Sheffield were colonized by Fig trees when waterborne seeds germinated, warmed by steelworks (Gilbert & Pearman 1988). Aquatic biotopes greatly influence the composition and diversity of urban avifaunas (Bozsko 1985).

Artificial light may advance breeding (Bartholomew 1949 in 2004) and light affects the starting time of the dawn chorus (Thomas et al. 2002). Urban daylight has high ultraviolet (UV) content (Heisler & Grant 2000); iridescence or reflectance affects prey visibility (Church et al. 1998; Siitari et al. 1999; Vulinec 1997). In Vienna, Kestrels caught flying moths at night around a floodlit tower but disappeared when the UV component of the light was filtered (Sachslehner 1996). A particular issue with nocturnal urban lighting is bird collisions (e.g.Cochran 1958), fatality rates can be ameliorated by lighting reduction (Ogden 2002). Coastal town illumination attracts migrating seabirds (Podolsky 2002) and birds also collide with buildings during the day (Bower 2000; Klem 1990) and with telecommunications towers (Jackson 2004); for a bibliography of bird impacts with structures see Trapp (1998). Urban noise may affect birds (Adams 1994b); their hearing differs from that of mammals (Slabbekoorn & Smith 2002) and many hunt by sound (Montgomerie & Weatherhead 1997) but some species cope with noise (Benson 1995; Rheindt 2003) by adjusting song volume (2004; Brumm & Todt 2002) or frequency (Slabbekoorn & Peet 2003). Pollution may contribute to urban House Sparrow declines, (J.D.Summers-Smith *pers.comm.*); birds absorb pollutants from food, water or dust deposition on their plumage (Dmowski 1999; Hui 2002). Nestling Blue and Great Tit faeces had increased concentrations of lead, cadmium, arsenic and copper at polluted sites (Dauwe et al. 2000) but pollution effects are hard to assess and species-dependent, for example pollution stress in Great Tit nestlings was detectable at morphological and ecological but not biochemical levels, whereas in Pied Flycatchers it was detectable at all three (Eeva et al. 2000).

Biotic factors differentiating urban habitats include disturbance and predation and vegetation composition and structure. Most studies of anthropogenic disturbance examine waders and waterfowl, in which recreational disturbance typically reduces breeding success and favours common opportunistic species (Hockin et al. 1992). Disturbance from adjacent urbanization affected Nightjar numbers on heathland (Liley & Clarke 2003), but in North America Caprimulgidae feed and nest in urban environments (Bowles 1921; Marzilli 1989; Wedgwood 1973). Some studies have found little or no effect (Bolger et al. 1997; Mörtberg 2001; Sauvajot et al. 1998), others negative effects (van der Zande et al. 1984 in Mörtberg 2001); avian disturbance literature in an urban context is reviewed by Fernandez-Juricic et al. (2001).

Two opposing factors influence urban nest predation. Optimum sites that minimise predation (e.g. Martin et al. 2000) may be scarce in urban habitats; predation rates were higher in Finnish town centres (Jokimäki & Huhta 2000; Jokimäki et al. 2005) and artificial nest predation rates in Florida suburbs increased with housing density (Thorington & Bowman 2003) although assessing predation with artificial nests is notoriously problematic (e.g. Blair 2004; DeGraaf et al. 1999; Grégoire et al. 2003). On the other hand, the absence of woodland nest predators from urban habitats can improve survival (Chamberlain 1994; Orell 1989; Simons et al. 2000; Snow 1988; Gering & Bair 1999 in Thorington & Bowman 2003; 1977). Relationships between predation and urbanisation are affected by differences in predator communities; in some countries mammals such as Martens predate urban nests, in others predation is dominated by birds such as Magpies (Clarkson & Birkhead 1987) and Jays, which experience increased predation themselves as larger corvids urbanise (Jerzak 1995; Marzluff & Balda 1992). In one study, birds attacked more nests near paths but mammalian predators were more active away from them (Miller & Hobbs 2000), in another, Blackbirds nesting nearer human activity were more productive and less discriminating in site selection (Osborne & Osborne 1980). Predation in Polish and London parks decreased with human activity (Tomialojc 1979; Tomialojc & Profus 1977) but Russo & Young (1997) found urban and especially suburban predation rates much higher than in rural habitat. The evidence is mixed; urban predation is sometimes lower than non-urban in Europe but higher in North America (Morneau et al. 1994), and "one can imagine reasons for both higher and lower rates" (Bland et al. 2004).

Urban bird habitats have built and vegetative components, both highly modified compared to natural alternatives. Buildings dominate in core urban areas where, in general, only species that nest on them sustain populations. Swift, House Sparrow, House Martin and Feral Pigeon are commensal, other flexible species exploit natural nest site substitutes, including Jackdaw, Raven, Peregrine Falcon, Kestrel and arboreal and montane pigeons such as the Speckled Pigeon and White-collared Pigeon in Africa (Goodwin 1979). Beijing was once known as 'the city of Swallows' (Jackson 1992 in Adams 1994). Where vegetation provides food, cavity nesters such as tits, Pied Wagtail, Wren and Robin exploit pipework and gaps in masonry; buildings clad with plants host a still wider range of nesters such as Blackbird and even Mallard. Fisk (1978) noted 22 species nesting on urban roofs, including cliff nesters, ground nesters and opportunists like gulls, which have been doing so for more than a century although numbers have increased recently (Belant 1997); UK urban gulls can have higher nesting success than traditional colonies (Raven 1997) but productivity was lower than non-urban colonies in Ohio, USA (Belant et al. 1993). Derelict buildings also support birds, Black Redstart most famously in the UK (Frith & Gedge 2000).

Urban vegetation often differs from that of surrounding areas and generally cannot replace natural forest in terms of bird communities (DeGraaf 1987). Even natural habitats retained within development change; between 1968 and 1986, 30% of plant species were lost from forest stands conserved within a Toronto development (Boyer et al. 1986 in Adams (1994)). Street trees exemplify structural and taxonomic simplification in urban vegetation; they produce a step increase in nest site availability upon attaining a suitable size; most London Plane trees in the UK are still growing, their parent species has mature girth of 12m (Chengappa 1999). Urban House Crows have tree morphology preferences (Soh et al. 2002) and street trees predicted Magpie distribution in Manchester, dense canopy species offering protection from Carrion Crows were preferred (Tatner 1982b). Canadian urban Merlins use abandoned corvid nests in urban trees (James 1988) and wooded Madrid streets were feeding or nesting habitat for 14 bird species although ground, scrub and hole nesters were absent and roads connecting parks had more diverse avifaunas (Fernandez-Juricic 2000).

One of the main vegetated habitats is amenity green space, typically grass with scattered trees and shrubs, controlled succession and simplified vertical structure (Adams 1994b), replicating early succession and climax vegetation (Niemela 1999) but offering little for disturbance-sensitive scrub nesters (Fernandez-Juricic et al. 2001), urban humans preferring sightlines and permeability (Harrison et al. 1995; Luymes & Tamminga 1995). Tree densities may approach those of non-urban forest (Lawrence 1995 in Pickett et al. 2001) and cavity-nesters do well, especially if provided with boxes (Luniak 1992). Generally, parks support more species than other urban habitats (Fernandez-Juricic & Jokimaki 2001), particularly if large (Baker 1988; Fernandez-Juricic & Telleria 1999; Gavareski 1976; Jokimäki 1999; Mason et al. in press; Mörtberg 2001; Park & Lee 2000; Sinclair et al. 2004), although Willow Tits use small forest fragments (Helle 1984 in Mörtberg 2001) but did not use similarly sized urban fragments. Assuming bigger is always better ignores the contribution of small patches to species accumulations, particularly in urban environments where conserving small patches is the only option (Fischer & Lindenmayer 2002). However, persistence in small fragments of aggressive species such as Noisy Miner (Mac Nally & Horrocks 2002; Major et al. 2001) or dominant synanthropes amplify the effects of patch size reduction on shyer species. Nonetheless, lower bird diversity in small parks does not always mean fewer birds; smaller forest remnants in Stockholm had higher bird densities (Mörtberg 1996 in Mörtberg 2001) and in Poland small parks have breeding densities higher than nearby forest (Tomialojc 1970; Tomialojc & Profus 1977). Other public areas providing habitat include city farms (Sorace 2001) and cemeteries (Thomas & Dixon 1974 in Adams 1994b; Kocian et al. 2003; Lussenhop 1977).

Parks exemplify the fragmentation of urban vegetation; much urban ecology literature invokes island biogeography and metapopulations (e.g. Fernandez-Juricic & Jokimaki 2001; Niemela 1999; Rudd et al. 2002). However, Tworek (2002) found some species responded positively to non-urban habitat fragmentation, though others were negatively affected (Roslin 2002). Simple 'habitat/non-habitat' island analogies fail to adequately describe urban habitats due to interspecific variation in fragmentation scale (Opdam & Wiens 2002) and preferred structure (Bolger et al. 2001), to birds' high mobility (Brotons et al. 2003) and because edges are as important as size; due to regeneration failure (Moran 1984 and Bagnall 1979 in Pickett et al. 2001) urban forest patches have the type of open margins at which nest predation, for example of Indigo Buntings (Suarez et al. 1997), is higher than at natural edges with plant succession. Reviews of habitat fragmentation and productivity (Maina & Jackson 2003; Paton 1994; Stephens et al. 2003) emphasise the roles of predation and disturbance in edge effects.

1.2. Differentiating urban avifaunas

The first section of this thesis examines the differentiation of urban and non-urban avifaunas. Certain avifaunal characteristics have become dogma of urban ornithology (e.g. Adams 1994b; Chace & Walsh 2006; Emlen 1974; Erz 1966; Huhtalo & Järvinen 1977; Marzluff 2001; Marzluff et al. 1996). Urban avifaunas are relatively species-poor with generalist, broad niche species doing well but specialists disadvantaged, and often high in overall biomass, largely accounted for by core urban species. The extent to which these characteristics apply depends on the degree of relative urbanisation from the birds' point of view. This can be hard to quantify, particularly in the little-studied habitat between the centres of cities and their periurban fringes that provides the case study for this thesis: high density residential areas that are highly-urbanised on most metrics yet support bird species that are not exclusively commensal, often originally of woodland edges (e.g. Simms 1962; Tomialojc 1998). The avifaunas of these 'second-tier urban' habitats show a characteristic duality (1998); core urban and non-urban avifaunas mingle. In a sense, they are a meeting point of 'resource breadth' and 'resource availability' bird distributions (Gregory & Gaston 2000); broad niche species such as Blackbird mix with commensals such as House Sparrow.

Bird communities simplified with increasing urbanization in all but one of 14 studies reviewed by Clergeau et al. (2001a), in Massachusetts (DeGraaf 1981), in Rennes and Québec (Clergeau et al. 1998) and in seven types of anthropogenic landscapes in Russia (Konstantinov 1996). Diversity can decline within urbanisation despite negligible apparent habitat change (Jones & Bock 2002). Its decline is not confined to temperate cities (Reynaud & Thioulouse 2000), nonetheless urban habitats do not always have the lowest integrity bird communities (O'Connell et al. 1998a; von Euler 1999) and diversity of some guilds can increase (Smith 2002). Typically, ten or fewer abundant species dominate core urban avifaunas (Johnsen & Vandruff 1987 in Adams 1994b; Huhtalo & Järvinen 1977; Luniak 1996) with density and species richness inversely related (Clergeau et al. 1997; Dulisz & Nowakowski 1996) although in smaller towns, central synanthrope concentrations may not arise (Huhtalo & Järvinen 1977; Vogrin 1998). Generalisation is complicated by variations in urban form, seasonality and rapid population change but city centre bird densities are frequently higher than in nearby non-urban habitats (Bland 1979; DeGraaf 1981; Tischler 1955 in Erz 1966; Luniak 1977; Mitschke & Baumung 2001; Sasvari 1990), and even raptors, such as Eastern Screech Owl (Gehlbach 1988) and Merlin (James 1988) achieve high urban densities.

Urban avifaunas are particularly interesting in terms of anthropogenic 'biotic homogenisation' (McKinney & Lockwood 1999), of which they provide an accessible case study (Blair 2001a; Blair 2001b; Clergeau et al. 2005, in press; Crooks et al. 2004) although Jokimäki & Kaisanlahti-Jokimäki (2003) found urbanisation did not homogenise avifaunas monotonically but above a threshold of anthropogenic influence. In addition to global homogenisation due to the ubiquity of cosmopolitan synanthropes, whose densities equalise quickly (Clergeau et al. 1998), avifaunas of widely-separated cities within biogeographic areas often show commonality (Bozsko 1985; Dinetti et al.

1996; Jokimäki et al. 2002), although dominance and commonality are not necessarily related (Tomialojc 1970 in Huhtalo & Järvinen 1977).

A further interesting feature of urban avifaunas is that many are changing rapidly, complicating attempts to differentiate them. A common pattern seems to be increasing species richness (Dinetti et al. 1996; Morneau et al. 1999; Nowakowski 1996) and colonisation of larger opportunists such as corvids (Aparova 2001; Kristan 2001; Soh et al. 2002; Vuorisalo et al. 2003), raptors (Bird et al. 1996; Bokotey 1996; Chace & Walsh 2006; Konstantinov et al. 1994; Rejt 2001; Warkentin & James 1988), pigeons (Slater 2001) and waterfowl (Adams et al. 1985; Bentz 1985; Bezzel 1985; Ilyichev et al. 1990; Jedraszko-Dabrowska & Debinska 1993; Jozkowicz & Górska-Klek 1996; Konstantinov et al. 1994; Traut & Hostetler 2003), together with declining small passerines (e.g. Rollinson et al. 2003), suggesting a major gain in net biomass (Luniak 1990). Species turnover has often been extensive even where there has been little change in species richness (e.g. Luniak 1996) and where richness has increased, it has often done so more in central than in suburban habitats (e.g. Witt 1996). Magpie is a particularly visible larger species which has rapidly urbanised since the 1950s, west to east across Europe and Asia (Jerzak 1995). Populations almost doubled between 1982 and 1992 in 11 Polish towns that had expanded around the Magpies' nesting habitat, from which they colonised older built-up areas as recently-planted trees matured (Gorski 1997). Longer lifespan and higher breeding success than non-urban birds helped their increase (Jerzak 1995). The Berlin population has greatly increased in the last 20 years (Witt 1997), while Dublin nest density increased by 12-13% per year between 1970 and 1987 with no sign of stabilisation (Kavanagh 1987a). Magpie colonisation of urban Kazan (Russia) only began in the 1980s but recent breeding densities reached 10 pairs km^{-2}, ten times typical non-urban density (Vodolajskaia 2001).

As urbanisation intrudes into landscapes worldwide, it is important to identify which bird species tolerate its modification of their habitat and which do not adapt successfully. The core urban synanthropes are well-known, but can a more general subset of species within a national avifauna be identified that consistently associate more than other species with urbanisation? In the UK, bird species likely to urbanise have had time to do so; cities are long-established and despite urban sprawl and regeneration, many remaining extensive non-urban habitats are protected to some degree. Chapter two takes advantage of this relatively stable mosaic of urban and non-urban habitats, across which both land cover and the distribution of the breeding avifauna have been reliably mapped, to examine this issue on a broad scale.

1.3. Factors influencing the relative urbanisation of species

Chapter three builds on this analysis to consider whether ecological traits predispose bird species to be more or less urban, a question that has so far defied systematic answer. McClure (1989) compiled observations of 848 species from 30 locations in Asia and the USA between 1941 and 1988 and classified each species according to 113 characteristics, of which 29 were common to at least 50% of 70 species designated as 'urban'. No firm conclusions could be drawn. Synanthropy, the degree to which species "gain some benefit from use of habitats modified by humans" (Johnston 2001), is not necessarily directly related to urbanisation and can vary seasonally (e.g. Nuorteva 1971) and geographically. For example, Konstantinov et al. (1994) categorised Song Thrush as a species for which increased urbanization does not favour breeding and it was lost from 50% of breeding atlas plots in Berlin between 1977-83 and 1989-91 but is still abundant in adjacent forests (Witt 1996). In contrast, urban London gardens in the 1960s supported stable populations (Simms 1962) and in the U.K. the built environment is now more important than the countryside for this species (Mason 2000). The ongoing and often rapid changes in urban avifaunas referred to above complicate defining birds consistently as 'urban', for example Great Spotted Woodpecker and Coal Tit are non-urban in Finland (Jokimäki & Suhonen 1998) but increasingly urbanised in the UK (Cannon 2000), linked to positive population trends (Baillie et al. 2001). Species which ordinarily never urbanise, such as South African montane sunbirds, can do so if driven by extreme events such as fires and drought (Harrison 2000).

In general, urban environments disadvantage habitat specialists except those whose speciality is commensality; this effect is even apparent in exurban settlements among pristine habitat (Fraterrigo & Wiens 2005). Urbanised generalists are typically edge species, naturally occurring where habitats meet and tending to be residents or partial migrants, granivores or omnivores (Adams 1994). In Australia, generalists such as Torresian Crow, Australian Magpie and Noisy Miner are abundant in urban and suburban habitats (Rollinson & Jones 2002). In Finland, omnivores were more prevalent in urban environments, Carrion Crow and House Sparrow abundances correlating with proportion of built-up area and, together with Feral Pigeon, with human density

(Jokimäki & Suhonen 1998). In Naples, species occurring in all habitat types were Feral Pigeon, Blackbird and two resident granivores, Italian Sparrow and Serin (Fraissinet 1995). It is hard to measure species' dependence on urbanisation as it is rarely reversed. However, Konstantinov (1996) monitored birds along a habitat gradient from a small town centre to settlements that were being abandoned. Synanthropes declined and disappeared with settlements and a forest bird community started to reappear. Again, ongoing worldwide urbanisation raises the question of whether the species which adapt to it successfully and, perhaps more importantly, those which fail to adapt, can be predicted on a broader scale, ideally based on a small number of measurable traits.

1.4. The role of gardens

Localised and/or seasonal surveys (Cannon 1999) suggest that private gardens provide substantial resources for significant numbers of wild birds, and they form a significant, if variable, proportion of the vegetative bird habitat in urban areas. The second analytical section of this thesis, chapters four, five and six, examines the year-round use of this habitat by wild birds, and its seasonal variation, on a larger scale than previously attempted, firstly across the UK as a whole and secondly examining variation between urban and non-urban gardens. Cowie & Hinsley (1987) observed that, in Britain at least, gardens differ from parks in having fewer mature trees but often abundant supplementary food. Consequently, their avifaunas also differ, for example in parks Great Tit densities are often higher than those of Blue Tits (e.g. Berressem et al. 1983; Dhondt & Eyckerman 1980) but in gardens Blue Tit densities are often higher (Bland 1979). Gardens contribute to bird conservation (Cannon 1999) and Lepczyk et al. (2003a) found that more than half of the respondents to a survey of residents helped birds by providing food, nest boxes or bird-friendly shrubs. Rudd et al (2002) showed that wildlife linkages between half the urban green spaces in Vancouver could only be realised by backyards and that their enhancement was the best approach to connectivity. Nonetheless, garden Blue and Great Tit productivity was lower than in non-garden populations and, despite artificial food, appeared to be limited by natural food supply (Cowie & Hinsley 1987; Cowie & Hinsley 1988). Non-native plants are commonly blamed for hosting fewer invertebrates, although there is little evidence for this relationship in Sheffield (Gaston et al. 2004) and Belfast Blue Tits obtained up to 13% of their daily energy by extracting nectar from non-native flowers (Fitzpatrick 1994).

There is a need to examine the use of this habitat by birds nationally and, given its relative importance in urban landscape, to determine whether urban patterns of garden use are different from those elsewhere.

1.5. Case study: the breeding avifauna of urban gardens

The third analytical section of the thesis presents results from a field investigation of an urban case study avifauna. If the importance of urban habitats to birds is to be promoted and enhanced, it is important to understand the extent to which they support sustainable breeding populations; chapter seven shows how territory mapping can establish this despite the disadvantages of urban environments for fieldwork. Correlations between urbanisation and breeding success vary (Thorington & Bowman 2003) according to habitat structure, landscape context, species, predator communities and scale. Most evidence is from large, accessible or nestbox species, as shown in table 1.1, for which productivity generally equals or exceeds non-urban habitats (Marzluff et al. 1996). However, for smaller species urban clutches may be smaller, notably in garden Blue and Great Tits (Cowie & Hinsley 1987) and productivity lower (Luniak 1977; Schnack 1991) although in five box-using species in Warsaw and Poznan, clutch size and productivity were no worse than in adjacent non-urban areas (Luniak 1992). Lower adult mortality may compensate for low productivity (Erz 1966; Horak & Lebreton 1998; Tatner 1982a) although post-fledging mortality of suburban Australian Magpies (Rollinson & Jones 2002) and Warsaw Starlings (Luniak 1977) was higher than in rural conspecifics. Temporal advancement is also commonly observed in seasonal climates (Gehlbach 1988; Ilyichev et al. 1990; Perrins 1970; Rollinson & Jones 2002).

Again, most studies to date have been in either core urban habitats or parks; in contrast, chapter seven reports probably the first attempt to map in detail the breeding avifauna of an urban residential area in which private gardens are the primary habitat. If small urban gardens do provide a significant proportion of the wild bird habitat in urban areas and if they can support sustainable breeding avifaunas, it is important to understand which particular characteristics of the habitat best enable wild birds to breed and which, if any, are problematic for them. Chapter eight assesses correlations between breeding species richness, habitat structure variables and with two anthropogenic influences, one positive (supplementary food) and one negative (prevalence of domestic cats).

Table 1.1. Avian productivity studies in urban environments

Species	Location	Headline (with reference to non-urban habitat)	Reference
American Robin	Montreal, Canada	Larger clutch size (3.6) and higher success (90%)	(Morneau et al. 1994)
Blackbird	Manchester UK	Very low nesting success in urban parks, <5%	(Groom 1993)
Blackbird	Oxfordshire	50% nest success compared to woodland 14%	(Snow 1988)
Blackbird	Poland and UK	Breeding densities 10 times higher	(Luniak & Mulsow 1988 in Morneau et al. 1994; Snow 1958)
Canada Goose	N.America	Nestling survival comparable	(Master & Oplinger 1984)
Eastern Screech Owl	Waco, Texas USA	Earlier laying, larger fledglings, lower nest predation, higher adult mortality	(Gehlbach 1988)
Greenfinch	Krotoszyn, Poland	40-44% nest success, similar to rural	(Kosinski 2001)
Herring and Black-headed Gulls	UK, urban industrial building roof colony	Breeding success higher although lower than more dispersed roof colonies	(Raven 1997)
Herring and Ring-Billed Gulls	Cuyohoga, Ohio, USA	hatch success ≥ 41% lower	(Belant et al. 1993)
Magpie	Zielona Gora, Poland	Egg and clutch size similar but breeding success higher, 50.8% broods vs 32.8%	(Jerzak 1995)
Magpie	Slupsk, Poland	Mean breeding success 57% 2.7 fledged per brood	(Gorski & Kotlarz 1997)
Mallard	N.America	Nestling survival lower but urban warmth enabled compensatory repeat broods	(Adams 1994a)
Merlin	Canada	Higher breeding success	(Oliphant 1985 in James 1988)
Mississippi Kite	N.America	Twice as many young per nesting attempt	(Gennaro 1988 in Adams 1994b)
Peregrine Falcon	N.America	Breeding success similar	(Cade & Bird 1990 in Adams 1994b)
Starling	Warsaw	Survivors per nest 18 days lower in built-up area, egg failure rate similar	(Luniak 1977)
Swainson's Hawk	Regina, Canada	Mean 1.4 fledged per attempt, typical non-urban 1.2 – 1.5	(James 1992)
Wood Duck	Burlington, Iowa USA	Nestbox hatching success 80%, natural rural sites 50%	(Leopold 1951 and 1966 in Adams 1994b)

1.6. Case study: individual birds in urban gardens

The territory mapping study determined the breeding bird community and its relative stability but provided no information on winter use of the case study habitat, which was synonymous with use of feeders, the primary food resource. Chapters nine, 10 and 11 report information obtained from a year-round programme of catching birds at feeding stations and marking them with rings. This is complementary to the GBW reporting rate analysis, which shows seasonal patterns in urban feeder use but provides no data on individual birds, their fidelity to feeding stations and their persistence at them over time and between seasons. Another interesting issue is the relationship between the breeding avifauna and birds using feeders. If feeders are the primary resource, not just in winter, but through the year, there should be a strong correspondence between the breeding avifauna mapped in chapter seven and the species caught at feeders.

Marking individual birds is also the only way to study the degree of exchange between an urban garden population and other habitats. This question of mobility between urban and non-urban populations is important because it is still unclear whether urban and non-urban populations of even common and well-studied species are isolated from each other. For synanthropes in which urbanisation has fuelled range expansion, such as Collared Dove, the entire population may effectively be urban (Tomialojc 1988). Continuously distributed species such as Great Tit may have isolated urban populations (Schmidt & Einloft-Achenbach 1984), others such as House Sparrow mix breeding isolation with non-breeding dispersal and mingling. Blackbird, Eastern Screech-Owl and Woodpigeon have been shown to have freely mingling urban and non-urban populations and some urban Blackbird populations may depend on non-urban recruits (Groom 1993; Erz 1964 in 2004), although urbanised Blackbirds in Europe may have 'leapfrogged' non-urban populations to progressively colonise urban areas (Erz 1966; Steinbacher 1942 in Tomialojc 1998) and Batten (1973) considered that London's Blackbirds formed a stable and even a source population. Timescale may determine whether urban populations are sources or sinks; recently-established populations may not be self-sustaining (Luniak 1977) and source-sink relationships vary or even reverse with time (Opdam & Wiens 2002).

In the final part of the case study, specific ecological opportunities and/or constraints applicable to birds breeding and feeding in urban gardens are investigated, using Blue and Great Tits as study species. Urbanisation modifies food availability for birds, through anthropogenic input but also alters natural food availability. Invertebrates may respond in a similar way to birds with an increased proportion of generalists and declining diversity, for example Warsaw has only 15% of regional species (Luniak 1999) but the effects vary with species (Helden & Leather 2004; Zanette et al. 2005), season (Pouyat et al. 1994 in 1997) and scale (Gibb & Hochuli 2002) and are little-studied. Earthworms are sometimes more abundant in cities than elsewhere (Steinberg et al 1996 in 1997) while urban sites in the same regions have very different carabid assemblages and their completeness varies greatly (Eversham et al. 1996). Lower invertebrate populations may reduce parasitism, French rural Blackbirds had significantly higher prevalence of ticks than urban conspecifics (Gregoire et al. 2002).

Even small food quality differences in early life can affect trait expression in birds (Ohlsson et al. 2001); Estonian urban Great Tits were less brightly-coloured than non-urban conspecifics; cross-fostering suggested dietary deficiency, even though the urban birds had better health, lower reproductive effort and higher survival (Horak et al. 2001). It is therefore important in assessing the sustainability of urban avifaunas to understand more about the extent to which the diet of nestlings differs from that of non-urban conspecifics, as found in Song Thrushes in Vienna parks, for example, which provisioned nestlings with fewer snails than birds in an adjacent wood (Schnack 1991).

Overall, the taxonomic and structural incompleteness of urban vegetation seems likely to reduce the availability of invertebrates for nestling provisioning although some non-native urban plants provide nectar for adults, as in Greater Manchester where butterfly species richness decreased with urbanisation but Large White, Small White and Holly Blue showed potential to increase due to increasing area of host plants (Hardy & Dennis 1999). For Lepidoptera in general, light trapping shows urban and suburban faunas to be very impoverished although species associated with garden conifers have markedly increased their range recently (Taylor et al. 1978 in Davis 1978). Constraints in food availability may also be indirectly apparent, through, for example, variations in the energy budgets of adult birds finding food for their broods and it may result in heavy use of feeding stations, which could facilitate disease transmission; results of investigations into both these issues within the case study area are also reported.

1.7 Structure of the thesis

The research presented in the following chapters aimed to improve understanding of wild birds' use of urban gardens by applying a suite of fieldwork and analytical techniques at different biogeographical and taxonomic scales. Broadly, the chapters divide into three sections, analyses of the use of urban habitats and analyses of the use of gardens, followed by a case study. Chapters two and three consider the use of urban habitat at landscape level by a wide range of species within a national avifauna. Chapters four, five and six investigate the use of private gardens as a particular habitat by the species that frequent them most often, both generally and specifically in urban areas. Chapters seven to 12 examine the use of highly-urbanised gardens by a breeding bird community of relatively low diversity, and by individual birds.

In the first section, mapped breeding bird atlas data for 128 species across Great Britain is compared with land cover data to determine the species most closely associated with urbanisation (chapter two). The results of this spatial analysis enabled relationships between relative urbanisation and species traits to be tested; behavioural flexibility as measured by relative brain size is used in chapter three as an example of this approach. The second section evaluates the use of gardens as a habitat by 40 commoner bird species monitored in a volunteer survey, again across Great Britain. Trends and patterns in reporting rates are identified (chapter four) and those in urban gardens compared with gardens elsewhere (chapters five and six).

Results from fieldwork in an area of small urban gardens in Sheffield are then presented, first at the community level. Mapping the breeding territories of nine common species enabled relationships between habitat variables and breeding species richness to be analysed. At the species and individual levels, birds' use of gardens within the case study area was studied by catching them at feeding stations and marking individuals with coloured leg rings; this enabled analyses of their seasonal use of feeders (chapter nine), persistence and mobility (chapter 10) and biometrics and condition (chapter 11); the last chapter presents three specific field investigations into the opportunities or constraints affecting birds in the case study area.

2. Identifying the urban avifauna

Abstract

To identify ecological factors determining relative urbanisation in birds, it is first necessary to systematically construct a list of species ordered by some quantitative relative urbanisation parameter. Deriving such a metric from large-scale spatial distribution data has until now been hindered by a lack of formal methods that account for spatial autocorrelation in binary variables. A newly-developed implementation of autologistic regression for presence/absence data was used in this analysis to examine relationships between distribution and relative urbanisation for 128 British breeding bird species; 77 species showed significant associations, 42 positive and 35 negative. Because autologistic regression was an untried method, both traditional logistic regression and comparisons with other data were performed to validate the results; in general they were supported although there was more consistency and fewer surprises in the species negatively associated with urbanisation than among those positively associated.

2.1. Introduction

In this chapter the relative urbanisation of bird species is examined, using the breeding avifauna of Great Britain as a case study. Spatial distributions of breeding species from atlas data were modelled against land cover classification and hence the degree to which each breeding bird species is positively or negatively associated with urbanisation was estimated. Urban avifaunas are characteristically low in species richness compared to their 'host' avifauna i.e. to the naturally selected avifauna of the original pre-urban and surrounding non-urban landscapes (Chapter 1). Nonetheless, even within their relatively few species and despite their characteristic numerical dominance by a small number of synanthropes, they can retain considerable functional and taxonomic diversity. If there are any common ecological traits that predispose some species to successful urbanisation and render it less likely in others, they remain unidentified. To investigate this in any systematic way, it is necessary first to quantify the degree to which each species in a host avifauna has adapted to urban habitats.

Surveys enumerating species that occur regularly and sustainably in urban areas are scarce in the literature, as Luniak (1996) observed in compiling the surveys that make up half of table 2.1. which shows, as expected, that urban avifaunas have lower species richness than their host avifaunas; between 20% and 64% of species are represented. There are a number of problems with attempting to systematically associate bird species with their relative propensity to urbanise by using such published lists. Not only are few such lists available, they are temporally and biogeographically widely distributed. It would be unwise to compile lists that were even a few years apart in time due to the rapid and ongoing changes in urban avifaunas globally (Chapter 1) and, despite biotic homogenisation, urban avifaunas in different biogeographic areas feature very different species. Almost every city has its birders' checklist, but these are typically compiled in isolation with no methodological comparability and a species accumulation approach; almost any species from the host avifauna can be found among human habitation if observation is long and diligent enough, especially in winter. The published London 'bird list' contains 356 species recorded within 20 miles of St Paul's cathedral (Self 2005); clearly, only a small fraction of this number will be sustaining a viable population within the urban environment and hence relevant to this analysis.

Table 2.1. Relative species richness data from urban avifaunas. Pop = human population of city. Spp = number of species present, N = national or regional total avifauna, adjusted for comparability i.e. either breeding or all-year according to the urban data available.

Location	Pop	km^2	Spp	N	%	Reference
Hungary (8 towns)	–	–	117	208*	56	Bozsko (1985)
Italy (14 towns)	–	–	176	370	48	Fraissinet 1992/93 in Dinetti, Cignini et al (1996)
Olsztyn	174 k	88	41	233*	16	Dulisz and Nowakowski (1996)
Naples	4.4.M	117	62	250*	25	Fraissinet (1995)
La Plata	600 k	100	101	500†	20	Montalti and Kopij (2001)
Warsaw	2.4 M	520	169	233*	62	Luniak (1996)
Lodz	776 k	294	100	233*	43	Tranda et al. 1983 in Luniak (1996)
Berlin	3.4 M	900	127	247*	51	Witt 1984, Degen & Otto 1988 in Luniak (1996)
Prague	1.2.M	496	131	205*	64	Fuchs et al. 1990 in Luniak (1996)
Vilnius	540 k	402	105	201*	52	Idzelis 1993 in Luniak (1996)
Vienna	1.5 M	415	145	408	36	Boeck 1993 in Luniak (1996)
Washington DC	553 k	177	115	311	37	Hadidian, Sauer et al (1997)

* from Earthtrends (2005) † Buenos Aires Province

Another problem with compiling published lists is their area-dependence; from table 2.1, the percentage of the host avifauna recorded as urbanised is positively correlated with the area of the conurbation considered (Spearman's rank correlation, $r_s = 0.83$, $P = 0.003$, $N = 10$). Species-area relationships apart, as the survey area increases so does the number of habitat types included and the breadth of the definition of 'urban', compromising comparability of the lists in the absence of detailed land cover data.

The approach adopted in the following analysis is that systematic determination of the relative urbanisation of bird species requires a dataset collected using a uniform protocol, that covers both urban and non-urban habitat in the same way and (importantly, in the light of ongoing changes in urban avifaunas) at the same time; a broad-scale 'snapshot' rather than censuses that are exhaustive but spatially and temporally dispersed. There should be some uniform and unambiguous criterion for registration of a species as 'present', such as establishment of successful breeding, which overcomes problems of mobility and transience, and the dataset should be amenable to mathematical modelling and hence statistical testing of the hypothesis that the presence and/or proximity of urban development significantly affects the probability of a species being successfully established at any particular location. The availability of both national-scale breeding atlas data and systematic land cover classification data on the same spatial scale, combined with new developments in autologistic regression that enable the modelling of presence/absence data while accounting for spatial autocorrelation, enabled the evaluation of this proposal in the following analysis.

If bird species can be characterised as more or less urban than others, their geographic distribution should be predicted to some extent by corresponding variation in the geographic distribution of urban land cover within their range. To test this hypothesis, the probability of presence of breeding bird species in 10km grid squares across Great Britain was modelled against the proportion of urban land cover in each square. The objectives were to establish a reference list of the British bird species whose distributions are significantly associated (either positively or negatively) with relative urbanisation of their habitat, and to order this list by some quantitative measure of each species' relative urbanisation, for use in subsequent regression analysis of the ecological traits predicting relative propensity to urbanise (Chapter 3). Due to the novelty of modelling large presence/absence datasets with substantial spatial autocorrelation and the potential wide applicability of atlas data to correlative analyses if this problem can be solved, a subsidiary objective of this investigation was to validate the results of a novel implementation of autologistic regression against results produced by more traditional logistic regression and indications of relative urbanisation from other data.

2.2. Methods

Breeding bird distribution data for Great Britain were acquired from the second BTO/IWC/SOC breeding atlas of British and Irish birds, for which records were collected during the years 1988 – 1991 (Gibbons et al. 1993) in the form of binary presence/absence records for every 10km x 10km Ordnance Survey National Grid square. Contemporary land cover data as a percentage of area for each of 25 land classes in each 10-km square was obtained from the NERC Centre for Ecology & Hydrology Land Cover Map 1990. The urban land cover category (denoted landclass21) includes cities, large town centres, major industrial and commercial sites, major areas of concrete and tarmac and permanent bare ground such as car-parks and tips (CEH 2003). Figure 2.1 plots the proportions of this landcover class in each of the 2739 10km grid squares. Britain being a small island, 477 of these squares have land area less than 50%. For squares with increasingly small proportions of land area the occurrence of terrestrial breeding birds might become more strongly influenced by decreasing size of sample area than by habitat. One way to overcome this would be to model the proportion of urban land class in the land within the 10km square, i.e. if a square has urban landclass 10% but land area only 50%, the variable takes a value of 20%. However, as can be seen from figure 2.2, this approach disproportionately urbanises coastal squares containing small towns, adding some very highly urbanised squares on the south coast and distorting the urbanisation gradient by relocating its maximum values away from the most urbanised areas. The degree of this distortion is an artefact of the arbitrary positioning of the imposed sampling grid. Of the 477 10km grid squares with land area less than 50%, only 15 have a value of greater than 1% for landclass21 (urbanisation) so, arguably, little information about urban birds is lost by discarding them.

Also, exclusively coastal species such as Shag may occur in the same square as coastal towns but their distribution is determined by the square being coastal rather than by urbanisation. Conversely, synanthrophic species such as House Sparrow, Feral Pigeon and Swift frequently breed in British coastal towns but not in non-urban coastal habitat. Also, maritime species such as Lesser Black-Backed Gull are increasingly urban breeders. Hence, to discard all coastal squares thereby limiting the analysis to non-coastal species would not only sacrifice valid data on common synanthropes of conservation interest but would inappropriately bias the investigation of correlations between urbanisation and biological traits towards terrestrial passerines, perhaps sacrificing interesting information on the urbanisation of coastal non-passerines such as gulls. Hence, the compromise solution adopted was to discard squares with land area below 50%, leaving 2262 squares as the primary dataset for analysis. To restrict the analysis to a practical number of species with reasonable sample sizes and hence a reasonable likelihood of convergence in the iterative techniques used, only the 128 species (table 2.2) present in more than 10% of the atlas squares were considered.

Table 2.2. List of species recorded as breeding in more than 10% of the 10km squares and hence included in the analysis (see appendix B for scientific names).

Species
Barn Owl
Black Grouse
Black Guillemot
Blackbird
Blackcap
Black-headed Gull
Blue Tit
Bullfinch
Buzzard
Canada Goose
Carrion Crow & Hooded Crow
Chaffinch
Chiffchaff
Coal Tit
Collared Dove
Common Gull
Common Sandpiper
Common Tern
Coot
Corn Bunting
Crossbill & Scottish Crossbill
Cuckoo
Curlew
Dipper
Dunlin
Dunnock
Eider
Feral pigeon
Fulmar
Garden Warbler
Goldcrest
Golden Plover

Species
Goldfinch
Goosander
Grasshopper Warbler
Great Black-backed Gull
Great Crested Grebe
Great Spotted Woodpecker
Great Tit
Green Woodpecker
Greenfinch
Teal
Grey Heron
Grey Partridge
Grey Wagtail
Greylag Goose
Hen Harrier
Herring Gull
House Martin
House Sparrow
Jackdaw
Jay
Kestrel
Kingfisher
Lapwing
Lesser Black-backed Gull
Lesser Redpoll
Lesser Spotted Woodpecker
Lesser Whitethroat
Linnet
Little Grebe
Little Owl
Little Ringed Plover
Long-eared Owl

Species
Long-tailed Tit
Magpie
Mallard
Marsh Tit
Meadow Pipit
Merlin
Mistle Thrush
Moorhen
Mute Swan
Nightingale
Nuthatch
Oystercatcher
Peregrine
Pheasant
Pied Flycatcher
Pied Wagtail
Raven
Red-breasted Merganser
Red-legged Partridge
Redshank
Redstart
Reed Bunting
Reed Warbler
Ring Ouzel
Ringed Plover
Robin
Rock Pipit
Rook
Sand Martin
Sedge Warbler
Shag
Shelduck

Species
Short-eared Owl
Siskin
Skylark
Snipe
Song Thrush
Sparrowhawk
Spotted Flycatcher
Starling
Stock Dove
Stonechat
Swallow
Swift
Tawny Owl
Tree Pipit
Tree Sparrow
Treecreeper
Tufted Duck
Turtle Dove
Twite
Wheatear
Whinchat
Whitethroat
Willow Tit
Willow Warbler
Willow/Red Grouse
Wood Warbler
Woodcock
Woodpigeon
Wren
Yellow Wagtail
Yellowhammer

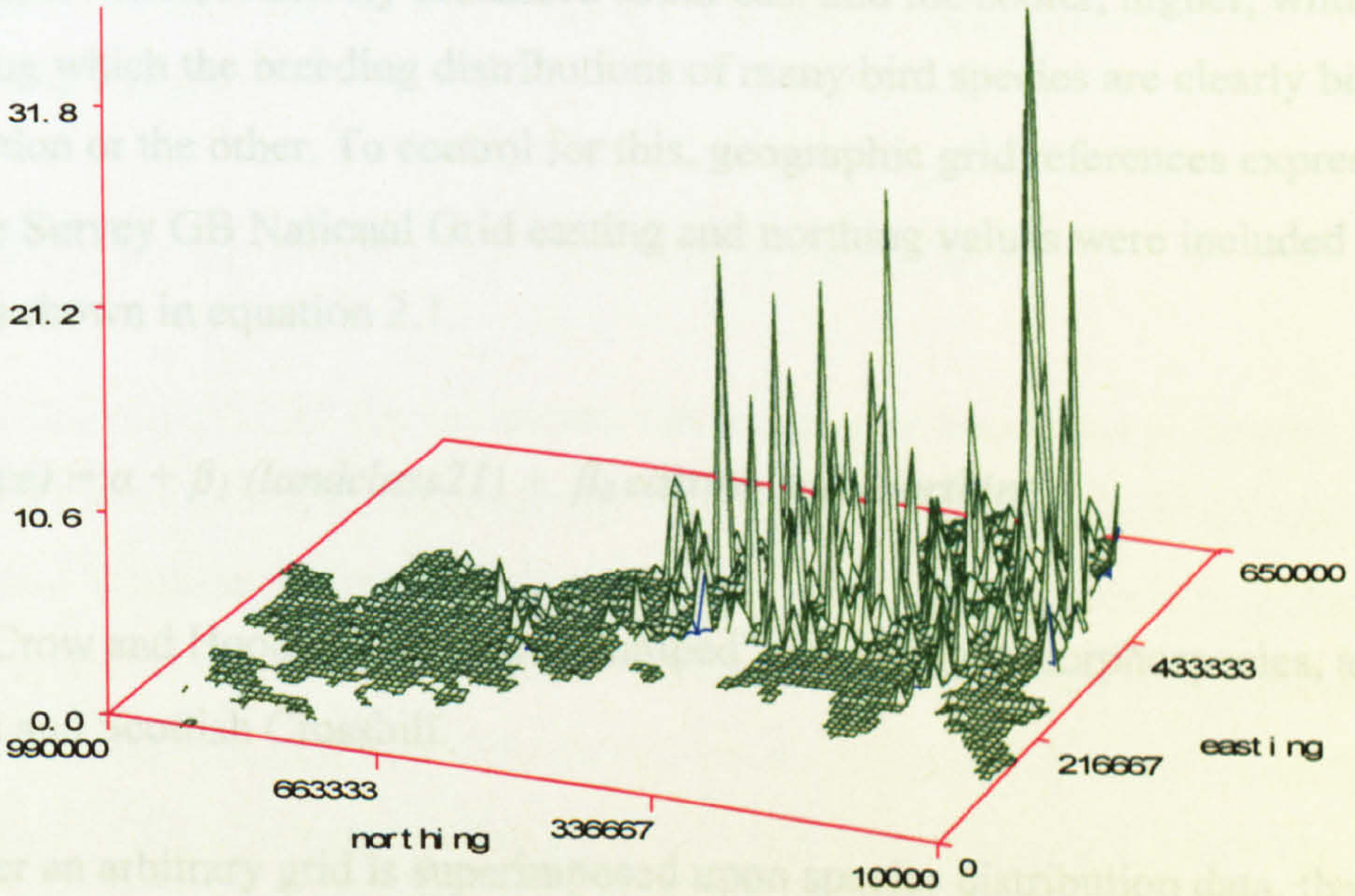

Fig. 2.1. Plot of proportion of urban landcover in each 10km square (landclass21)

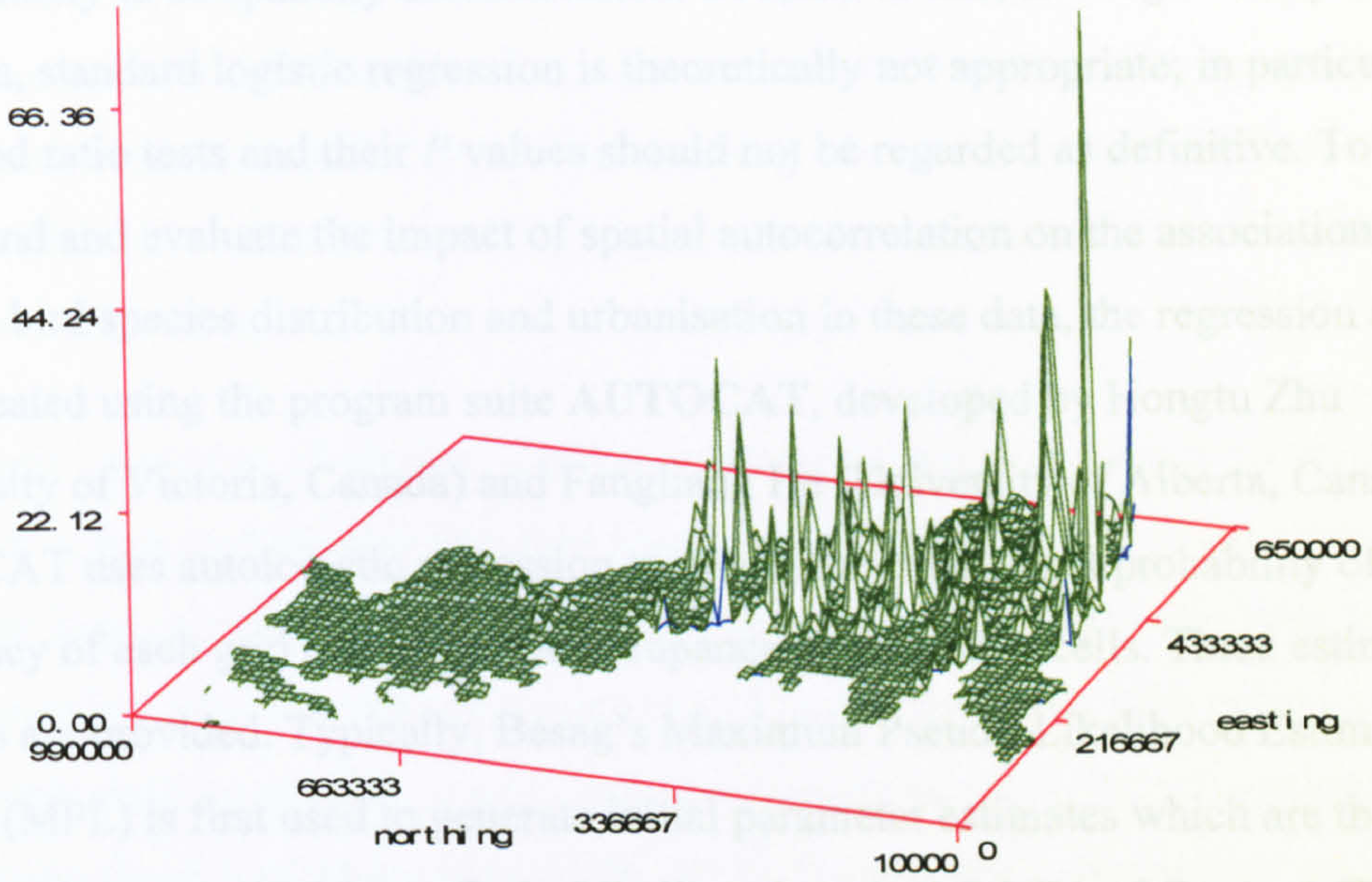

Fig. 2.2. Plot of ratio of urban landcover to land area in each 10 km square

As a 'first cut' analysis to determine the likelihood of a sufficient number of species being significantly associated with degree of urbanisation to make subsequent investigation worthwhile, logistic regression for each of the 128 species individually was performed in SAS procedure GENMOD using binomial error distribution and type 3 sums of square analysis. Species for which type 3 analysis was significant at $P \leq 0.05$ were sorted in decreasing order of the regression parameter estimate (logit coefficient) for the variable landclass21 (continuous urban development) and are presented in table 2.4. A feature of the biogeography of the British Isles is a general habitat cline between the milder, lowland, relatively urbanised south-east and the cooler, higher, wilder north-west, along which the breeding distributions of many bird species are clearly biased in one direction or the other. To control for this, geographic grid references expressed as Ordnance Survey GB National Grid easting and northing values were included in the model, as shown in equation 2.1.

$$p(presence) = \alpha + \beta_1 (landclass21) + \beta_2\, easting + \beta_3\, northing \qquad (2.1.)$$

Carrion Crow and Hooded Crow were 'lumped' into a single morphospecies, as were Crossbill and Scottish Crossbill.

Whenever an arbitrary grid is superimposed upon species distribution data, the presence of a species in one grid square is likely to influence and/or be influenced by its presence in adjacent squares, hence the presence/absence scores for the bird species in the atlas data are likely to be spatially autocorrelated. Because of this, although widely used with such data, standard logistic regression is theoretically not appropriate; in particular, likelihood ratio tests and their P values should not be regarded as definitive. To better understand and evaluate the impact of spatial autocorrelation on the associations between bird species distribution and urbanisation in these data, the regression analysis was repeated using the program suite **AUTOCAT**, developed by Hongtu Zhu (University of Victoria, Canada) and Fangliang He (University of Alberta, Canada). AUTOCAT uses autologistic regression to model the conditional probability of occupancy of each grid cell given the occupancies of all other cells. Three estimation methods are provided. Typically, Besag's Maximum Pseudo-Likelihood Estimation method (MPL) is first used to generate initial parameter estimates which are then input as starting values to the Monte Carlo Likelihood method (MCL) of Geyer & Thompson. Should the MCL method fail, the program also provides the Markov Chain Monte Carlo Stochastic Approximation (MCMC-SA) of Gu & Zhu as an alternative (He et al. 2000; He et al. 2003 and references therein).

Although Maximum Pseudo-Likelihood (MPL) is by far the quickest estimation method implemented in AUTOCAT, it does not give valid variance estimates and is not efficient in cases of strong spatial correlation (He et al. 2003). To obtain goodness of fit information the appropriate procedure is to use the parameter estimates produced by the MPL model as starting values for either of the Monte Carlo methods. Full second order spatial autocorrelation i.e. four non-equal spatial correlation coefficients, two cross and two diagonal, for each cell ($\gamma_1 \neq \gamma_2 \neq \gamma_3 \neq \gamma_4$) was incorporated into the model, the form of which was therefore:

$$p(presence) = \alpha + \beta_1(landclass21) + \beta_2\gamma_1 + \beta_3\gamma_2 + \beta_4\gamma_3 + \beta_5\gamma_4 \qquad (2.2.)$$

and the initial values of all six parameters (intercept α, urbanisation parameter β_1 and the four spatial autocorrelation parameters $\beta_2 - \beta_5$) were set to zero. The Markov Chain Monte Carlo Stochastic Approximation method is a two stage process requiring two sets of pre-assigned constants (Gu & Zhu 2001; He et al. 2003). Based on values suggested in He et al. (2003) and practical experience, the stage 1 gain constants which force the estimates into a feasible region were set to $a_1 = 0.3$, $b_1=10$, $\eta_1 = 0.1$, while the stage 2 true estimation constants were set to $a_2=0.6$, $b_2=1$. The stopping criterion was initially set to $\eta_2=0.001$ but this resulted in long run times (up to 20,000 iterations for sparse species) and a number of species failed to converge to this accuracy. As 128 species had to be processed and as 0.001 precision was not essential to achieve the two objectives of a significance test for association and the ordering of species by their parameter estimates, this was reduced to $\eta_2=0.01$ whenever convergence failed to occur after 10,000 iterations at $\eta_2=0.001$.

As a simple validation of species' associations with urbanisation, the proportions of the squares in which each species occurred that contained relatively large amounts of urban landcover were calculated. For each of the 77 species occurring in more than 10% of the 10km^2 breeding atlas squares and having significant associations with urbanisation under autologistic regression, species-positive squares in which the proportions of urbanisation (landclass21) exceeded 20%, 10%, 5% and 1% were counted and these counts expressed as proportions of the species-positive squares. Further simple validation of the identification of the most urbanised species was done based on the approach of Bozsko (1985) who identified the species most frequently occurring in urban areas as the 'urban stock avifauna'. Experimentally, a selection criterion of [continuous urban development (landclass 21) + suburban/rural development (landclass 20)] >= 28% of area of square was found to select a subsample of approximately 10% (218 out of 2262) of the most developed 10km squares from the breeding atlas dataset. The frequency of occurrence of the 128 species in this subsample of highly developed squares was then calculated and those occurring within Bozsko's 'urban stock avifauna' frequency range of 80 – 100% of developed squares were tabulated. Finally, to compare the breeding atlas data with a more recent dataset, the latest breeding densities for various habitat types were obtained (S.E.Newson 2005 *in litt.*) from the BTO/JNCC/RSPB Breeding Bird Survey (see Newson et al. 2004 for methods). For species with non-zero density in habitat type 'human', the ratio of their density in this habitat type to their mean density in other habitat types was calculated.

2.3. Results & Discussion

Table 2.3 lists 67 species for which type 3 $P \leq 0.05$ in logistic regression of presence/absence against landclass21. Blackbird, Starling and House Sparrow are the 'top three' in terms of size and sign of their landclass21 parameter estimate, all species commonly found in urban habitats, the latter two generally regarded as synanthropic

(Johnston 2001). Four of the next six species are water birds that are found in urban habitats but are unlikely to have their distributions primarily determined by urbanisation, Great Crested Grebe especially. Collared Dove, Magpie, Feral Pigeon and Swift are all highly but not exclusively urbanised species. Mute Swan and Canada Goose are significantly urbanised species, but Little Ringed Plover and Little Grebe are unlikely to have distributions primarily determined by urbanisation. At a 10km square scale, the presence of gravel pits and reservoirs serving cities within the same squares as patches of urbanisation may cause these habitat associations in water birds. Further down the list of positive associations, none of Lesser Whitethroat, Bullfinch, Nuthatch, Lesser Spotted Woodpecker, Reed Bunting or Reed Warbler would normally be considered significantly urbanised. Species negatively associated with urbanisation in table 2.3 are generally less surprising, only Jackdaw might be considered to any extent an urban breeder. Siskin also now breeds in suburban habitats but only in very recent years, post-dating the survey on which these data are based. The 17 most negatively associated species are species of remote and upland landscapes. For comparison, the models were re-run using all 2739 10km squares, coastal squares included (not tabulated); 74 species had type 3 $P \leq 0.05$ as opposed to only 67 when squares with less than 50% land area were excluded. Species losing significance with the exclusion of coastal squares were Blackcap, Blue Tit, Crow, Great Tit, Greenfinch, Little Grebe, Mistle Thrush, Robin, Shag, Song Thrush, Treecreeper and Jay. Species gaining significance when coastal squares were excluded were Cuckoo, Spotted Flycatcher, Teal, Swallow and Woodlark.

All three autologistic regression methods produce six parameter estimates, for the intercept, urbanisation (landclass21) and the four spatial autocovariates γ_1 - γ_4. The parameter estimates for urbanisation and their t values for all 128 species using all the three methods are given in table 2.4. Estimates with t values of magnitude greater than 1.98 (critical value for $p < 0.05$ at 120 DF) are deemed to be significant (N= 2262 squares) and are shown in bold in table 2.4. Although MPL provided initial parameter estimates for all species except Cuckoo, for the majority of species the MCL method failed to converge even when using these as starting values. The MCMC-SA method, however, did converge for all species except Eider, Black Guillemot (exclusively coastal and very restricted distributions) and Nightingale. These were the three least frequently occurring species in the dataset, incidentally supporting the decision to only include species occurring in more than 10% of grid squares in the analysis.

Table 2.3. Results of simple logistic regression with coastal grid squares (land area of less than 50%) excluded. The 67 species for which type 3 $P \leq 0.05$ are sorted in descending order of their model parameter estimates for landclass21 (P-est) i.e. from 'most urban' to 'least urban'.

Species	P-est	*P*	Species	P-est	*P*	Species	P-est	*P*
Blackbird	3.3266	0.0062	Herring Gull	0.0917	0.0099	Swallow	-0.2095	<.0001
Starling	2.7353	0.0002	Reed Warbler	0.0912	0.002	Oystercatcher	-0.2124	<.0001
House Sparrow	1.2917	0.0014	Common Tern	0.0878	0.0015	Curlew	-0.2265	<.0001
Moorhen	0.5729	0.0003	Great Spotted Woodpecker	0.0849	0.0308	Rook	-0.2286	<.0001
Mallard	0.5125	0.013	Kingfisher	0.0794	0.0037	Crossbill	-0.2884	0.0002
Magpie	0.3889	0.0021	Tufted Duck	0.078	0.0048	Red Grouse	-0.3049	<.0001
Coot	0.3269	<.0001	Woodlark	-0.0624	0.0184	Common Sandpiper	-0.3153	<.0001
Collared Dove	0.2753	0.0004	Tree Pipit	-0.072	0.0064	Dipper	-0.3384	<.0001
Great Crested Grebe	0.268	<.0001	Cuckoo	-0.0742	0.0027	Siskin	-0.3715	<.0001
Feral Pigeon	0.2214	<.0001	Spotted Flycatcher	-0.0756	0.0224	Short-eared owl	-0.373	0.0002
Swift	0.1936	0.0036	Teal	-0.0887	0.041	Wheatear	-0.4055	<.0001
Little Ringed Plover	0.1784	<.0001	Pied Flycatcher	-0.0989	0.0176	Peregrine Falcon	-0.5047	<.0001
Canada Goose	0.1631	<.0001	Turtle Dove	-0.105	0.0007	Merlin	-0.5098	<.0001
Little Grebe	0.1525	<.0001	Barn Owl	-0.1061	0.0006	Buzzard	-0.5676	<.0001
Mute Swan	0.1348	0.0002	Red-legged Partridge	-0.1109	<.0001	Raven	-0.6402	<.0001
Bullfinch	0.13	0.0083	Marsh Tit	-0.1252	<.0001	Ring Ouzel	-1.1455	<.0001
Whitethroat	0.1292	0.0448	Nightingale	-0.1434	0.0004	Common Gull	-1.2301	0.0017
Nuthatch	0.1215	0.0004	Yellowhammer	-0.1437	<.0001	Goosander	-1.5382	<.0001
Tawny Owl	0.1168	0.0051	Whinchat	-0.1639	0.0002	Red-breasted Merganser	-1.5732	0.0006
Lesser Spotted Woodpecker	0.1113	0.0001	Jackdaw	-0.1748	<.0001	Hen Harrier	-4.3483	<.0001
Lesser Black-backed Gull	0.1011	0.01	Golden Plover	-0.1916	0.0225	Black Grouse	-4.7922	<.0001
Lesser Whitethroat	0.0972	0.0037	Redstart	-0.208	<.0001			
Reed Bunting	0.0962	0.0212	Pheasant	-0.2082	<.0001			

Table 2.4. Parameter estimates (P-est) and *t* values, autologistic regression. *see text.

Species	MPL*: P-est and *t*		MCL*: P-est and *t*		MCM-SA*: P-est and *t*	
Blackbird	**7.963797**	**3.471323**	fail	fail	**9.633414**	**4.091979**
Blackcap	0.106016	1.411368	fail	fail	**0.356287**	**4.058435**
Bullfinch	**0.134919**	**2.241513**	fail	fail	**0.222322**	**3.677297**
Black-headed Gull	-0.025233	-0.626904	**-0.066935**	**-2.008282**	**-0.073781**	**-2.276424**
Black Grouse	**-3.228639**	**-3.458245**	fail	fail	**-3.570969**	**-4.253441**
Barn Owl	-0.026177	-0.746668	-0.027040	-1.394243	-0.025613	-1.390408
Blue Tit	**4.313498**	**3.207261**	fail	fail	**6.593086**	**4.509902**
Buzzard	**-0.406050**	**-3.462903**	fail	fail	**-0.342945**	**-5.065800**
Crow	0.080644	0.898060	0.389136	1.149923	0.153679	1.555677
Corn Bunting	-0.045532	-1.268220	fail	fail	0.003055	0.287513
Chiffchaff	0.023082	0.540829	fail	fail	**0.102378**	**2.604282**
Collared Dove	**0.002789**	**2.642347**	fail	fail	**0.005634**	**5.010815**
Canada Goose	0.026843	0.652685	fail	fail	**0.082154**	**2.775096**
Chaffinch	0.405454	1.494888	0.564289	1.839558	0.581816	1.916061
Cuckoo	fail	fail	fail	fail	-0.021615	-1.242940
Common Gull	**-2.322943**	**-3.301541**	fail	fail	**-2.946956**	**-4.612074**
Common Tern	0.016667	0.566662	**0.038118**	**2.273778**	**0.039478**	**2.441968**
Coot	**0.222172**	**2.547877**	fail	fail	**0.377423**	**4.679348**
Crossbill	**-0.203730**	**-2.124921**	fail	fail	**-0.267202**	**-3.183681**
Common Sandpiper	-0.161759	-1.788008	fail	fail	**-0.290908**	**-4.468510**
Coal Tit	-0.002361	-0.063734	0.011066	0.365175	0.012781	0.441139
Curlew	**-0.164016**	**-3.287488**	fail	fail	**-0.133800**	**-4.498616**
Dunnock	**0.366987**	**2.142409**	fail	fail	**0.818784**	**3.877130**
Dipper	**-0.156084**	**-2.257704**	fail	fail	**-0.236915**	**-4.706578**
Dunlin	**-0.394543**	**-2.235572**	fail	fail	**-0.363649**	**-2.817691**
Eider	**-2.010799**	**-2.001533**	fail	fail	fail	fail
Fulmar	0.006425	0.089296	fail	fail	-0.167156	-1.780318
Feral pigeon	**0.114422**	**2.550426**	**0.116437**	**2.110610**	**0.141493**	**4.000547**
Green Woodpecker	-0.040749	-1.374851	fail	fail	0.003062	0.252945
Great Black-backed Gull	**-1.203169**	**-2.287006**	fail	fail	**-1.870491**	**-8.611099**
Goldcrest	-0.034705	-1.366880	-0.034985	-1.788942	-0.034219	-1.769357
Goosander	**-0.966056**	**-3.294853**	fail	fail	-0.858780	-0.858780
Great Crested Grebe	**0.102473**	**2.548688**	fail	fail	**0.143398**	**4.180526**
Grasshopper Warbler	0.004713	0.172930	0.010401	0.550325	0.010018	0.538782
Greylag Goose	0.005303	0.175498	0.013008	0.853844	0.012592	0.852172
Grey Wagtail	-0.019939	-0.687105	fail	fail	**-0.039104**	**-2.608782**
Goldfinch	0.065319	1.041430	fail	fail	**0.232707**	**3.283162**
Golden Plover	-0.232323	-1.784028	fail	fail	**-0.294933**	**-8.906704**
Greenfinch	**0.281284**	**2.152869**	fail	fail	**0.746222**	**4.659664**
Great Spotted Woodpecker	0.055294	1.218502	fail	fail	0.003921	0.309356
Great Tit	**1.043859**	**2.775474**	fail	fail	**1.933210**	**4.224437**
Garden Warbler	-0.001405	-0.040690	0.024727	0.376526	0.031230	1.395030
Grey Heron	-0.012607	-0.502540	-0.005274	-0.226848	-0.005570	-0.239055
Herring Gull	0.037366	1.162359	fail	fail	-0.026034	-0.899211
Hen Harrier	**-5.043718**	**-3.486363**	fail	fail	**-5.726342**	**-4.561980**
House Martin	0.188598	1.419272	fail	fail	**0.615942**	**3.504378**
House Sparrow	**2.240166**	**3.358714**	fail	fail	**3.887160**	**4.943616**
Jay	0.011551	0.320641	0.045533	1.644859	**0.048216**	**2.105757**
Jackdaw	-0.042815	-1.459145	fail	fail	-0.028907	-1.455668
Kestrel	0.061988	1.168370	fail	fail	**0.157541**	**2.707062**
Kingfisher	0.049854	1.739211	fail	fail	**0.053413**	**2.776697**
Lapwing	-0.044812	-1.542318	fail	fail	-0.011968	-0.557127
Lesser Black-backed Gull	0.046464	1.306537	-0.008997	-0.232086	0.000877	0.029054
Long-eared Owl	-0.005133	-0.134973	fail	fail	0.007233	0.325768
Little Grebe	0.062568	1.853837	**0.111424**	**2.971433**	**0.104244**	**3.759753**
Linnet	-0.007815	-0.158035	fail	fail	**0.217749**	**3.067511**
Little Owl	**-0.060200**	**-2.105619**	fail	fail	0.006482	0.539732
Little Ringed Plover	0.054955	1.768754	fail	fail	**0.092597**	**3.803955**
Lesser Redpoll	-0.010448	-0.397508	-0.004072	-0.268886	-0.003423	-0.238931
Lesser Spotted Woodpecker	0.056916	1.699685	fail	fail	**0.041094**	**2.445781**
Long-tailed Tit	0.066370	1.262698	fail	fail	**0.140496**	**2.680139**
Lesser Whitethroat	0.025696	0.730178	fail	fail	**0.051841**	**2.432990**

Mistle Thrush	**0.211500**	**2.041841**	0.490067	1.925631	**0.324639**	**2.951896**
Mallard	**1.335205**	**3.408380**	**1.770452**	**3.899765**	**1.735365**	**4.097109**
Magpie	0.312058	1.881368	fail	fail	**0.790087**	**4.809028**
Moorhen	**0.661970**	**2.966612**	fail	fail	**1.442998**	**5.649366**
Merlin	**-0.538697**	**-2.871096**	fail	fail	**-0.537861**	**-3.426379**
Meadow Pipit	**-0.051889**	**-1.969577**	fail	fail	**-0.063381**	**-3.382912**
Mute Swan	**0.095217**	**2.327471**	fail	fail	**0.122983**	**3.514207**
Marsh Tit	-0.030823	-0.923490	fail	fail	-0.018857	-1.755018
Nightingale	-0.027576	-0.461173	fail	fail	fail	fail
Nuthatch	**0.098497**	**2.090108**	fail	fail	0.011775	0.695788
Oystercatcher	-0.077299	-1.693643	fail	fail	**-0.121270**	**-3.691952**
Grey Partridge	-0.021319	-0.730346	0.032995	0.650454	0.012678	0.869176
Peregrine	**-0.393924**	**-2.788138**	fail	fail	**-0.643530**	**-5.160561**
Pied Flycatcher	-0.027120	-0.602748	fail	fail	**-0.042529**	**-2.335285**
Pheasant	**-0.071165**	**-2.380168**	fail	fail	-0.029439	-1.866660
Pied Wagtail	-0.021525	-0.503458	-0.009854	-0.246507	-0.009704	-0.246810
Robin	**1.206025**	**2.227711**	**1.492270**	**2.559377**	**1.455602**	**2.517253**
Reed Bunting	0.060336	1.281142	fail	fail	**0.170430**	**3.419031**
Rock Pipit	-0.305185	-1.545527	fail	fail	**-0.609022**	**-2.785758**
Willow/Red Grouse	-0.161222	-1.648744	fail	fail	**-0.238773**	**-3.431726**
Redshank	-0.019224	-0.702401	0.001333	0.055840	-0.015183	-1.009578
Red-legged Partridge	**-0.075404**	**-2.182760**	fail	fail	-0.010081	-0.877260
Red-breasted Merganser	**-3.110654**	**-3.395296**	**-4.344941**	**-4.238204**	**-3.640265**	**-4.622192**
Raven	**-0.573207**	**-2.710247**	fail	fail	**-0.798009**	**-4.226196**
Rook	**-0.082450**	**-2.218376**	fail	fail	**-0.039494**	**-2.709709**
Ringed Plover	-0.003885	-0.134220	-0.008745	-0.422806	-0.007871	-0.398353
Redstart	**-0.112729**	**-2.273180**	**-0.128259**	**-3.642510**	**-0.120791**	**-4.052150**
Reed Warbler	0.029200	0.980441	fail	fail	**0.040793**	**2.453277**
Ring Ouzel	**-0.851605**	**-3.210439**	fail	fail	**-0.687561**	**-5.950166**
Skylark	0.026531	0.410281	0.058706	0.822784	0.061315	0.883990
Shag	**-3.744398**	**-2.478179**	fail	fail	-4.966107	-0.036192
Stonechat	**-0.177433**	**-2.138399**	fail	fail	**-0.240807**	**-3.488162**
Stock Dove	-0.010071	-0.303219	fail	fail	**0.047565**	**2.485087**
Short-eared Owl	**-0.322563**	**-2.248237**	fail	fail	**-0.339076**	**-2.930842**
Spotted Flycatcher	-0.020949	-0.610341	0.000458	0.015346	-0.000791	-0.026753
Starling	**5.220525**	**3.722802**	fail	fail	**6.884786**	**5.093922**
Sparrowhawk	0.004761	0.177914	0.032968	1.284117	0.029300	1.332681
Swift	**0.237706**	**2.674361**	fail	fail	**0.445478**	**4.707670**
Siskin	**-0.206480**	**-2.226847**	fail	fail	**-0.353695**	**-4.146415**
Swallow	-0.042589	-1.179487	-0.025115	-0.523858	-0.027129	-0.732854
Sand Martin	0.007841	0.312951	-0.008663	-0.507903	-0.008317	-0.479074
Snipe	-0.046425	-1.451249	fail	fail	**-0.066048**	**-3.136463**
Song Thrush	**0.613759**	**2.275810**	0.935428	2.520570	**0.823645**	**2.760078**
Shelduck	0.003490	0.115781	fail	fail	0.005964	0.407603
Sedge Warbler	0.003558	0.130234	fail	fail	0.033467	1.540622
Teal	-0.048804	-1.091013	fail	fail	**-0.104424**	**-2.613919**
Treecreeper	0.039356	1.088070	0.069664	1.781690	0.057716	1.893716
Turtle Dove	-0.018324	-0.543533	fail	fail	-0.009769	-0.917834
Tawny Owl	**0.111407**	**2.213947**	**0.147507**	**2.888424**	**0.146088**	**3.131089**
Tree Pipit	-0.041053	-1.391432	**-0.064796**	**-3.019233**	**-0.061441**	**-3.225101**
Tree Sparrow	-0.031178	-1.179202	fail	fail	0.023943	1.656681
Tufted Duck	0.032608	1.041553	fail	fail	**0.062334**	**2.768716**
Twite	**-0.516626**	**-2.790729**	fail	fail	**-0.317746**	**-2.988930**
Black Guillemot	-1.783501	-1.701257	fail	fail	fail	fail
Wheatear	**-0.201099**	**-2.312249**	fail	fail	**-0.348828**	**-9.032336**
Whinchat	**-0.107993**	**-2.105061**	fail	fail	**-0.183010**	**-4.229690**
Whitethroat	0.083662	1.112095	fail	fail	0.365007	4.001259
Woodcock	-0.047025	-1.418911	-0.020001	-1.102951	-0.025023	-1.471156
Wood Warbler	-0.039365	-1.176977	fail	fail	**-0.050261**	**-2.417586**
Woodpigeon	**0.894353**	**2.670267**	fail	fail	**1.855388**	**4.428392**
Wren	0.446560	1.617832	0.588398	1.883590	0.584409	1.953252
Willow Tit	-0.035445	-1.095420	fail	fail	0.004432	0.390131
Willow Warbler	0.290074	1.655116	0.350890	1.949173	0.345910	1.910929
Yellowhammer	-0.065239	-1.920821	fail	fail	-0.004225	-0.196294
Yellow Wagtail	-0.015236	-0.574025	fail	fail	0.014303	1.143576

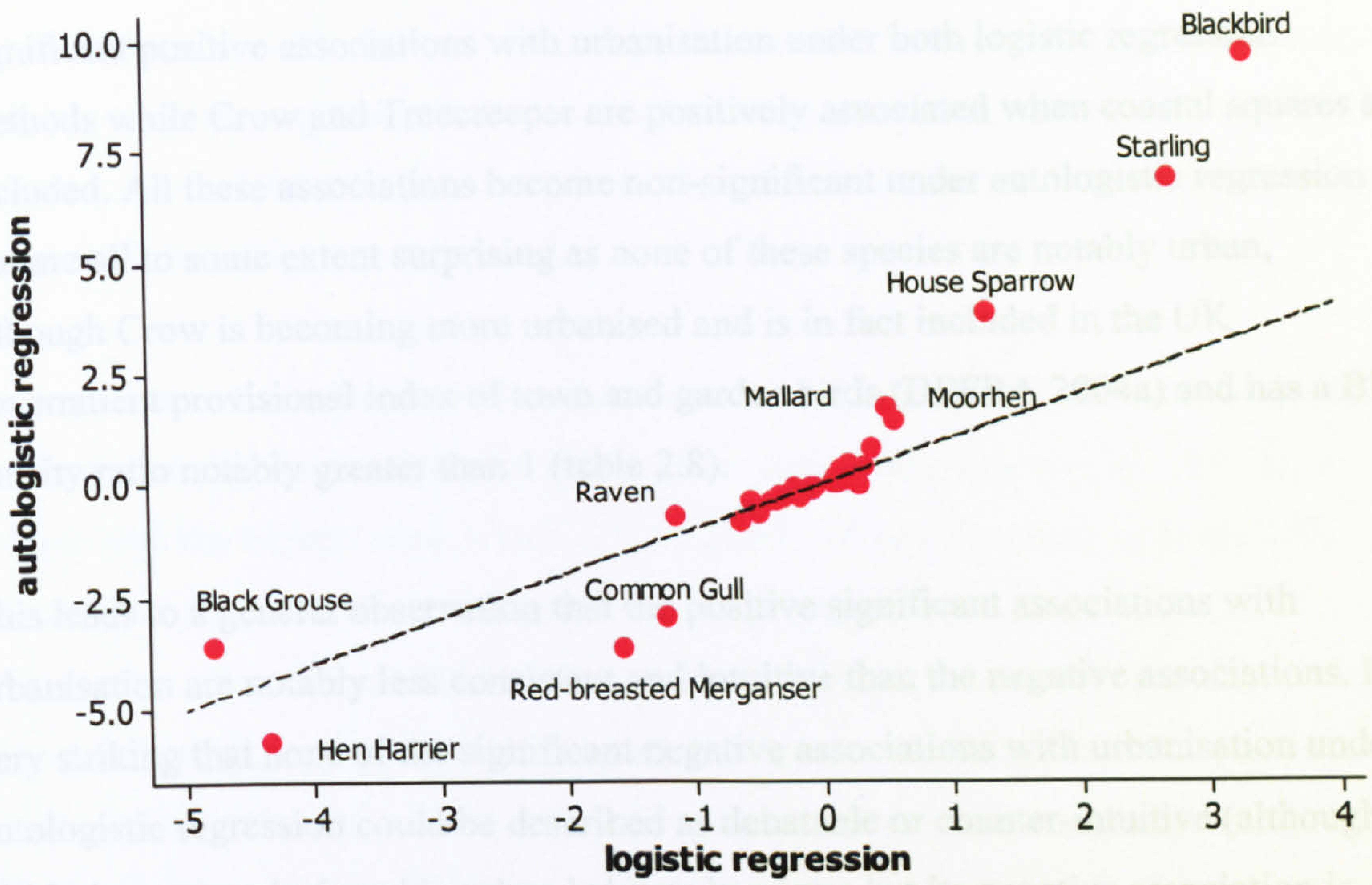

Figure 2.3. Comparison of the parameter estimates from autologistic and logistic regression of breeding bird species' presence/absence in 2262 × 10 km squares against landclass21 (relative urbanisation), for 50 species with significant (type 3 $P \leq 0.05$) associations under both methods. 1:1 line shown for reference.

Figure 2.3 shows that for the 50 species that have significant associations under both regression methods, there is good correlation between the parameter estimates produced (Pearson correlation $r = 0.892$, $P < 0.001$). The 'top 20' species under logistic regression i.e. those with the 20 most positive parameter estimates all have significant positive associations under autologistic regression as well, with the exception of Nuthatch. The 'bottom 20' under logistic regression all have significant negative associations under autologistic regression as well, except Goosander. Nine species (Turtle Dove, Barn Owl, Red-legged Partridge, Marsh Tit, Nightingale, Yellowhammer, Jackdaw, Pheasant and Goosander) are significantly negatively associated with urbanisation (all nine as would be expected) under logistic regression but, perhaps unexpectedly for such non-urban species, this association loses significance under autologistic regression. Woodlark, Cuckoo, Spotted Flycatcher and Swallow are significantly negatively associated with urbanisation (again as would be expected) in logistic regression when coastal squares are excluded but this significance is lost under autologistic regression (and if coastal squares are included in logistic regression). The significant negative association between Shag and urbanisation when coastal squares are included does not occur when coastal squares are excluded, as would be expected given that Shag is an exclusively coastal species.

Nuthatch, Lesser Black-backed Gull, Herring Gull and Great Spotted Woodpecker show significant positive associations with urbanisation under both logistic regression methods while Crow and Treecreeper are positively associated when coastal squares are included. All these associations become non-significant under autologistic regression and are all to some extent surprising as none of these species are notably urban, although Crow is becoming more urbanised and is in fact included in the UK government provisional index of town and garden birds (DEFRA 2004a) and has a BBS density ratio notably greater than 1 (table 2.8).

This leads to a general observation that the positive significant associations with urbanisation are notably less consistent and intuitive than the negative associations. It is very striking that none of the significant negative associations with urbanisation under autologistic regression could be described as debatable or counter-intuitive (although Siskin is commonly found in urban habitats in winter but its negative association is nonetheless reasonable for the breeding season). In contrast, a number of the positive associations with urbanisation are surprising, most notably among those unique to the autologistic method Linnet, Kestrel, Chiffchaff, and Stock Dove. Other surprising positive associations under autologistic regression are Whitethroat, Blackcap, Bullfinch, Reed Bunting, Tawny Owl, Little Grebe, Little Ringed Plover, Kingfisher, Lesser Whitethroat, Lesser Spotted Woodpecker, Reed Warbler and Common Tern; all these associations gain further support from logistic regression.

Lower consistency in the positive associations than in the negative can also be seen in that all eight of the species that have no significant association with urbanisation under logistic regression with no coastal squares but do have significant associations under both autologistic regression with no coastal squares and logistic regression with coastal squares have positive associations. It is again striking that this inconsistency does not occur for any of the negatively associated species. However, the numbers of species acquiring a significant association under autologistic regression despite having no significant association under either logistic regression method were 9 out of 42 for positively associated species and 10 out of 35 for negatively associated species and these proportions are not significantly different (χ^2 test, $p = 0.47$).

Table 2.5 shows a clear general decline in the proportions of species-positive squares that are relatively highly urbanised as species' associations with urbanisation become less positive under autologistic regression, this is confirmed by the correlation coefficients (table 2.6). Again, it is striking that the species with negative associations under autologistic regression behave as expected, most of them having zero or very low proportions of urbanised squares, whereas the species with positive associations behave much less intuitively.

Sorting the species in descending order of their proportions of squares over each of the thresholds of relative urbanisation in turn gives some surprising results. The 'top 7' species with the highest proportions of their species-positive squares over the 20% urbanisation threshold are Common Tern, Little Ringed Plover, Lesser Spotted Woodpecker, Great Crested Grebe, Tufted Duck, Canada Goose and Kingfisher with the first species that might normally be regarded as urban, Feral Pigeon, in 8th position. Sorting by the 10%, 5% and 1% threshold proportions produces similarly counter-intuitive rankings, the >=5% ranking gives Little Ringed Plover, Reed Warbler, Great Crested Grebe, Lesser Spotted Woodpecker, Common Tern, Lesser Whitethroat, Canada Goose, Little Grebe, Kingfisher, Tufted Duck, Mute Swan and Coot as the 'top 12' with Feral Pigeon only appearing in 13th rank, followed by further surprising species before the species with high positive associations under autologistic regression finally start to appear midway down the rankings. House Sparrow, for example, is ranked at 34 out of 77 species, Blackbird at 42 and Starling at 37.

Table 2.5. Proportions of the squares in which the species whose distributions had positive associations with landclass 21 under autologistic regression occurred that had percentage cover of landclass 21 exceeding four different thresholds.

Species	autologistic regression		Proportion of species-positive squares with urbanisation >= threshold percentages			
	rank	P-est	>= 20%	>= 10%	>= 5%	>= 1%
Blackbird	1	9.6334	0.001859	0.0079	0.02277	0.121283
Starling	2	6.8848	0.001954	0.008305	0.023937	0.127504
Blue Tit	3	6.5931	0.001909	0.008115	0.023389	0.124582
House Sparrow	4	3.8872	0.001978	0.008408	0.024233	0.128586
Great Tit	5	1.9332	0.001952	0.008297	0.023914	0.126403
Woodpigeon	6	1.8554	0.001989	0.008454	0.024366	0.128294
Mallard	7	1.7354	0.001935	0.008224	0.023706	0.124819
Robin	8	1.4556	0.001829	0.007773	0.022405	0.118884
Moorhen	9	1.443	0.002424	0.010303	0.029091	0.155152
Song Thrush	10	0.8236	0.001871	0.007951	0.022919	0.119738
Dunnock	11	0.8188	0.002014	0.00856	0.024169	0.128399
Magpie	12	0.7901	0.002551	0.010842	0.03125	0.161352
Greenfinch	13	0.7462	0.002227	0.009465	0.026726	0.139755
House Martin	14	0.6159	0.00203	0.008122	0.024365	0.129442
Swift	15	0.4455	0.002616	0.011118	0.030739	0.155657
Coot	16	0.3774	0.00299	0.012706	0.035874	0.17713
Whitethroat	17	0.365	0.001814	0.009674	0.028416	0.149335
Blackcap	18	0.3563	0.002506	0.010652	0.029449	0.149749

Mistle Thrush	19	0.3246	0.002048	0.008705	0.024066	0.128008
Goldfinch	20	0.2327	0.002398	0.010192	0.027578	0.142086
Bullfinch	21	0.2223	0.002489	0.009956	0.029247	0.143746
Linnet	22	0.2177	0.002341	0.008777	0.026331	0.142188
Reed Bunting	23	0.1704	0.002533	0.008866	0.029132	0.145028
Kestrel	24	0.1575	0.002281	0.008552	0.025086	0.13569
Tawny Owl	25	0.1461	0.00253	0.010753	0.02783	0.13852
Great Crested Grebe	26	0.1434	0.005806	0.018868	0.056604	0.249637
Feral pigeon	27	0.1415	0.003562	0.014248	0.035619	0.170971
Long-tailed Tit	28	0.1405	0.002336	0.009346	0.025701	0.134346
Mute Swan	29	0.123	0.003378	0.01098	0.036318	0.170608
Little Grebe	30	0.1042	0.003315	0.01326	0.040884	0.196685
Chiffchaff	31	0.1024	0.002716	0.010862	0.028513	0.149355
Little Ringed Plover	32	0.0926	0.006369	0.025478	0.079618	0.321656
Canada Goose	33	0.0822	0.004315	0.015102	0.042071	0.206041
Tufted Duck	34	0.0623	0.004338	0.011931	0.037961	0.170282
Kingfisher	35	0.0534	0.00375	0.01125	0.04	0.18875
Lesser Whitethroat	36	0.0518	0.003394	0.014706	0.044118	0.209276
Jay	37	0.0482	0.003325	0.011638	0.030756	0.162926
Stock Dove	38	0.0476	0.003056	0.009931	0.029794	0.151261
Lesser Spotted Woodpecker	39	0.0411	0.006061	0.022222	0.048485	0.226263
Reed Warbler	40	0.0408	0.003559	0.016014	0.05694	0.224199
Common Tern	41	0.0395	0.007782	0.015564	0.046693	0.178988
Collared Dove	43	0.0056	0.002522	0.010719	0.030265	0.152585
Grey Wagtail	44	-0.0391	0.002581	0.007742	0.019355	0.098065
Rook	45	-0.0395	0	0.002865	0.017765	0.130659
Pied Flycatcher	46	-0.0425	0	0.003759	0.011278	0.071429
Wood Warbler	47	-0.0503	0	0.00369	0.01476	0.087331
Tree Pipit	48	-0.0614	0.000858	0.003433	0.012876	0.090129
Meadow Pipit	49	-0.0634	0.000557	0.005568	0.018931	0.105791
Snipe	50	-0.066	0	0.001835	0.015596	0.089908
Black-headed Gull	51	-0.0738	0	0.003906	0.011719	0.068359
Teal	52	-0.1044	0	0.002012	0.014085	0.054326
Redstart	53	-0.1208	0	0.002035	0.005086	0.061038
Oystercatcher	54	-0.1213	0	0	0.006048	0.047379
Curlew	55	-0.1338	0	0.000841	0.004205	0.063078
Whinchat	56	-0.183	0	0.001055	0.004219	0.048523
Dipper	57	-0.2369	0	0.00096	0.001919	0.037428
Red Grouse	58	-0.2388	0	0.001493	0.001493	0.028358
Stonechat	59	-0.2408	0	0	0.003333	0.041667
Crossbill	60	-0.2672	0	0	0.002667	0.042667
Common Sandpiper	61	-0.2909	0	0	0.001078	0.02694
Golden Plover	62	-0.2949	0	0	0.001894	0.028409
Twite	63	-0.3177	0	0	0	0.035714
Short-eared Owl	64	-0.3391	0	0	0	0.033033
Buzzard	65	-0.3429	0	0	0.00197	0.031527
Wheatear	66	-0.3488	0	0	0	0.02893
Siskin	67	-0.3537	0	0	0.001471	0.030882
Dunlin	68	-0.3636	0	0	0.003788	0.026515
Merlin	69	-0.5379	0	0	0	0.031884
Rock Pipit	70	-0.609	0	0.001961	0.02549	0.127451
Peregrine	71	-0.6435	0	0	0.003527	0.017637
Ring Ouzel	72	-0.6876	0	0	0	0.017857
Raven	73	-0.798	0	0	0.001894	0.011364
Great Black-backed Gull	74	-1.8705	0	0	0	0.012821
Common Gull	75	-2.947	0	0	0	0
Black Grouse	76	-3.571	0	0	0	0.003676
Red-breasted Merganser	77	-3.6403	0	0	0	0
Hen Harrier	78	-5.7263	0	0	0	0

Table 2.6. Correlations between autologistic parameter estimates and proportions of species-positive squares with urbanisation (landclass 21) greater than or equal to threshold percentages:

threshold % urbanisation	Pearson correlation coefficient	*P* value
20	0.227	0.047
10	0.289	0.011
5	0.278	0.015
1	0.337	0.003

Looking at the occurrence frequencies in the most developed squares (table 2.7), there are few surprises in the top third of the species with 80-100% occurrence frequencies, except perhaps for Mallard which is consistently positively associated with urbanisation on all measures so far analysed. Swallow has a surprisingly high occurrence frequency and the presence of widely distributed species such as Pied Wagtail, Willow Warbler, Blackcap and Skylark in the upper half of this ranking suggests that this result is strongly influenced by overall high abundance and uniform distribution, as might be expected at a 10 km spatial scale, rather than by urbanisation *per se*. Thirty-nine (17.6%) of the 221 species logged as breeding in Britain during the fieldwork for the atlas dataset meet the 80-100% criterion. From table 2.1 it can be seen that this is much lower than the typical proportion of national avifaunas breeding in urban habitats but remarkably similar, in number if not in exact species composition, to the 'urban stock avifauna' for Hungary of 33 species (15.8% of national breeding avifauna) identified by Bozsko (1985).

Table 2.7. Species having occurrence frequencies (%) of 80 – 100% in the 218 most developed 10km squares, sorted in descending order of occurrence frequency.

Species	%	Species	%	Species	%
Mallard	99.5	Magpie	96.3	Whitethroat	90.8
Blackbird	98.6	Pied Wagtail	95.9	Collared Dove	90.4
Blue Tit	98.6	Willow Warbler	95.4	Spotted Flycatcher	89.4
Chaffinch	98.6	Blackcap	95.0	Long-tailed Tit	88.5
Robin	98.6	Skylark	95.0	Pheasant	87.6
Starling	98.6	Song Thrush	95.0	Swift	86.2
Wren	98.6	Goldfinch	94.5	Yellowhammer	85.8
House Sparrow	98.2	Mistle Thrush	94.5	Coal Tit	83.9
Great Tit	97.2	Moorhen	94.0	Reed Bunting	83.5
Swallow	97.2	Jackdaw	93.6	Bullfinch	83.0
Crow	96.8	Greenfinch	93.1	Treecreeper	82.6
Dunnock	96.8	Rook	92.2	Great Spotted Woodpecker	82.1
Woodpigeon	96.8	Chiffchaff	90.8	Lapwing	81.7
House Martin	96.3	Linnet	90.8	Tawny Owl	80.7

Table 2.8 provides further support for positive associations with urbanisation for the 'top 6' most positively associated species under autologistic regression, although the BBS ratios cast doubt on the urban credentials of Mallard, Robin and Song Thrush which certainly persist in urban areas but could not be claimed to be quintessentially urban species, and, further down the rankings, Coot, Whitethroat and Blackcap.

Table 2.8. Species with significant associations between distribution and urbanisation under autologistic regression and having non-zero density in 'human' habitat classification of the BBS, sorted and ranked by autologistic regression parameter estimate with logistic regression parameter estimates also shown for comparison. BBS ratio is ratio of density in human habitat to mean density in other BBS habitat classes in which density was non-zero. **Bold**: BBS ratio >1. *Italics*: BBS ratio < 1.

species	**logistic regression**	**autologistic regression**	**rank**	**BBS ratio**	**BBS ratio rank**
Blackbird	3.3266	9.6334	1	**4.188**	6
Starling	2.7353	6.8848	2	**14.634**	2
Blue Tit		6.5931	3	**1.734**	14
House Sparrow	1.2917	3.8872	4	**13.396**	3
Great Tit		1.9332	5	**1.202**	16
Woodpigeon		1.8554	6	**2.057**	12
Mallard	0.5125	1.7354	7	*0.594*	27
Robin		1.4556	8	*0.819*	22
Moorhen	0.5729	1.443	9	**1.417**	15
Song Thrush		0.8236	10	*0.772*	23
Dunnock	-0.1916	0.8188	11	**2.724**	9
Magpie	0.3889	0.7901	12	**5.238**	5
Greenfinch		0.7462	13	**3.492**	8
House Martin		0.6159	14	**1.084**	19
Swift	0.1936	0.4455	15	**3.636**	7
Coot	0.3269	0.3774	16	*0.245*	35
Whitethroat	0.1292	0.365	17	*0.374*	33
Blackcap		0.3563	18	*0.436*	30
Mistle Thrush		0.3246	19	**1.142**	17
Goldfinch		0.2327	20	*0.979*	20
Bullfinch	0.13	0.2223	21	*0.429*	31
Linnet		0.2177	22	*0.659*	24
Kestrel		0.1575	24	*0.615*	26
Feral Pigeon	0.2214	0.1415	27	**49.444**	1
Long-tailed Tit		0.1405	28	*0.517*	28
Mute Swan	0.1348	0.123	29	**1.946**	13
Chiffchaff		0.1024	31	*0.157*	38
Canada Goose	0.1631	0.0822	33	*0.508*	29
Tufted Duck	0.078	0.0623	34	*0.018*	39
Jay		0.0482	37	*0.974*	21
Stock Dove		0.0476	38	**1.111**	18
Collared Dove	0.2753	0.0056	43	**7.867**	4
Grey Wagtail		-0.0391	44	*0.229*	36
Rook	-0.2286	-0.0395	45	*0.164*	37
Oystercatcher	-0.2124	-0.1213	54	**2.115**	11
Crow	ns	ns		**2.352**	10
Jackdaw	-0.1748	ns		*0.622*	25
Great Spotted Woodpecker	0.0849	ns		*0.405*	32
Nuthatch	0.1215	ns		*0.346*	34

Moorhen persistently appears among the most urbanised species, having the 15th most positive BBS ratio. Mistle Thrush too is positively urbanised in BBS as well as the atlas data; this result is supported by observations of sustainable urban Mistle Thrush populations in Sheffield (Chapter 7). The BBS ratios for Feral Pigeon and Collared Dove are much more convincing in terms of demonstrating urbanisation than the rankings of their associations under autologistic regression, similarly the relative urbanisation of Crow is strongly supported by BBS despite the lack of a significant association under autologistic regression. This may be a reflection of the recentness of this species' urbanisation, the BBS data are 20 years more recent than the atlas data. Positive BBS ratios for Stock Dove and Oystercatcher, however, may cast some doubt on the validity of this relatively simple analysis, although Stock Dove breeds in urban Sheffield (pers. obs.) and Oystercatchers among urban sewage works (pers. obs.). For those species with non-zero BBS density in the 'human' habitat class, there is a significant correlation between autologistic regression parameter estimate and BBS ratio (Spearman's rank correlation, $r_s = 0.417$, $N = 35$, $P = 0.0126$)

2.4. Conclusions

There are no surprises in the 'bottom 30' species most negatively associated with urbanisation. The 'top 15' positively associated species are also familiar in urban environments; the strong positive associations for Coot and Moorhen perhaps supported by their use of periurban reservoirs as well as urban waterways and park lakes. In terms of known species habitat preferences, the assumption that the parameter estimate is directly proportional to relative urbanisation appears to work well for non-urban species but perhaps less consistently for positive associations; Feral Pigeon, for example, is ranked by the autologistic regression method as only the 17th most urban species and Collared Dove is ranked as less urbanised than Lesser Spotted Woodpecker. However, the results for these species may be influenced by their strong associations with non-urban human habitats in villages and farms. Little Grebe appears surprisingly urbanised, but Bozsko (1985) noted that many developed areas in Hungary include or are adjacent to water bodies and that Little Grebe, as well as Great Crested Grebe, Mallard, Coot and Moorhen, readily bred in her urban study areas where suitable habitat was present, despite high levels of disturbance. Little Ringed Plover may also appear to have a surprisingly positive association with urbanisation, but according to the Urban Wildlife Trust (2005) "this species primarily favours man-made habitats in Britain" and its primary habitat in Norway is "urban areas" (State of the Environment Norway 2005).

In addition to spatial autocorrelation, a key technical issue with this kind of analysis is the question of scale appropriateness and its interspecific variation (Hostetler 2001); 10 km squares represent a fairly coarse resolution. Over the contiguous USA, a huge area with significant biogeographic variation, spatial resolution of land-cover classification did affect the results of models predicting the occurrence of bird species, especially with regard to aridity and altitude (Lawler et al. 2004). The UK is much smaller and has much less variation, in those parameters especially. However, the issue of controlling for altitude might be worth further investigation. Whitethroat, Lesser Whitethroat and Bullfinch are species of lowland scrub and farmland that have surprisingly positive associations with urbanisation in this analysis; in reality this may be a negative association with altitude, which should co-vary negatively with urbanisation, most British cities being historically ports (although it will also co-vary to some extent with northing and easting, which were included in the models). There is also the perennial concern with any evaluation of wildlife associations with man-made habitats; human delineations of urban and non-urban may not match the assessments made by birds, the effects on birds of many aspects of urbanisation remaining largely unknown (Miller et al. 2001)

Despite the complications of spatial autocorrelation and the highly significant confounding association between urbanisation and position ($P<0.0001$ for both easting and northing) in the Great Britain dataset, autologistic regression has successfully generated a list of species ordered by relative urbanisation that not only makes a great deal of ornithological sense and is supported by other less rigorous analyses but is sufficiently extensive and diverse to facilitate further analysis of causal factors. At the time of writing, this is the first large-scale correlative investigation of relative urbanisation in birds that formally takes account of spatial autocorrelation.

3. Predicting the relative urbanisation of British breeding bird species

Abstract

If urban environments differ from non-urban in their ecological opportunities and constraints, a degree of behavioural flexibility may be required if bird species are to persist in them successfully. Some bird species exploit urbanised habitats more readily than others; for 72 commoner British breeding species of a wide range of taxa, a measure of relative propensity to urbanise was compared with an index of relative brain size, as a surrogate of behavioural flexibility, using phylogenetically independent contrast regression. There was no significant relationship between relative urbanisation and brain size. Natural habitats used, population trends and taxonomy also have little influence on relative urbanisation; it is broadly associated with the number of other habitats exploited but as urban environments and avifaunas are actually quite diverse, probably not consistently with any one trait or even suite of traits.

3.1. Introduction

The question of whether the bird species that adapt successfully to urban environments differ in any consistent, measurable ways from those that do not urbanise is of increasing research interest given greater awareness of urban ecology specifically and, more generally, the need to predict the responses of species and assemblages to habitat modification. Comparative techniques that control for phylogeny offer opportunities to conduct large-scale, multi-species analyses, if datasets quantifying the relative urbanisation of a suite of species can be constructed. In this chapter, the relative urbanisation dataset derived for British breeding birds in chapter 2 is utilised to investigate the relationship between species urbanisation and a measure of relative behavioural flexibility: brain size.

Are urbanised birds adapting to completely novel habitat or are they simply exploiting remnants of recognisably 'natural' habitat or functionally equivalent habitat surrogates? If adaptation to a novel environment has taken place, some degree of intraspecific population differentiation in behaviour, morphology and perhaps eventually in genotype might be expected to arise, indeed Diamond (1986) has proposed that urbanising birds offer an opportunity to study rapid evolution. On the other hand, urbanised species may have sufficient *a priori* behavioural and/or morphological plasticity to give their pre-urban phenotypes an inherent ability to tolerate urban habitats (e.g. Jedraszko-Dabrowska & Debinska 1993), with behavioural differences between urban and non-urban birds reflecting this plasticity and genetic differentiation unlikely. Ecological reality probably involves varying combinations of both adaptation and plasticity. Aspects of behaviour observed to change in urbanised birds include aggression and/or vocalisation (e.g. James 1988; Jedraszko-Dabrowska & Debinska 1993; Jozkowicz & Górska-Klek 1996), nest construction (e.g. Jerzak 1995; Tatner 1982a) and prey selection (e.g. Wright 1973). In general, these changes seem within the range of *a priori* phenotypic plasticity; even physiological differences such as in the timing of gonadal growth in urban Blackbirds (Partecke et al. 2004) and in the blood of urban Rufous-collared Sparrows (Ruiz et al. 2002) disappeared under identical captive conditions.

Nonetheless, there is a common assumption that urban environments are more hostile and unpredictable than non-urban, and that adaptation to a relatively inhospitable habitat will drive genetic differentiation. Alternatively, another plausible ecological basis of genetic differentiation in urban birds is reduced genetic diversity due to relative stability and predictability of urban environments reducing selection pressure on those species whose inherent phenotypic plasticity allowed them to colonise what might in fact be a relatively benign environment (Rejt et al. 2004). One possible mechanism is seen in the Great Tit, in which two 'personality' traits determining behaviour in novel environments ('fast' or 'slow' explorers) are heritable and affect survival, but vary in their distribution between sexes from year to year. The annual balance of the two types alternates adaptively between sexes based on inter-year variations in food availability and consequent intraspecific competition (Dingemanse et al. 2004). If the urban food supply were more predictable, there would be less selection pressure to retain this variation as one of the two 'personalities' is better adapted than the alternative to abundant food in each sex (Dingemanse et al. 2004) and genetic diversity would decrease, assuming the urban population was to some extent reproductively isolated. Unfortunately, other studies have suggested that exploratory behaviour 'personalities' in Great Tits, although heritable, may have a common genetic basis that constrains their independent evolution within populations (van Oers et al. 2004).

Aspects of urban environments more benign for birds include higher night temperatures, abundant nest and roost sites for cavity and ledge using species and relatively low parasite incidence (e.g. Gregoire et al. 2002), which may reduce selection pressure for immunocompetence. Conversely, some aspects of urban environments may promote genetic differentiation; mutation rates in Herring Gulls nesting in an industrial urban harbour were more than twice those of non-urban nesters (Yauk & Quinn 1996). In highly-urbanised Britain, patches of built habitat provide a more or less continuous availability of urbanisation across much of the landscape; it seems unlikely that there is no population exchange between birds of built and rural habitats and genetic differentiation would therefore perhaps be surprising, particularly on the very recent timescale of large-scale urbanisation. However, the possibility cannot be discounted, given that spatial genetic differentiation in small passerine birds has been documented in populations as little as 25km apart (Moore et al. 2005) and can occur within a single woodland in Great Tits (Garant et al. 2005).

Nonetheless, among the British avifauna at the present time and stage in the urbanisation process, some species such as Blue Tit, Robin and Dunnock regularly and sustainably occur in built habitats whereas others such as Willow Tit, Stonechat and Meadow Pipit do not. Among the 47 British breeding species having positive associations with urbanisation (Chapter 2) there is some ambiguity; a few of the species with weak positive associations would not normally be considered highly urbanised. This probably arises because many of these species occur in both types of habitat. In contrast, among the 35 species negatively associated with urbanisation there are few, if any surprises; as these species tend to only occur in non-urban habitat and never urbanise. Some species clearly do urbanise, and this may both require phenotypic plasticity and promote adaptation, but the overarching biological issue remains of what *a priori* factors apparently prevent some other species from ever urbanising at all.

Some apparent trait biases have been observed in comparisons of urban and non-urban avifaunas. In a US study, degraded rural habitats of similar bird community integrity to urban assemblages had significantly more ground nesters (O'Connell et al. 1998b). There may also be taxonomic bias. In Italy, for example, Apodiformes and Columbiformes are the most diversely represented urban non-passerine families and among the Passeriformes, Fringillidae and Corvidae have the most urban species (Dinetti et al. 1996). This may be a common pattern elsewhere (Erz 1966) but such calculations are rarely comparable between studies. Urban biotic homogenisation (Chapter 1) suggests that a measure of ubiquity might predict a species' relative propensity to urbanise; within biogeographic areas the subsamples of bird species present in even widely separated urban areas often show considerable commonality (e.g. Bozsko 1985). Relative biogeographical origin may be another interesting bias; Luniak

(1996) noted that the biogeographical origins of Warsaw's avifauna were similarly proportioned to those of other central European cities, but it seems unlikely that this observation could be generalised globally and Bozsko (1985) observed that despite their commonality, the primary determinant of urban avifaunas' species composition was their host avifauna. Measures of ubiquity and biogeographical origin are likely to be at best supplementary or subsidiary to ecological traits in quantifying species' relative tendencies to urbanise.

The most commonly observed ecological trait bias in the composition of urban avifaunas is ecological versatility, with habitat specialists typically disadvantaged except for those whose speciality is commensality (Adams 1994a) or early ecological succession (Johnston 2001). Hence, measures of ecological versatility such as exploitation indices might predict species' urbanisation. In North America, for example, non-urban taxa include woodland warblers, vireos and flycatchers, which are mainly migrant insectivores, while urbanised generalists are typically habitat edge species and either residents or partial migrants, granivores or omnivores (Adams 1994). Unfortunately, quantifying ecological versatility is very difficult due to practical and conceptual problems in accurately evaluating ecological opportunities and constraints from the perspective of the target species, aggravated by mobility and seasonal variation in resource exploitation (Mac Nally 1995). Also, in any direct correlative analysis of relative versatility it would be very hard to control for differences in the relative availabilities of resources between urban and non-urban habitats and for the effects of competitive release within the urbanised subsample of a host avifauna, perhaps aggravated by variations in colonisation sequence.

Nonetheless, accepting the reasonable proposition that urban environments are to some extent novel to birds, species that successfully urbanise may well require a degree of behavioural flexibility and adaptability which can loosely be described as 'intelligence'. If this is the case, relative urbanisation should hypothetically be predicted by a measurable morphological trait: brain size, which is correlated with a number of behavioural traits in birds. Relative brain size in birds has been shown to be related to frequency of opportunistic foraging innovations (Lefebvre et al. 1997), indicators of relative immune system function correlated with behavioural repertoire (Møller et al. 2005), social complexity (Burish et al. 2004), song complexity (Garamszegi et al. 2005), developmental traits (Iwaniuk & Nelson 2003), extent of food hoarding

(Garamszegi & Eens 2004) and cognitive ability (Iwaniuk et al. 2005). On the other hand, the extent of cooperative breeding (a measure of sociality) in Corvidae was not associated with brain size (Iwaniuk & Arnold 2004). In other taxa, primates show a positive correlation between behavioural innovation, social learning frequency and brain size (Reader & Laland 2002), while brain centres related to flight and neuronal capabilities increased with habitat complexity in bats (Safi & Dechmann 2005).

A result of particular relevance to the prediction of species' persistence in putatively novel and challenging urban environments was that of Sol et al. (2002), who showed that relative brain size predicted successful establishment of bird species introduced to new locations; this was subsequently replicated in a larger database of >600 introduction events (Sol et al. 2005a). Brain size was also related to a disinclination to migrate, which implies flexibility to tolerate seasonal change (Sol et al. 2005b) and, more recently, Shultz et al. (2005) showed it was significantly related to population persistence in UK farmland, a habitat undergoing changes that have proved challenging for many of its bird species. Even more relevantly, Timmermans (1999) showed that relative forebrain size, along with feeding innovation rate, was significantly associated with taxonomic bias in propensity to urbanise and weakly associated within taxa with urbanisation frequency; as determined by consulting field guides for records in urban situations. The present study benefits from the availability of a rather more sophisticated measure of relative urbanisation.

Aspects of avian life in an urban environment that could be considered to require behavioural flexibility include the need for feeding innovations to deal with novel foods and food sources such as artificial feeders. Competition may differ between urban and non-urban populations, for example at feeding stations and other clumped food resources, from non-native synanthropes not encountered in non-urban habitats and for limited nest sites. On the other hand, lower competition than that encountered in natural forests may account for very high bird densities in some urban parks (Tomialojc & Profus 1977). A more subtle aspect of birds' behavioural flexibility is their relative use of 'public' and 'private' information when foraging. Poor sightlines and high background noise in urban habitats may distort or attenuate the information received by birds, affecting, for example, their responses to disturbance and their foraging efficiency. In the Yellowhammer *Emberiza citrinella* (a species of open country that has not urbanised), foraging birds that heard conspecifics' predator alarm calls but did not observe the actual predator remained alert and lost feeding time longer than birds that saw the predator and had complete information (van der Veen 2002). Woodland edge species, such as Blackbird, which readily urbanise may be better adapted to incomplete information, arguably an example of greater behavioural flexibility. For example, poor visibility in urban gardens might prevent birds from discovering food without observing other birds, but Blackbirds do not take such preharvest 'public information' into account when selecting food patches, paying more attention to avoiding dominant conspecifics and revisiting known rich patches (Smith et al. 2001).

The following analysis examines the hypothesis that the relative propensity of species within a host avifauna to adapt to urban habitat is associated with relative intelligence expressed quantitatively as relative overall brain size. Supporting analyses aim to determine whether other ecological factors might be associated with relative urbanisation, specifically whether urbanisation is associated with the preferential exploitation of one or more other habitat types and whether it is simply a reflection of general population increase. Taxonomic bias of urbanised species is investigated and the degree to which relative urbanisation is associated with the number of habitat types exploited, as a measure of relative niche breadth, is also examined.

3.2. Methods

Brain sizes were obtained from literature (Iwaniuk & Nelson 2003; Møller et al. 2005) and data for additional species were kindly provided by Dr Andrew N. Iwaniuk of the University of Alberta, Canada (2005, *in litt.*) who holds a database of avian brain sizes compiled from a number of primary sources and his own work. Data were available for 72 of the 78 species whose distributions had been found to be significantly associated with urbanisation under autologistic regression ('significant' species, see chapter 2) and for 106 of the 128 species breeding in 10% or more of grid squares ('breeding' species). Significant species for which brain sizes were not available were Black Grouse, Grey Wagtail, Ring Ouzel, Rock Pipit and Twite. Brain masses and volumes appear to be used interchangeably in the literature and endocranial volume has been shown across 82 species to provide a reliable estimate of brain size (Iwaniuk & Nelson 2002), the two are linearly related by the generally agreed value for fresh brain density of 1.036g ml^{-1}.

Most of the data available were expressed as brain volumes, any masses were converted to volumes for consistency.

The expected negative allometric relationship between brain volume and body mass is given by equation 3.1 where Y = brain volume, X = body mass and the exponent b is less than one for negative allometry.

$$Y = aX^b \quad \text{and hence} \quad log Y = log\, a + b\, Log\, X \qquad (3.1.)$$

The hypothesis to be tested predicted that the more successfully urbanised bird species will have brain sizes deviating positively from this baseline relationship, and conversely the brain sizes of less urbanised species will deviate negatively; the first part of the investigation was therefore to estimate the deviations of each species' relative brain size from this baseline. According to Boire & Baron (1994) a traditional and widely-accepted method is to calculate fitted brain sizes from a regression of brain size against body size for a reference group of species. This reference group should be ideally of related species having the same level of encephalisation but also of a wide range of body weights (Boire & Baron 1994). In fact, Garamszegi & Eens (2004) considered the inclusion of a large range of species for the baseline regression to be very important (more so than controlling for phylogeny). Accordingly, OLS regression of log brain volume against log body size (using MINITAB 13) in the 106 breeding species was used to construct this regression baseline. Mute Swan and Canada Goose were identified by MINITAB as outliers with disproportionate influence on the regression equation and so were removed from the analysis (see below for further discussion). A simple method of testing the hypothesis that deviations of brain size from the baseline is associated with relative urbanisation would be to regress urbanisation against the residuals of the log brain /log body regression; Boire & Baron (1994), however, recommended the brain size index as used by Stephan (1967 in Boire & Baron 1994), the ratio of actual brain volume to the fitted brain volume in the baseline regression, expressed as a percentage. This was therefore the metric used for the regression analysis of relative urbanisation against brain size, which was initially performed using OLS linear regression to indicate any general trend.

However, an issue with multi-species statistical analysis is that species' values of parameters cannot be treated as independent data points due to the confounding effect of common descent. Accordingly, the program Comparative Analysis by Independent Contrasts (CAIC) was additionally used in a second, phylogenetically controlled analysis (Purvis & Rambaut 1995b). Firstly, CAIC's regression facility was used to perform phylogenetically independent regression of urbanisation on brain index, again to inspect the basic trend. Secondly, a definitive analysis was performed using CAIC to generate independent contrasts for the variables $\log_{10}$(brain volume), $\log_{10}$(body mass) and urbanisation with $\log_{10}$(body mass) set as the independent variable, in effect asking CAIC to compare urbanisation with $\log_{10}$(brain volume) while holding constant the effects of $\log_{10}$(body mass) (Purvis & Rambaut 1995a). The resulting contrast values from CAIC were then modelled in a multiple regression of *contrast[urbanisation]* against *contrast[log(body mass]* and *contrast[log(brain volume)]* with the 'no intercept' option set in SAS PROC REG to force the regressions through the origin.

The relationship was further investigated by removal of outlier species and taxonomic focusing. Raven, Canada Goose and Mute Swan are outliers (figure 3.4.) due to their unusually large body mass; their removal from the analysis can be justified on ecological as well as statistical grounds. Raven was formerly widely distributed across both urban and non-urban habitats and is only non-urban in modern times due to persecution. Canada Goose is a recently- introduced feral species and as such has not adapted to urbanisation in the progressive 'natural' way typical of native species. Mute Swan is sparsely but very widely distributed, its breeding distribution is primarily determined by the presence of almost any suitable water body, urban or non-urban. These species are also highly variable in body mass, depending on sex and age. Datasets without waterbirds and consisting solely of passerines were also examined.

As in chapter 2, the BTO/JNCC/RSPB Breeding Bird Survey (BBS) (Noble et al. in press) provided supporting data on breeding densities in different habitat types. To examine the issue of whether relative urbanisation is associated with the degree to which species exploit other habitat types either uniformly or preferentially, OLS multiple regression analysis (PROC REG in SAS) was used to examine how breeding densities in nine habitat types (plus a tenth 'miscellaneous' habitat type) estimated from the BBS might jointly predict relative urbanisation. BBS figures were available for 47 of the significant species. Automatic backwards elimination of predictors at $P \geq 0.1$ was used. Distributions of the predictors were highly skewed with many zeroes so all ten were log transformed (with 0.1 added to allow logarithms of the zeroes).

To examine the association of relative urbanisation with the direction of population trends, the significant species were coded as 1 or 0 respectively for positive and negative associations with urbanisation and 1 or 0 for either generally rising or generally falling population trends (www.bto.org). Where trends have changed in recent years, subjective judgement was used to assign a trend direction more or less contemporary with the Atlas data gathering period (1988-91); 52 species had trends that could be unambiguously classified in this way. The resulting contingency table was tested for association using a χ^2 test (PROC FREQ in SAS).

Detailed analysis at family level of taxonomic bias in propensity to urbanise was not possible due to the sparse representation of many families among the 128 breeding species. However, relative distributions of the species between seven intermediate taxa within the three categories of association with urbanisation (positive, negative and no significant association) were examined graphically. In addition, the association between whether a species is passerine or non-passerine and the direction of the relationship of its breeding distribution with urbanisation (positive, negative and no significant association) was evaluated using a χ^2 test.

To investigate whether relative urbanisation is associated with the number of different habitat types exploited by a species, the 83 species for which BBS breeding density data were available was coded either 1 (positive association with urbanisation), -1 (negative association) or 0 (no significant association) and the number of different BBS habitat codes in which each species attained a non-trivial breeding density (Newson et al. 2004) was counted (maximum 9, including 'miscellaneous' habitat). A two sample t-test was used to compare the mean number of habitat types exploited by positively and negatively urbanised species, one-way ANOVA was used to compare the numbers of habitats used by species positively, negatively and non-significantly associated with urbanisation. As a further indicative analysis, OLS linear regression was performed of species' degree of association with urbanisation (autologistic regression parameter estimate) against the number of habitats in which they had non-trivial BBS breeding densities, for the 49 of the significant species having BBS densities.

3.3. Results

Although the distribution of the autologistic regression parameter estimate values for landclass21 (subsequently referred to as urbanisation) for the 72 species considered was not formally normal (Kolmogorov-Smirnov test $P < 0.01$) it was considered adequately symmetrical about the mean for regression analyses to be informative.

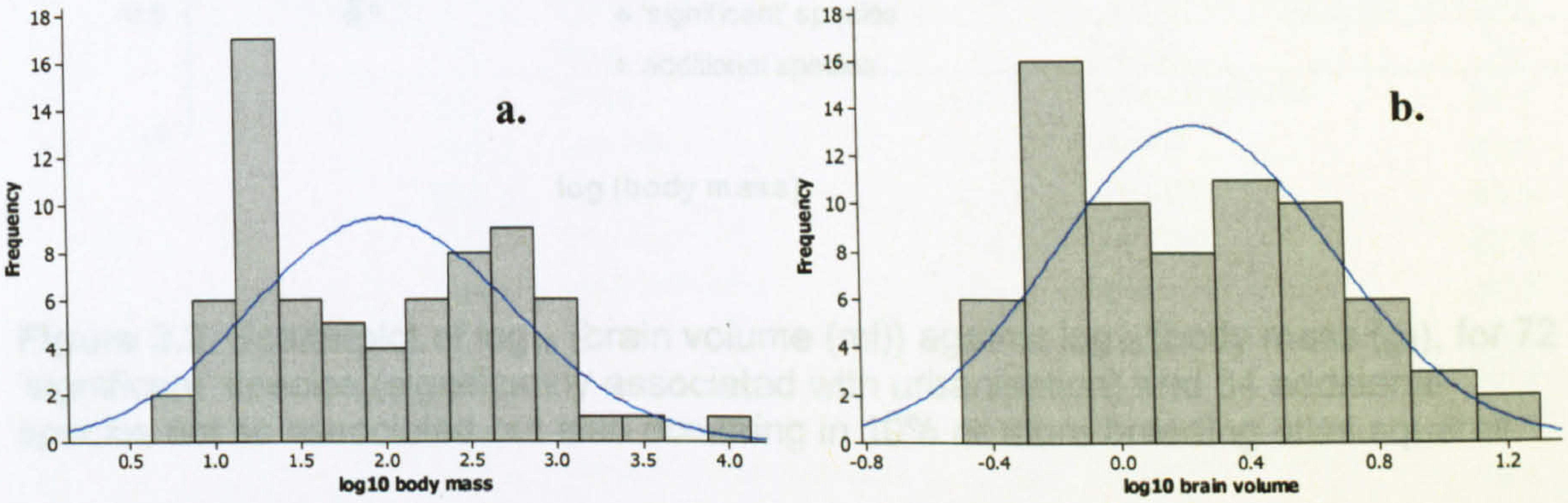

Figure 3.1.a. Frequency distribution of $\log_{10}$ (brain volume (ml)) with normal distribution (blue), for the 72 significant species **Figure 3.1.b.** Frequency distribution of $\log_{10}$ (body mass (g)) with normal distribution (blue), for the 72 significant species

Similarly both brain volume (K-S test, $P<0.01$) and body mass (K-S test, $P<0.01$) failed formal normality tests but, as expected for a negative allometric relationship their logarithms were fairly symmetrical, although still formally non-normal (both K-S test, $P<0.01$) in distribution with some bimodality apparent (figures 3.1.a. and b.). As expected, there was a highly significant correlation between log(brain volume) and log(body mass), as shown in figure 3.2. 'Significant' species ($N = 72$) are those for which there was a significant association of distribution with urbanisation under autologistic regression, 'additional' species are the additional 34 species out of the 128 occurring in 10% or more breeding atlas squares (table 2.2.) for which brain data were available (total $N = 106$). Species are tightly clumped at low values.

Linear regression of brain volume against body mass was highly significant ($F_{1,70} = 69.1$, $P < 0.001$, $r^2 = 49.3\%$), as was linear regression of $\log_{10}$ (brain volume) against $\log_{10}$ (body mass), equation 3.1 is the regression equation for the 72 significant species.

$$\log_{10}(\text{brain volume}) = -0.837 + 0.541 \log_{10}(\text{body mass}) \qquad (3.1.)$$

$$(P < 0.001, F_{1,70} = 617.5, r^2 = 89.8\%)$$

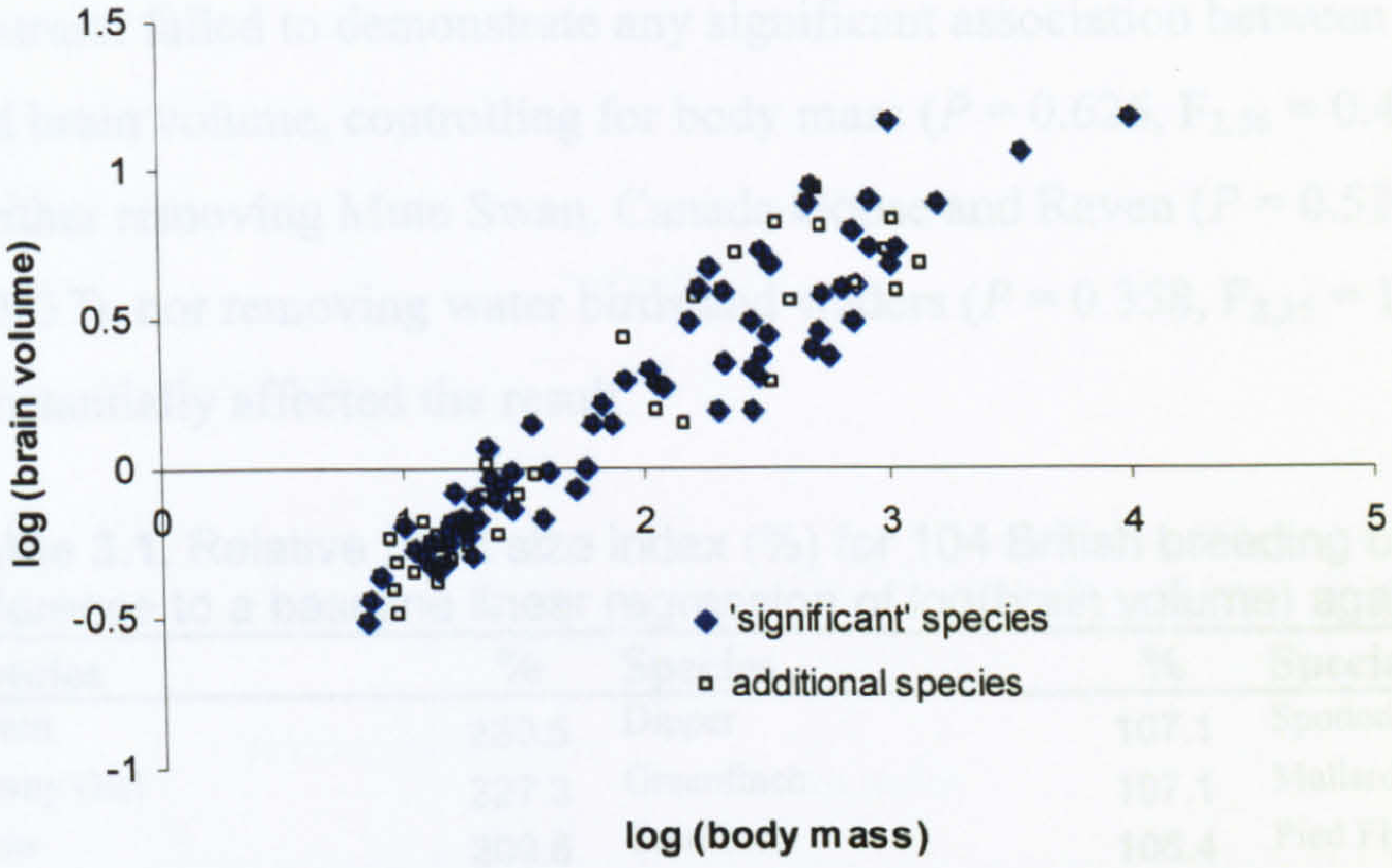

Figure 3.2. Scatterplot of $\log_{10}$ (brain volume (ml)) against $\log_{10}$ (body mass (g)), for 72 'significant' species (significantly associated with urbanisation) and 34 additional species not so associated but also occurring in 10% or more breeding atlas squares.

The equation for 104 species (Mute Swan and Canada Goose removed) was little different (equation 3.2.) Table 3.1. shows brain size indices predicted by equation 3.2.

$$\log_{10} (brain\ volume) = - 0.88 + 0.557 \log_{10} (body\ mass) \qquad (3.2.)$$

($P < 0.001$, $F_{1,102} = 857.37$, $r^2 = 89.4\%$)

The parameters log(a) and b of equation 3.2. remained unchanged to 2 decimal places when two alternative sets of body mass data for the same species (one independently collected from literature by a colleague (K.L.Evans *pers comm*) and one compiled by the BTO (Robinson 2005)) having up to 10% mean variance with respect to the original dataset were experimentally substituted in the regression. OLS linear regression of urbanisation against relative brain size index for all 72 of the significant species indicated no significant association (figure 3.3). Removing gulls, waders and waterbirds from the regression analysis made little difference ($P = 0.936$, $F_{1,46} = 0.01$, $r^2 = 0.0\%$) and regression for passerines only was also non-significant ($P = 0.856$, $F_{1,34} = 0.03$, $r^2 = 0.1\%$) even when outliers such as Raven and Blackbird were removed.

Phylogenetically independent regression of urbanisation on brain size index using CAIC's own bivariate regression facility failed to show any significant association ($P = 0.982$, $r^2 = 0.00$). For all 72 significant species, multiple regression of the urbanisation contrasts produced by CAIC against the log (brain volume) and log (body mass) contrasts failed to demonstrate any significant association between relative urbanisation and brain volume, controlling for body mass ($P = 0.626$, $F_{2,56} = 0.47$, $r^2 = 0.017$). Neither removing Mute Swan, Canada Goose and Raven ($P = 0.529$, $F_{2,56} = 0.64$, $r^2 = 0.0237$), nor removing water birds and waders ($P = 0.358$, $F_{2,35} = 1.06$, $r^2 = 0.0570$) substantially affected the result.

Table 3.1. Relative brain size index (%) for 104 British breeding bird species, with reference to a baseline linear regression of log(brain volume) against log(body mass)

Species	%	Species	%	Species	%
Raven	239.5	Dipper	107.1	Spotted Flycatcher	84.1
Tawny Owl	227.3	Greenfinch	107.1	Mallard	83.5
Crow	209.6	Goldfinch	106.4	Pied Flycatcher	83.4
Barn Owl	200.6	Tree Sparrow	104.6	Tree Pipit	82.8
Rook	199.9	Long-tailed Tit	104.6	Snipe	80.8
Jackdaw	194.7	Lesser Black-backed Gull	103.7	Red-breasted Merganser	80.5
Magpie	185.0	Yellowhammer	102.6	Shelduck	80.4
Great Spotted Woodpecker	184.2	Black-headed Gull	102.2	Pied Wagtail	80.1
Jay	183.4	Great Black-backed Gull	101.9	Swallow	79.4
Short-eared Owl	171.1	Wren	101.7	Curlew	78.6
Lesser Spotted Woodpecker	163.7	Goldcrest	100.9	Wood Warbler	76.1
Little Owl	156.5	Black Guillemot	100.7	Meadow Pipit	75.9
Kestrel	156.3	Linnet	100.6	Tufted Duck	75.3
Buzzard	149.9	Whitethroat	100.5	Chiffchaff	74.8
Hen Harrier	147.4	Blackcap	100.0	Mute Swan	74.5
Crossbill	139.5	Stonechat	99.8	Kingfisher	73.9
Nuthatch	139.4	Reed Bunting	99.1	Sand Martin	73.8
Marsh Tit	132.8	Little Ringed Plover	98.5	House Martin	73.5
Blue Tit	129.7	Common Tern	98.5	Willow Warbler	73.5
Starling	128.8	Siskin	96.9	Moorhen	71.8
Coal Tit	126.3	Garden Warbler	96.7	Common Sandpiper	69.2
Bullfinch	126.3	Skylark	96.6	Goosander	69.1
Peregrine	124.6	Robin	94.8	Stock Dove	66.6
Great Tit	124.2	Wheatear	93.1	Swift	66.5
Fulmar	124.2	Canada Goose	92.7	Turtle Dove	65.1
House Sparrow	117.7	Reed Warbler	90.1	Great Crested Grebe	62.9
Lesser Redpoll	117.7	Whinchat	89.7	Collared Dove	62.5
Merlin	117.5	Golden Plover	89.3	Pheasant	62.1
Lesser Whitethroat	115.1	Oystercatcher	89.2	Woodpigeon	61.9
Song Thrush	114.1	Redstart	88.5	Feral pigeon	60.2
Mistle Thrush	114.0	Teal	88.0	Red-legged Partridge	59.7
Blackbird	112.5	Sedge Warbler	87.9	Little Grebe	59.4
Chaffinch	111.2	Treecreeper	87.9	Red Grouse	54.6
Common Gull	110.1	Cuckoo	87.3	Coot	51.8
Herring Gull	109.0	Dunlin	87.3		
Dunnock	108.8	Yellow Wagtail	85.0		

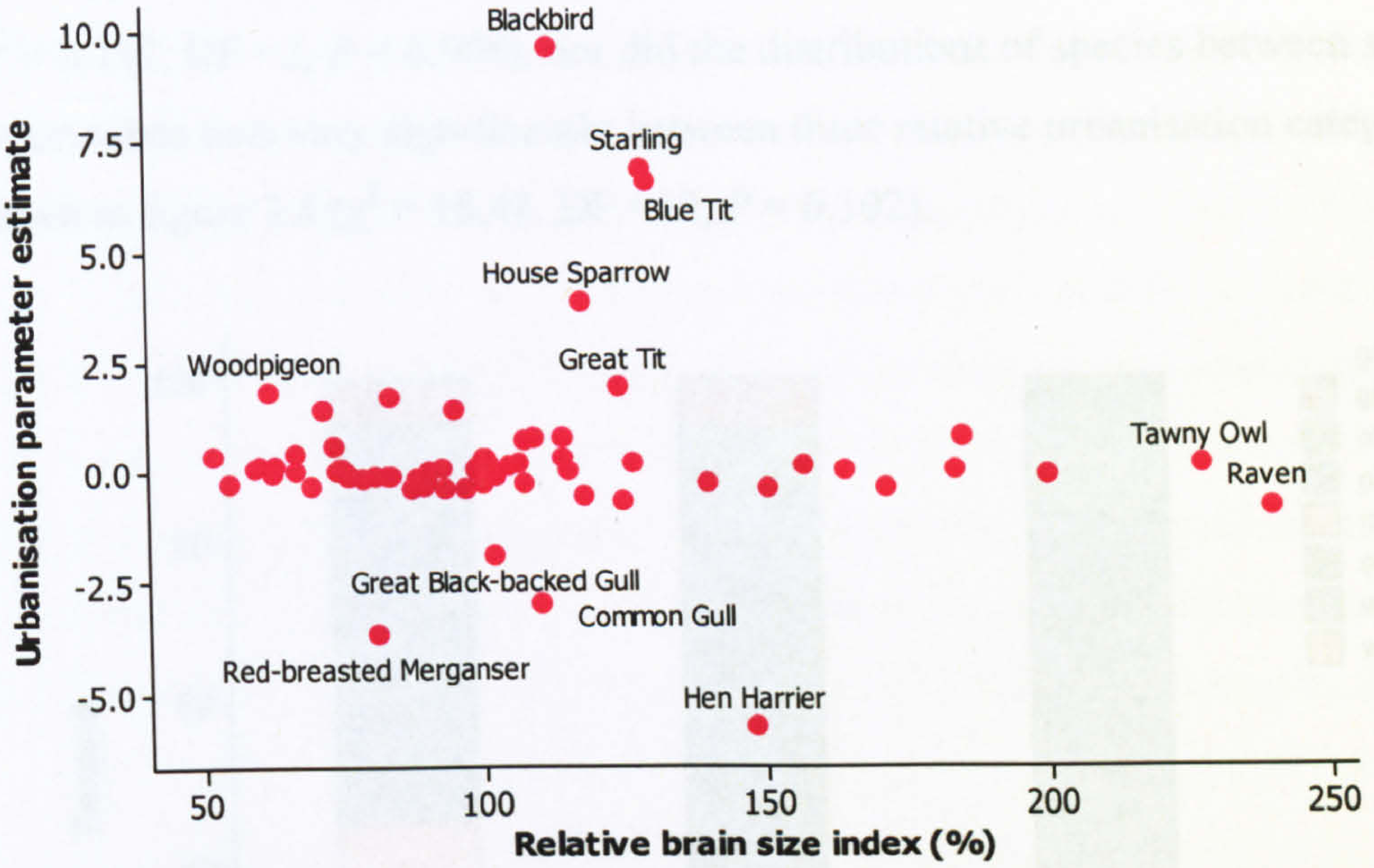

Figure 3.3. Scatterplot of relative urbanisation (model parameter estimate from chapter 2) against relative brain size index, for the 72 species with breeding distributions significantly associated with urbanisation (Chapter 2). OLS linear regression not significant ($P = 0.93$, $F_{1,70} = 0.01$, $r^2 = 0\%$).

Multiple regression of relative urbanisation against the ten BBS densities estimated equation 3.3 ($P < 0.0001$, $F_{5,41} = 11.32$, $r^2 = 0.58$). Log transformed predictors representing inland water, broadleaved woodland, moor and hill bog, improved grassland and arable were removed by automatic backwards elimination at $P >= 0.1$.

$$\begin{aligned} urbanisation = 0.752 &+ 0.3 \log(SNGRASS + 0.1) + 0.406 \log(HUMAN + 0.1) \\ &- 0.2 \log(CONIFER + 0.1) - 0.22 \log(COASTAL + 0.1) \\ &+ 0.48 \log(MISC + 0.1) \end{aligned} \tag{3.3}$$

It is unlikely that breeding densities in each habitat are independent, so this analysis is indicative rather than definitive but it suggests that use of semi-natural grassland (SNGRASS) for breeding is positively associated with relative urbanisation, as is use of human habitats (HUMAN) (as expected). Use of coniferous woodland (CONIFER) and coastal (COASTAL) habitats is negatively associated with urbanisation. The largest parameter estimate is for 'miscellaneous' habitats (MISC), which makes interpretation of the model difficult. Habitat codes are from LCM2000 (Chapter 5).

There was no significant association between direction of association of breeding distribution with relative urbanisation and direction of overall population trend ($\chi^2 = 3.02$, DF =1, $P = 0.082$), nor between direction of association of breeding distribution with relative urbanisation (+ or –) and whether species were passerine or non-passerine ($\chi^2 = 0.197$, DF =2, $P = 0.906$), nor did the distributions of species between seven intermediate taxa vary significantly between three relative urbanisation categories, as shown in figure 3.4 ($\chi^2 = 18.48$, DF =12, $P = 0.102$).

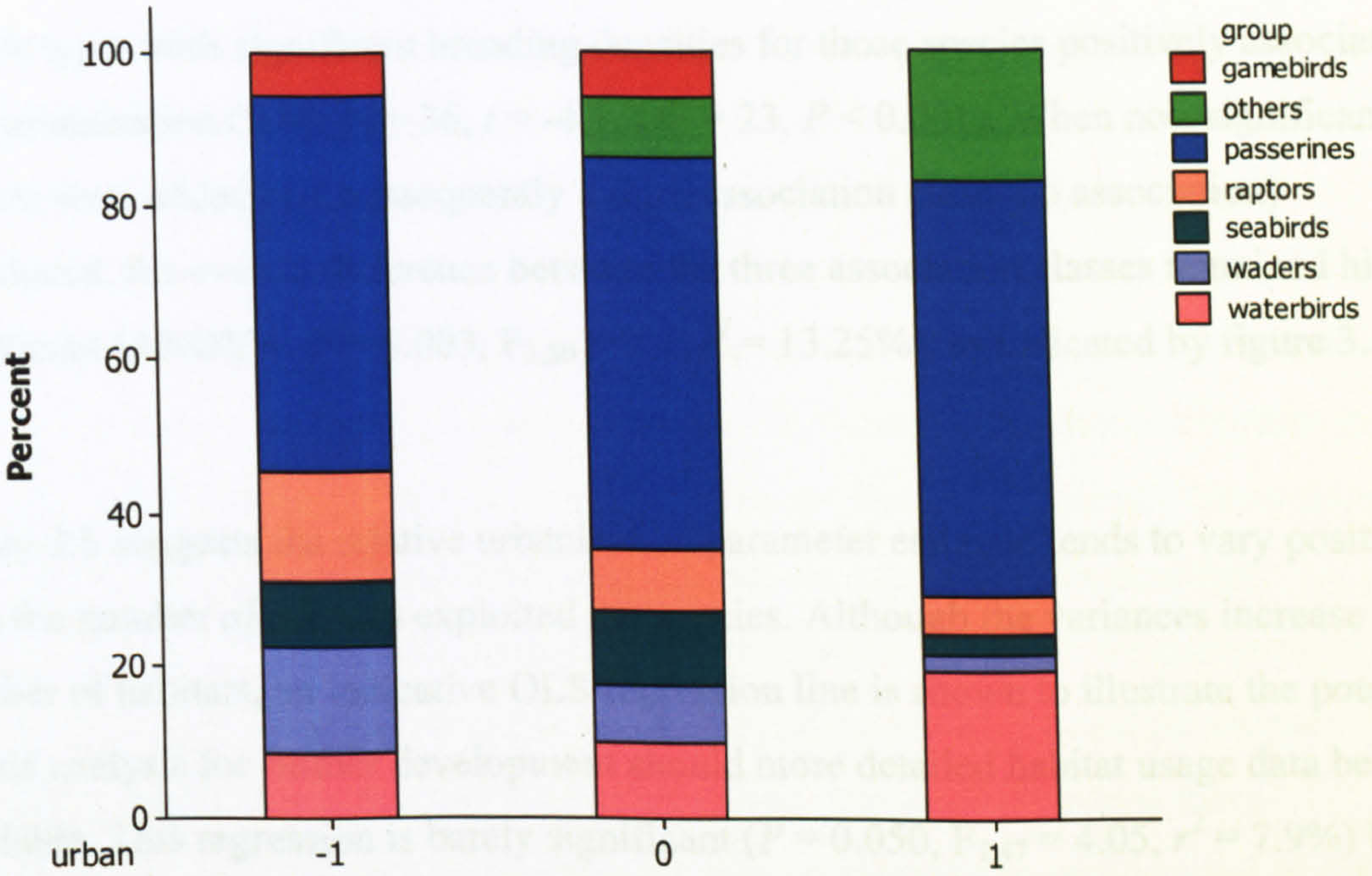

Figure 3.4. Assortment of the 128 breeding species into seven taxonomic groups within the three categories of association of distribution with urbanisation (1 = positive association, 0 = no significant association, -1 = negative association).

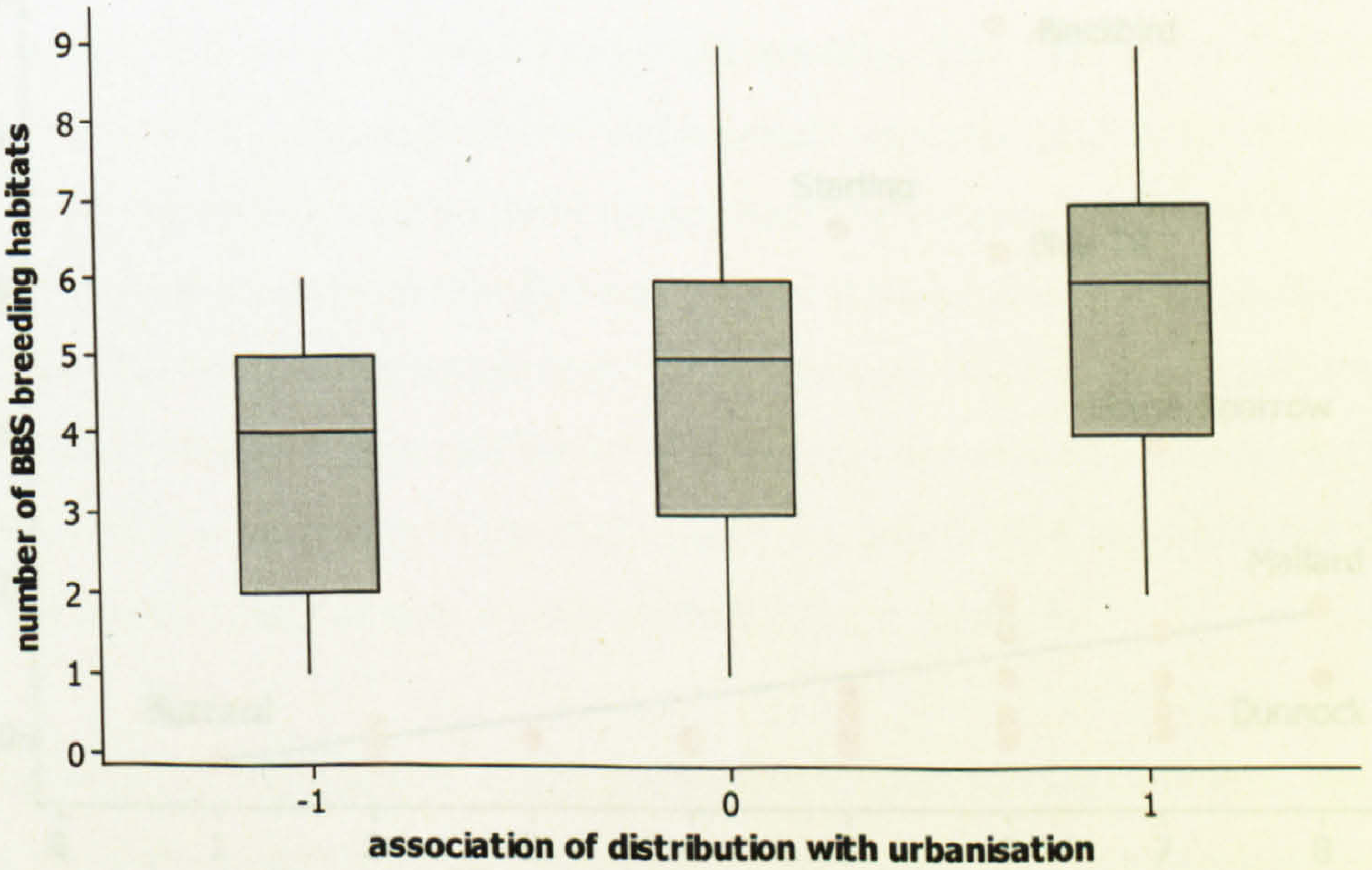

Figure 3.5. Boxplot of numbers of habitat types in which 83 BBS species had non-trivial breeding densities, by direction of association of each species' breeding distribution with relative urbanisation (–1 = negative association, 0 = no significant association, 1 = positive association) as determined by autologistic regression. Bar = median, box = first and third quartiles, whiskers = highest and lowest values respectively within upper (Q3 + 1.5 Q3 – Q1) and lower (Q1 – 1.5 (Q3 – Q1) limits.

The numbers of BBS habitat types per species were normally distributed (Kolmogorov-Smirnov test $P = 0.15$). Among the 49 of the 'significant' species for which BBS densities were available, the mean number of habitat types with non-trivial breeding densities for the species whose distributions were negatively associated with urbanisation was 3.62 (N = 13). This was significantly lower than the mean number of habitat types with significant breeding densities for those species positively associated with urbanisation (5.67, N = 36, $t = -4.1$, DF = 23, $P < 0.001$). When non-significant species were added and consequently a third association class (no association) introduced, the overall difference between the three association classes remained highly significant (ANOVA, $P = 0.003$, $F_{2,80} = 7.1$, $r^2 = 13.25\%$), as indicated by figure 3.5.

Figure 3.6 suggests the relative urbanisation parameter estimate tends to vary positively with the number of habitats exploited per species. Although the variances increase with number of habitats, an indicative OLS regression line is shown to illustrate the potential of this analysis for further development should more detailed habitat usage data become available. This regression is barely significant ($P = 0.050$, $F_{1,47} = 4.05$, $r^2 = 7.9\%$) but if the outliers Starling, Blackbird and Blue Tit are removed the fit considerably improves ($P = 0.018$, $F_{1,44} = 17.44$, $r^2 = 28.4\%$).

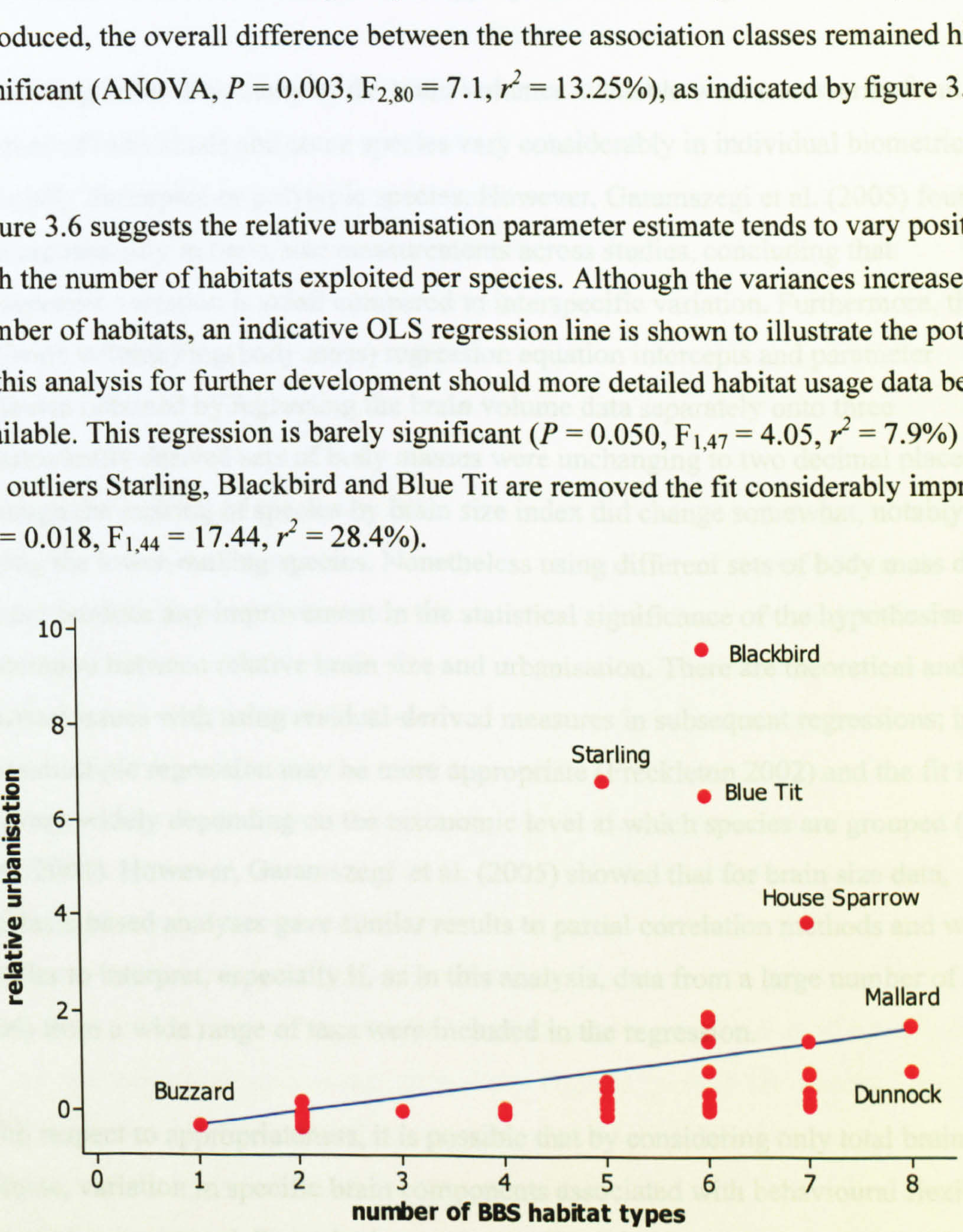

Figure 3.6. Scatterplot of autologistic regression parameter estimate for association of breeding distribution with urbanisation against number of BBS habitat types with non-trivial breeding densities per species, indicative OLS regression line shown (blue)

3.4. Discussion

For commoner British breeding bird species, the relative urbanisation parameter produced by modelling species distribution against land cover under autologistic regression is not predicted in any statistically significant way by brain volume, even when controlling for body size and phylogeny. Relative propensity to urbanise successfully is therefore not linked to behavioural flexibility; at least in as far as the brain volume data used are reliable and appropriate as its surrogate measure.

Concerning reliability, many of the brain volumes available were necessarily from small samples of individuals and some species vary considerably in individual biometrics, especially dimorphic or polytypic species. However, Garamszegi et al. (2005) found high repeatability in brain size measurements across studies, concluding that intraspecific variation is small compared to interspecific variation. Furthermore, the log(brain volume)/log(body mass) regression equation intercepts and parameter estimates obtained by regressing the brain volume data separately onto three independently derived sets of body masses were unchanging to two decimal places, although the ranking of species by brain size index did change somewhat, notably among the lower-ranking species. Nonetheless using different sets of body mass data did not produce any improvement in the statistical significance of the hypothesised association between relative brain size and urbanisation. There are theoretical and practical issues with using residual-derived measures in subsequent regressions; in some cases multiple regression may be more appropriate (Freckleton 2002) and the fit lines can vary widely depending on the taxonomic level at which species are grouped (Burish et al. 2004). However, Garamszegi et al. (2005) showed that for brain size data, residuals-based analyses gave similar results to partial correlation methods and were simpler to interpret, especially if, as in this analysis, data from a large number of species (106) from a wide range of taxa were included in the regression.

With respect to appropriateness, it is possible that by considering only total brain volume, variation in specific brain components associated with behavioural flexibility has not been captured. Some brain components vary in size more between species than total brain volume, for example telencephalon has a greater increase in size with body mass than other brain components and a larger range of variation (Boire & Baron 1994 and references therein). Opinions vary as to which measure of relative brain size is the most appropriate to consider in terms of association with behavioural traits, Burish, Kueh et al. (2004) concluded that telencephalic volume per whole brain volume F_{tel} was 'the most prominent structural correlate of behavioural traits' in birds, outperforming residuals-based measures of relative brain size, whereas Lefebvre, Whittle et al. (1997) preferred component size / brain stem size. Also, different brain components are associated with different specific aspects of behaviour than others, for example telencephalon with social complexity (Burish et al. 2004) but hippocampus with spatial learning and degree of food hoarding (Garamszegi et al. 2005), the latter perhaps only in an experience-dependent manner (Francis 2005; Healy et al. 2005). Nonetheless, correlation between the brain size indices calculated in this chapter and Burish, Kueh et al's F_{tel} values was good (linear regression, $P < 0.001$, $F_{1,41} = 73.89$, $r^2 = 64.3\%$). Despite the uncertainty, it remains reasonable to use relative total brain size as a 'best guess' indicator of overall relative intelligence (A.N.Iwaniuk 2005 *pers. comm.*). In fact Garamszegi, Eens et al. (2005) explicitly state that according to their review "studies testing for ecological and behavioural correlates of encephalisation tend to use total brain size as a focus of study, even if selection may act on individual brain structures".

In the light of this analysis, the question of what factors might influence the relative propensity of different bird species to exploit urban habitats remains. Historical colonisation sequence may have an influence, as in the observed mutual exclusion of House Sparrow and Tree Sparrow from their apparently preferred built habitats depending on which of the two species arrived in each particular urbanised area first (Summers-Smith 1988). Another intuitive predictor of failure to urbanise is a species' association with homogeneous, open landscapes such as open farmland, wetland or moorland. Comparison of relative urbanisation with BBS habitat use data does not immediately appear to support this but the data are not ideally partitioned for testing this particular hypothesis, they suggest that breeding in semi-natural grassland is positively associated with propensity to urbanise whereas use of coastal and coniferous habitats is negatively associated with urbanisation; birds highly visible in semi-natural grassland may of course actually be woodland edge species. More detailed breakdown of habitat use, notably dissection of the 'miscellaneous' BBS habitat type that is the largest significant predictor of urbanisation and probably obscures important differentiating niche breadth information, would be required to develop this analysis further.

Relative propensity to urbanise in bird species may not be measurable on a linear scale, as assumed in this analysis; there is probably a need to distinguish between those species that merely tolerate urban environments, those that never use them and those that actually persist or even thrive in them, in order to understand what factors enable or prevent successful urbanisation. Ecological niches provided by urban habitats may differ from those in non-urban niches and may be rather narrow but they could nonetheless be highly diverse, allowing substantial ecological diversity in urban avifaunas. Having said that, the BBS data on habitat utilisation support the urban ornithology dogma that niche breadth is linked in some general way to propensity to urbanise in bird species. However, phylogenetically controlled regression analysis clearly shows that whatever traits may be significantly associated with this apparent broadening of a species' niche to encompass urban environments, behavioural flexibility as measured by relative brain size is not one of them.

4. National trends in the use of gardens by birds in Great Britain

Abstract

Trends in the use of private residential gardens by wild birds in Great Britain were investigated using weekly bird records from 18,300 gardens over eight years. Plotting reporting rates for 40 species showed that the use of this habitat is seasonal and cyclic with the timing and regularity of its periodicity variable between species. Using logistic regression modelling with trigonometric terms, the significances of underlying trends in the cyclic reporting rates were evaluated; 18 species showed clear trends, the three with the most negative year term parameter estimates being 'red-listed' as of high conservation concern. Correlations with national scale survey data suggested that garden reporting rates are related to general population trends in a number of species, including several of conservation importance. Other species exhibit important differences between national and garden trends.

4.1. Introduction

In Great Britain private gardens contribute a significant proportion of the total available bird habitat, garden ownership being a traditional and widely held aspiration (Dunnett & Beer 2001). Owen (1991) estimated their total area in England and Wales as 485,000 ha or 3% of total land area. Based on a net annual increase in residential land use of 5,000 ha year^{-1} in England (ODPM 2003), and assuming around one third of such development is garden, they may cover as much as 500,000 ha of England and Wales today. This compares well with approximately 120,000 ha of national and local nature reserves in England (English Nature 2004) and 115,000 ha of Royal Society for the Protection of Birds (RSPB) reserves in the U.K. (RSPB 2002). Hence, it is likely that private gardens support a significant proportion of the national populations of some bird species; in the case of some species of conservation concern, such as House Sparrow perhaps a large proportion (Robinson et al. 2002b).

Human residential habitats in which gardens are the primary resource support important populations of a number of wild bird species (Gregory & Baillie 1998), perhaps more important than previously suspected (Bland et al. 2004), and appear to be refuges for some declining species such as the Song Thrush (Mason 2000; Peach et al. 2004). Although most typical gardens support only a reduced avifauna due to a variety of factors, including high levels of disturbance and predation, lack of nesting cover and predominantly alien plant species, some garden bird species are effectively subsidized in this habitat by artificial feeding and provision of nest boxes (Beebee 2001; Cannon 1999). Despite the recent upsurge in urban ornithological activity (Marzluff et al. 2001a), most research has remained focused on larger green spaces such as parks or on gradient studies. However, in many cities the overall area of private gardens may be very extensive, extimates include 23% of Sheffield (Gaston et al. in press), 27% of Leicester (Jeffcote 1993) and 20% of London (London Biodiversity Partnership 2001). Questionnaire data suggest that Sheffield's private gardens contain 25,000 ponds, 350,000 trees and 45,000 bird nest boxes (Gaston et al. in press), a very significant habitat resource

Being adjacent to human habitations, gardens are amenable to detailed year-round monitoring by volunteers, an obvious opportunity to increase public engagement in bird conservation and obtain data on a population that is otherwise inadequately monitored despite its potential conservation importance. Volunteer garden bird surveys have been attempted in a number of countries (Cannon 1999). Since 1970, around 250 volunteers have recorded exact numbers of birds using feeding stations over the winter period for the British Trust for Ornithology (BTO) Garden Bird Feeding Survey (Chamberlain et al. 2005; Toms 2003), which offers a uniquely long time series of feeder use data but is limited by small scale and issues with modelling the free-format data. At the other extreme of scale, Project FeederWatch collects data from thousands of volunteers across North America, demonstrating continental-scale movements as well as trends (Wells et al. 1998) but unfortunately only in the winter half of the year. The Canberra bird survey (Veerman 2002) exemplifies the comprehensive data available on smaller geographical scales; resources generally limit this intensive approach to local survey areas.

The BTO/CJ Wildbird Foods Ltd Garden BirdWatch (GBW) is presently the only garden bird survey collecting systematic weekly data from thousands of sites on a national scale and throughout the year (Cannon 2000; Toms 2003). In this chapter, the first eight years' data from GBW are analysed to determine seasonal patterns of garden usage and their variation between species, and the occurrence or otherwise of inter-annual directional trends and other temporal variations. By comparing GBW reporting rates with national population indices, the extent to which changes in garden usage by bird species reflect or differ from patterns in overall population levels is investigated, and the implications for species of conservation concern are considered.

4.2. Methods

GBW is an open-access project funded by volunteers' subscriptions; participation has grown from around 5,000 sites in January 1995 to over 16,000 in 2004 (figure 4.1).

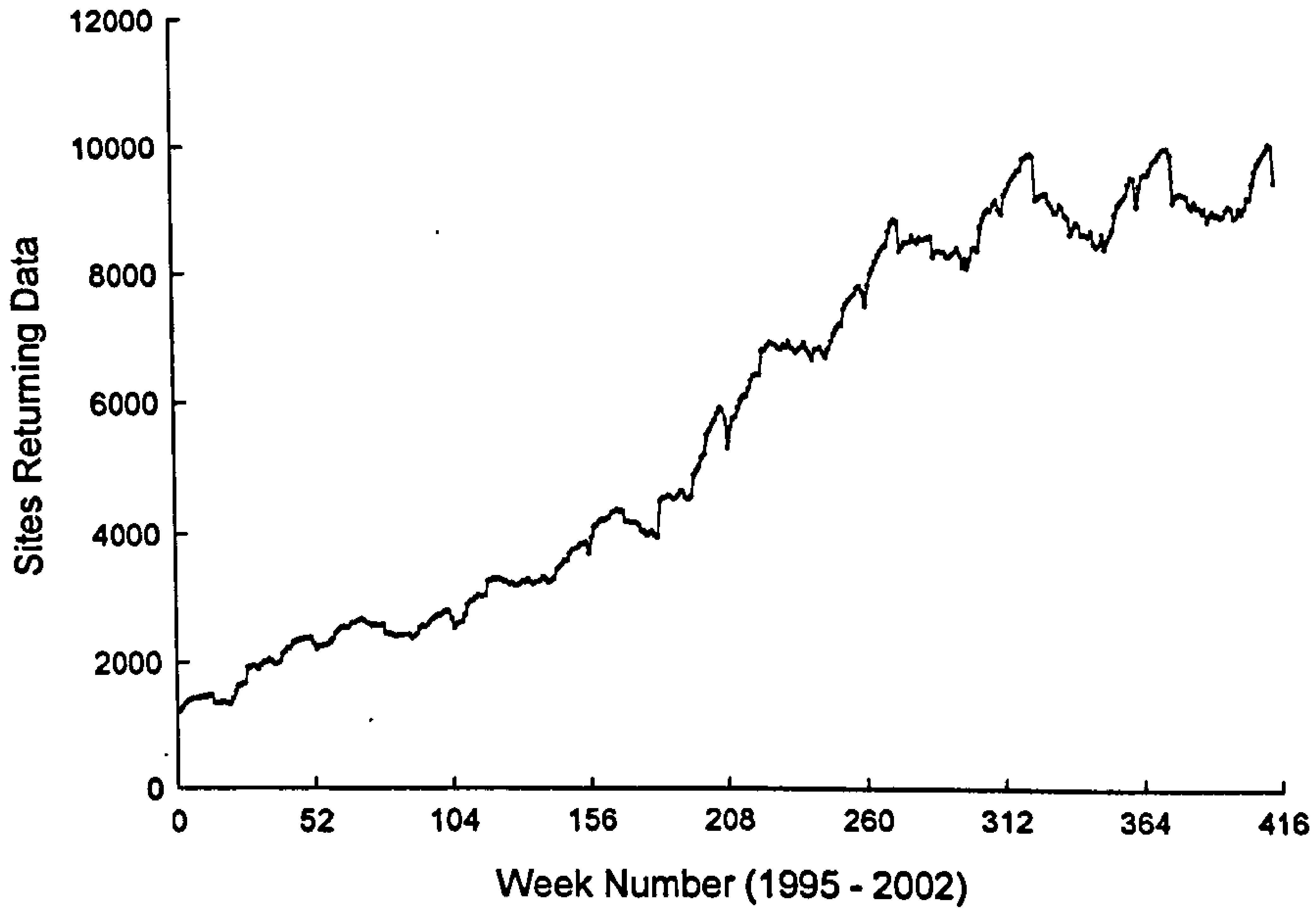

Figure 4.1. Numbers of sites contributing data to the analysis each week. Week numbers 1- 416 run from January 1995 to December 2002.

All available data for the years 1995 – 2002 were used in this analysis. The data are incomplete longitudinally as sites may join or leave the project at any time. Figure 4.2 shows that despite inevitable concentration in areas of highest human population density the survey covers the whole of Great Britain reasonably well.

Figure 4.2. GBW sites in Great Britain, November 2003. Map:www.dmap.co.uk

Presence/absence data were collected weekly using a standard checklist of 40 bird species. This method overcomes the zero records problem observed by Rushton, Ormerod & Kerby (2004), in that 'absence' records can be confidently interpreted as zeroes. Carrion Crow and Hooded Crow (Parkin et al. 2003) were recorded as a single species, few Hooded Crows visit gardens and in this habitat the ecological role of the two is similar. Volunteers were instructed to define their own consistent 'study area' within which if a species was observed at any time during a week it would be recorded as 'present' for that week. No restrictions were imposed on the type of garden observed. Almost all volunteers provided artificial food of some kind and feeding stations were generally the focal point of the study areas. Volunteers were asked to maintain consistent observation effort each week and encouraged to discard data from under- or over-observed weeks. Some variation in observer effort and competence is inevitable, but this does not detract from the ecological interest of these unique data when examined at a national scale and over an eight-year timescale. The full volunteers' instructions are available at www.bto.org.

For each of the 40 species and 416 weeks a weekly reporting rate was calculated, i.e. the proportion of the sites returning data that week at which the species was recorded. The procedure GENMOD in SAS was used to fit a Generalized Linear Model (GLM) with a logit link function and binomial error distribution ('logistic regression') appropriate to the dichotomous dependent variable *count*, which has values of either 'present' or 'absent' for each species and week (Allison 1999). This procedure estimates the logarithm of the odds of occurrence in week *i*, $ln\ (p_i\ /\ 1\text{-}p_i)$ where p_i is probability of occurrence in week *i*. A notable feature of the GBW reporting rates is strong cyclic variation with period of one year. The objective of the modelling being to examine longer-term trends underlying this periodicity, it was accounted for in the model by using trigonometric terms, following Flury and Levri (1999). The initial form of the model for all species was:

$$ln\ (p_i\ /\ 1\text{-}p_i) = \theta \quad where \qquad (4\ 1)$$

$$\begin{aligned}\theta = \alpha \quad &+ \quad \beta_1\,(year) + \beta_2\,(year^2) + \beta_3\,(cosweek) + \beta_4\,(sinweek)\\ &+ \quad \beta_5\,(cosweek * sinweek) + \beta_6\,(sinweek * year) + \beta_7\,(cosweek * year)\end{aligned}$$

where α is the value of the GLM intercept returned by GENMOD and $\beta_{1\text{-}7}$ are the GLM parameter estimates for each term. The term *year* took integer values between 1 and 8 representing 1995 – 2002, *cosweek* and *sinweek* were the cosine and sine respectively of the week number (1 – 52) within each year. Likelihood ratio statistics for each term were obtained using the TYPE3 option in GENMOD, terms for which $P_r > \chi^2 > 0.05$ were successively removed until all remaining terms were significant at this level ('minimum adequate models'), at which point estimated values for weekly occurrence probability p_i were calculated from the model parameter estimates using the formula:

$$p_i = e^{\theta} / 1 + e^{\theta} \qquad (4.2)$$

As the same sites provide data many times over the life of the project, the weekly observations are not independent. Therefore, rather than the default maximum likelihood estimation method in GENMOD, the generalized estimating equations (GEE) option for longitudinal data was selected, which produces standard errors and test statistics that are adjusted for dependence (Johnston & Stokes 1997; Zeger & Liang 1986). GEE option TYPE=AR was chosen to impose a lag-1 autoregressive structure on the correlation matrix (Allison 1999).

Modelling was performed twice for each species, firstly using datasets containing all sites in order to model overall reporting rates ('all sites' models). For less frequently-occurring species a proportion of the sites might be inherently unsuitable (such as urban gardens for Treecreeper or Reed Bunting) and hence interesting trends in the use of suitable sites by such species might be obscured by the bulk of permanently negative observations. Accordingly, the modelling process was repeated using subsets of sites from which any gardens in which a species had never been recorded were removed ('species positive' models).

To examine the extent to which GBW reporting rates correlate with trends in national populations the means over weeks 14 – 26 annually of the GBW reporting rates predicted by the model were compared with the population indices (also model-derived) for Great Britain from the BTO/Joint Nature Conservation Committee (JNCC)/RSPB Breeding Bird Survey (BBS), which takes place between April and June (Spearman rank correlation coefficients, PROC CORR in SAS, N=7). Mean 'winter' predicted reporting rates for weeks 1 – 13 annually were also calculated and correlated with both the following BBS, i.e. that in the same calendar year (BBS/GBW winter_{y-1}, N=7), and with BBS from the preceding calendar year (BBS/GBW winter_{y+1}, N=6). The BBS field methodology and analytical procedures are described in detail elsewhere (Noble et al. in press; Raven et al. 2003); indices for Great Britain (not reported elsewhere) were calculated using standard BBS modelling procedures that correct for regional differences in sampling effort. No BBS index was available for the year 2001.

4.3. Results & Discussion

Weekly occurrence probabilities (predicted reporting rates) calculated from model parameter estimates, together with actual weekly reporting rates from the raw data were plotted; 14 examples are shown here (figures 4.3 – 4.16), figures for all 40 species are in appendix C. The two plots can easily be distinguished; the raw data plots (blue) are visibly 'noisy', the modelled values (black) are smoothed sinusoids. Cyclic patterns of seasonal habitat use are visible for almost all species, the primary cause of which is likely to be variation in exploitation of garden food supplies. Detailed examination of these cycles is beyond the scope of this chapter but other causal factors (varying in relative importance between species) probably include the effects of moult on bird visibility, preferential use of some types of artificial food by juveniles and the extent to which gardens are used as breeding, rather than merely feeding, habitat. Non-breeding winter visitors are clearly differentiated from residents, migrants (Fieldfare figure 4.3, Redwing and Brambling) having reporting rates of zero in the summer months while winter visitors (Black-headed Gull figure 4.4) have very low summer reporting rates.

Several species show progressive temporal reduction in the amplitude of their periodic seasonal cycles, notably Dunnock (figure 4.5), Robin, Blue Tit, Great Tit, Greenfinch and perhaps Starling and Chaffinch. General population increases leading to increased garden residency are a possible explanation, as is a general increase in year-round provision of artificial food (Cannon 2000). Reporting rates for winter visitors (including Siskin (figure 4.6) which increasingly breeds in Great Britain) are irregular from year to year as would be expected but notable irregularity is also present in the data for Pied Wagtail, Wren and Goldcrest (insectivorous species whose garden use is strongly weather-dependent) and in Jay, Nuthatch, and Bullfinch (low reporting rate species for which most gardens are probably ‘emergency’ habitat).

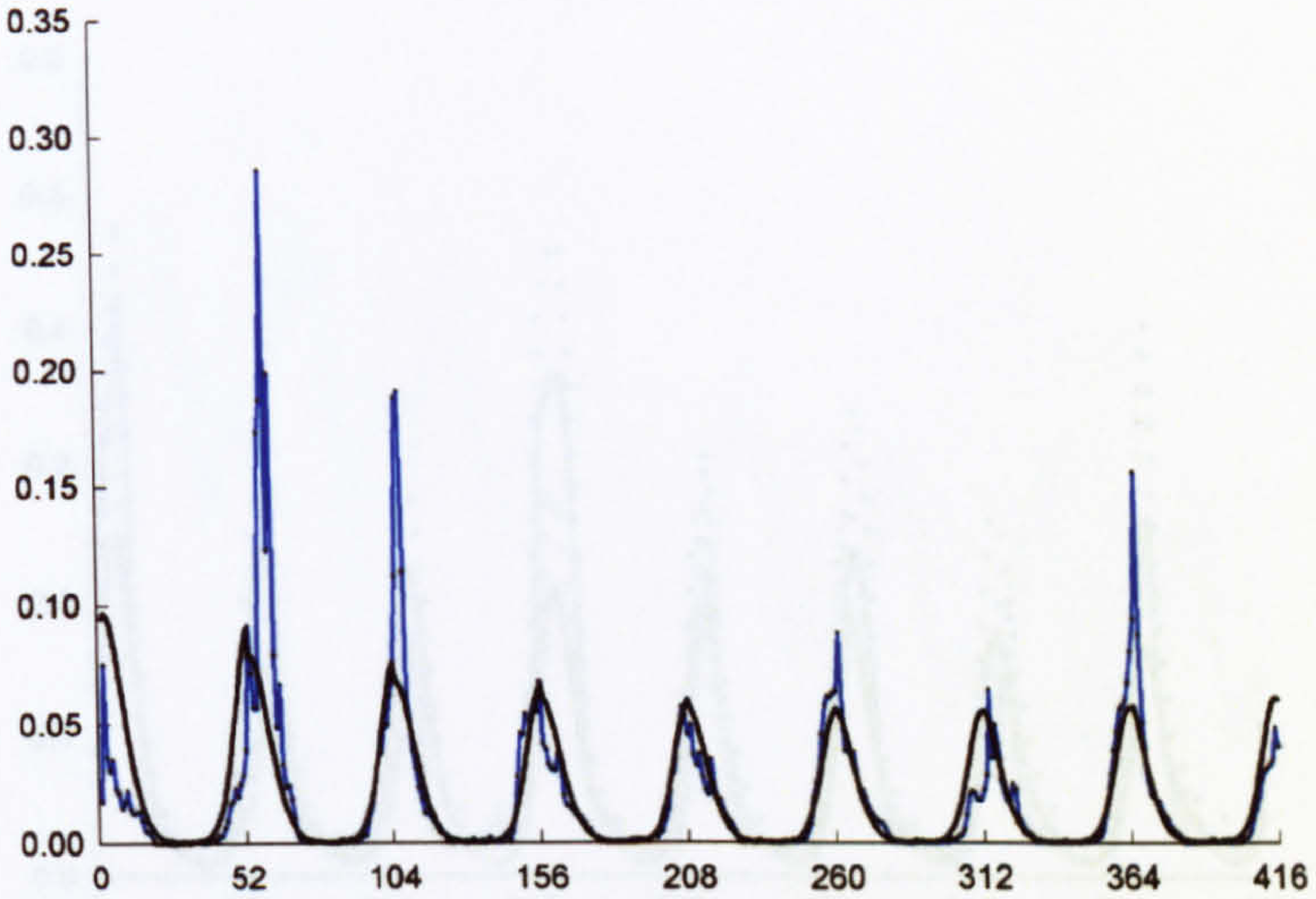

Figure 4.3. Fieldfare

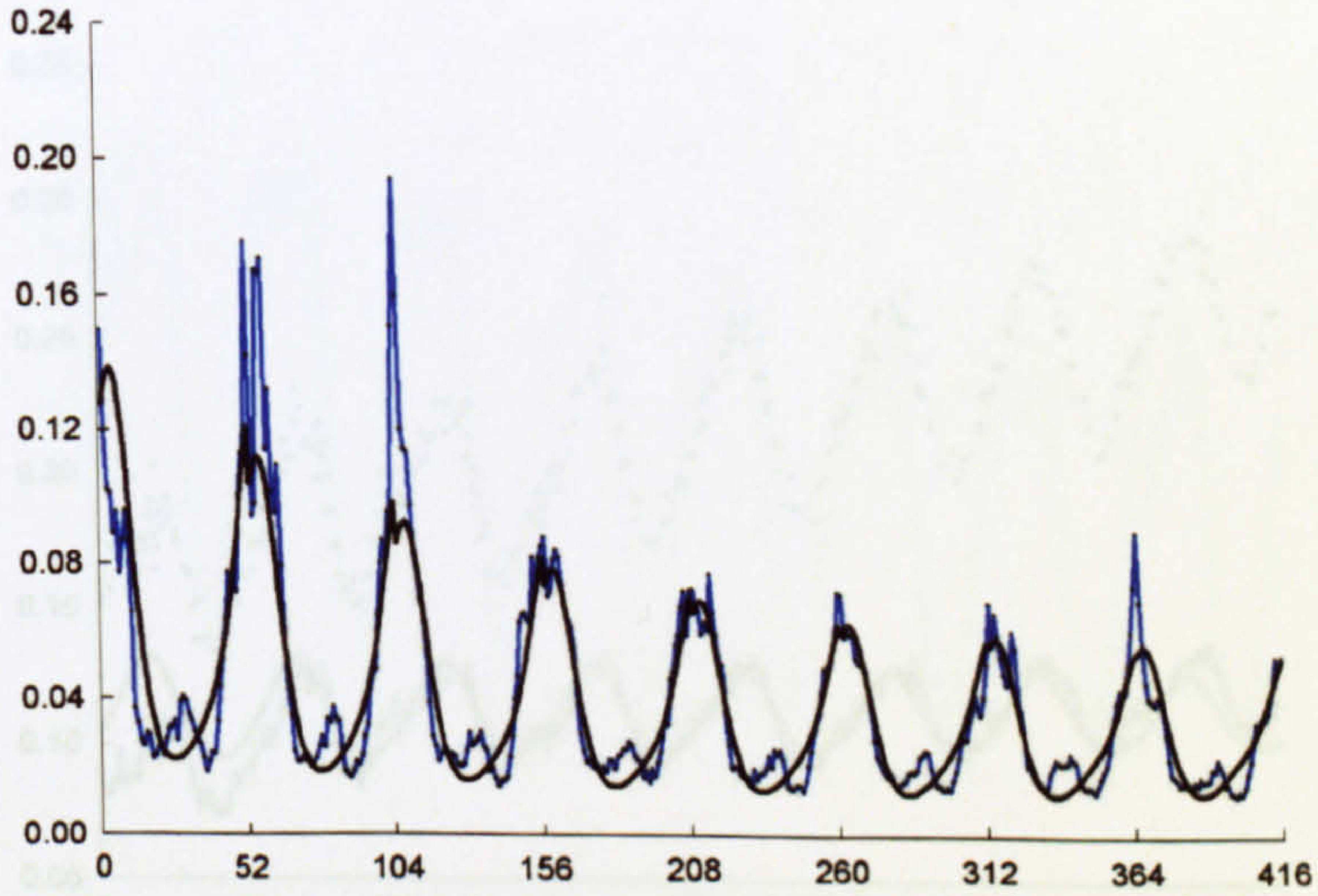

Figure 4.4. Black-headed Gull

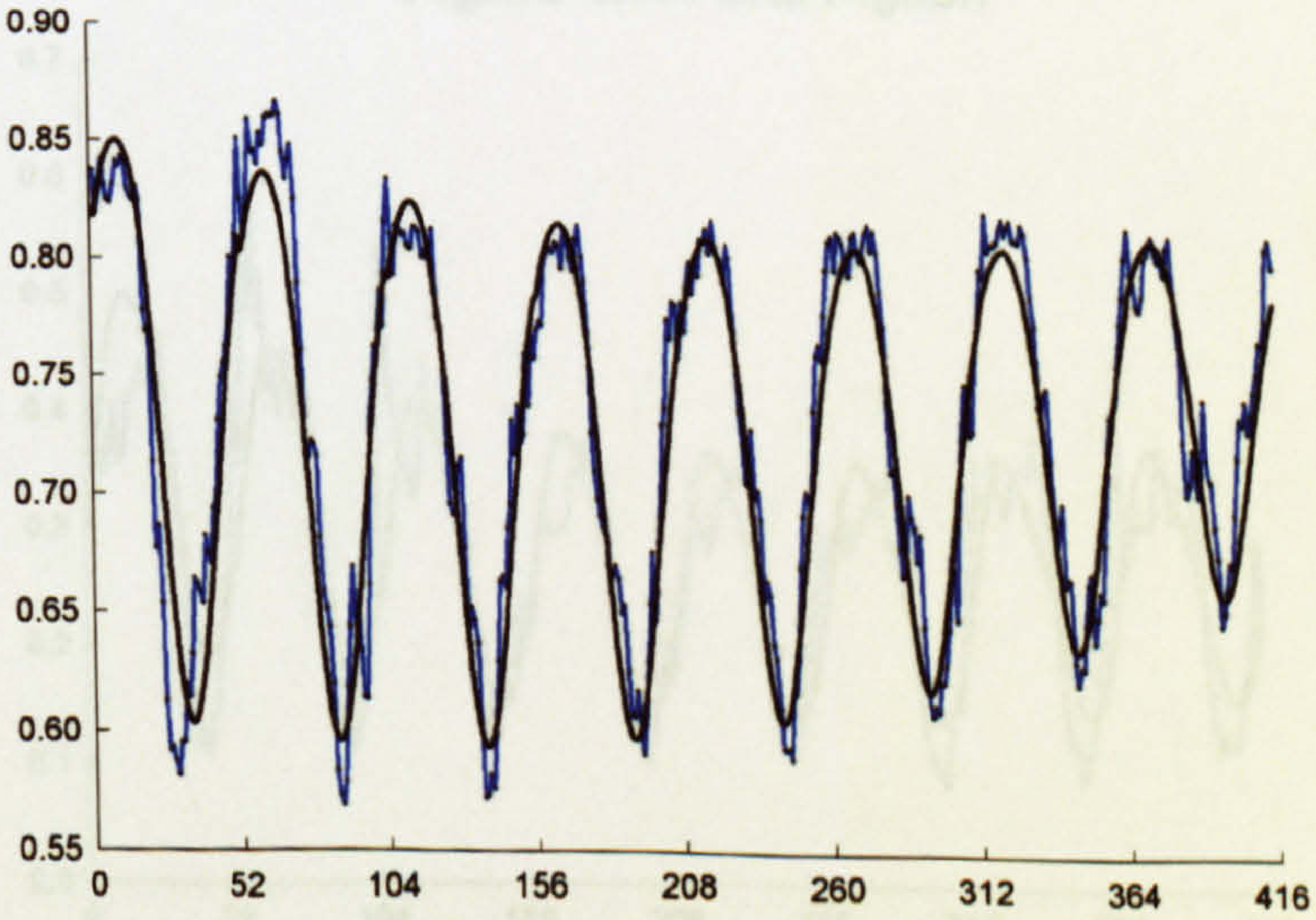

Figure 4.5. Dunnock

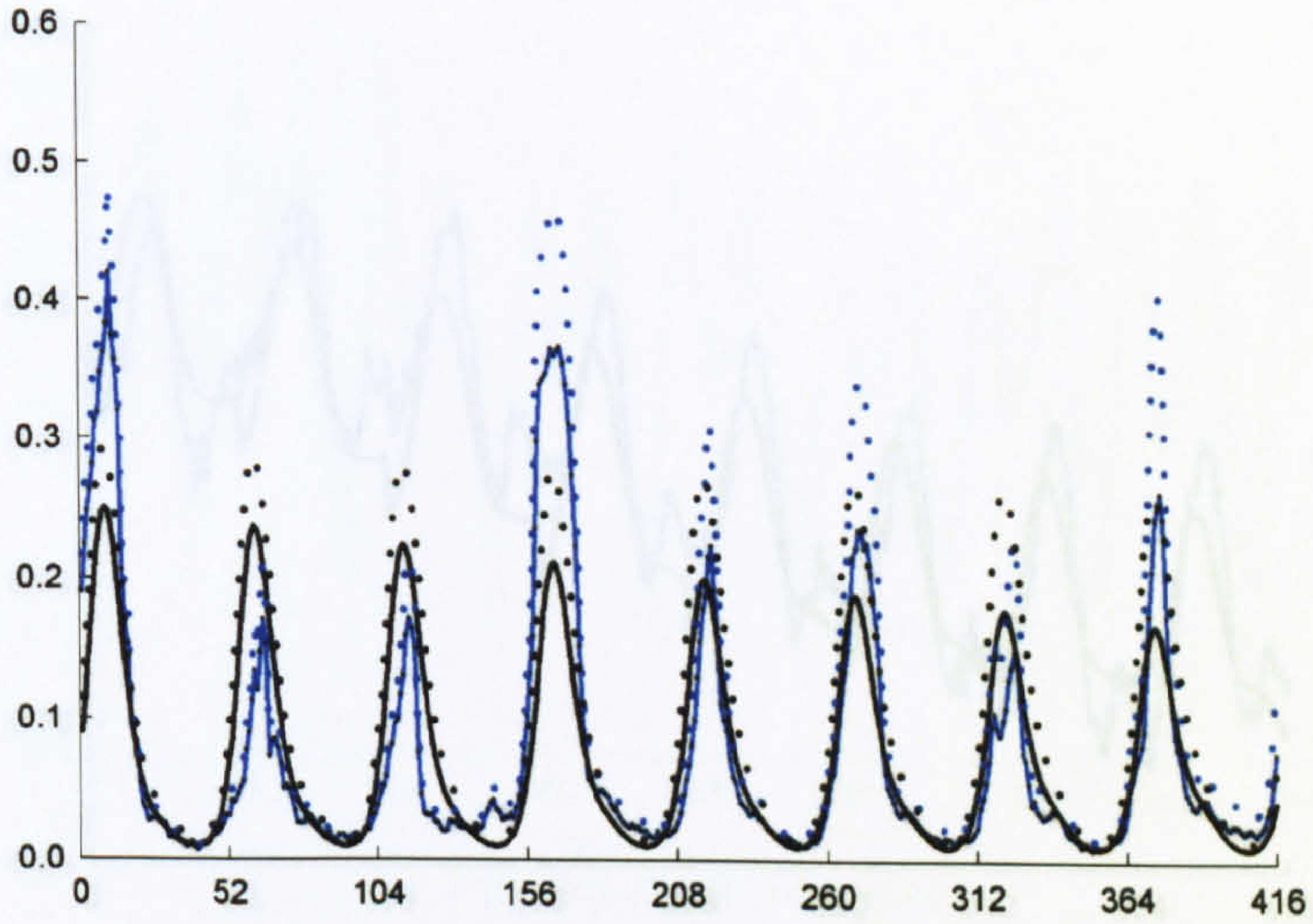

Figure 4.6. Siskin

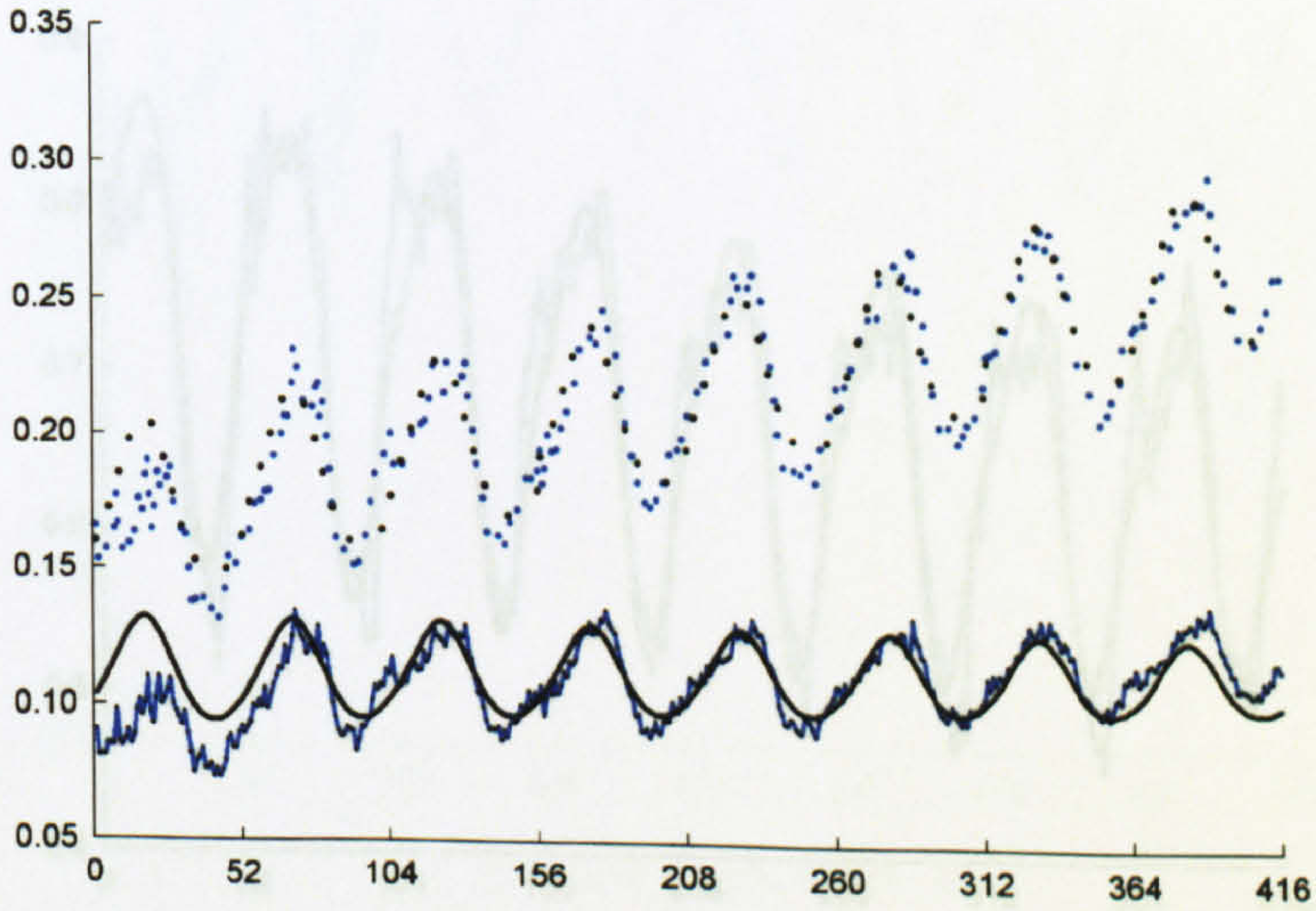

Figure 4.7. Feral Pigeon

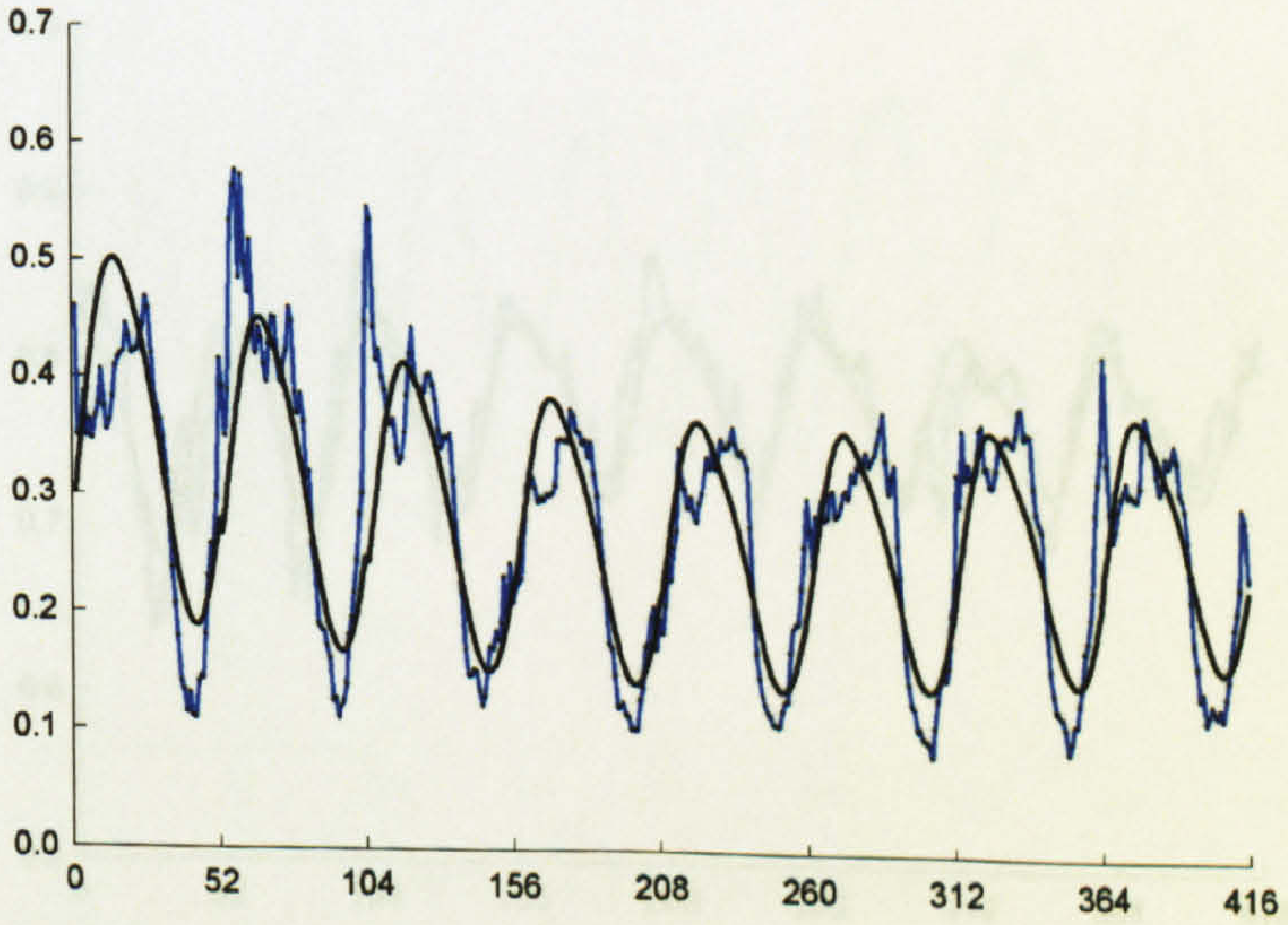

Figure 4.8. Song Thrush

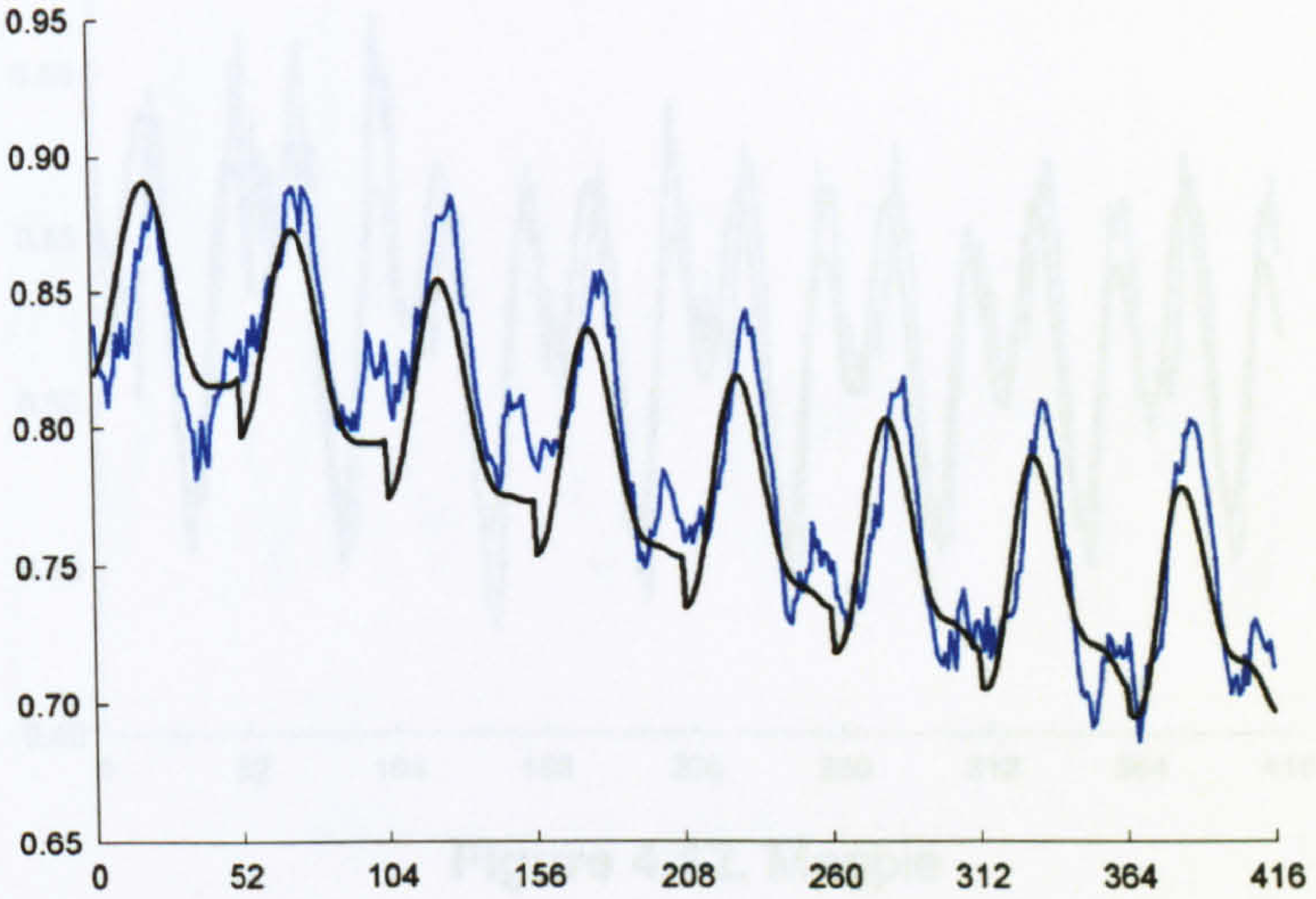

Figure 4.9. House Sparrow

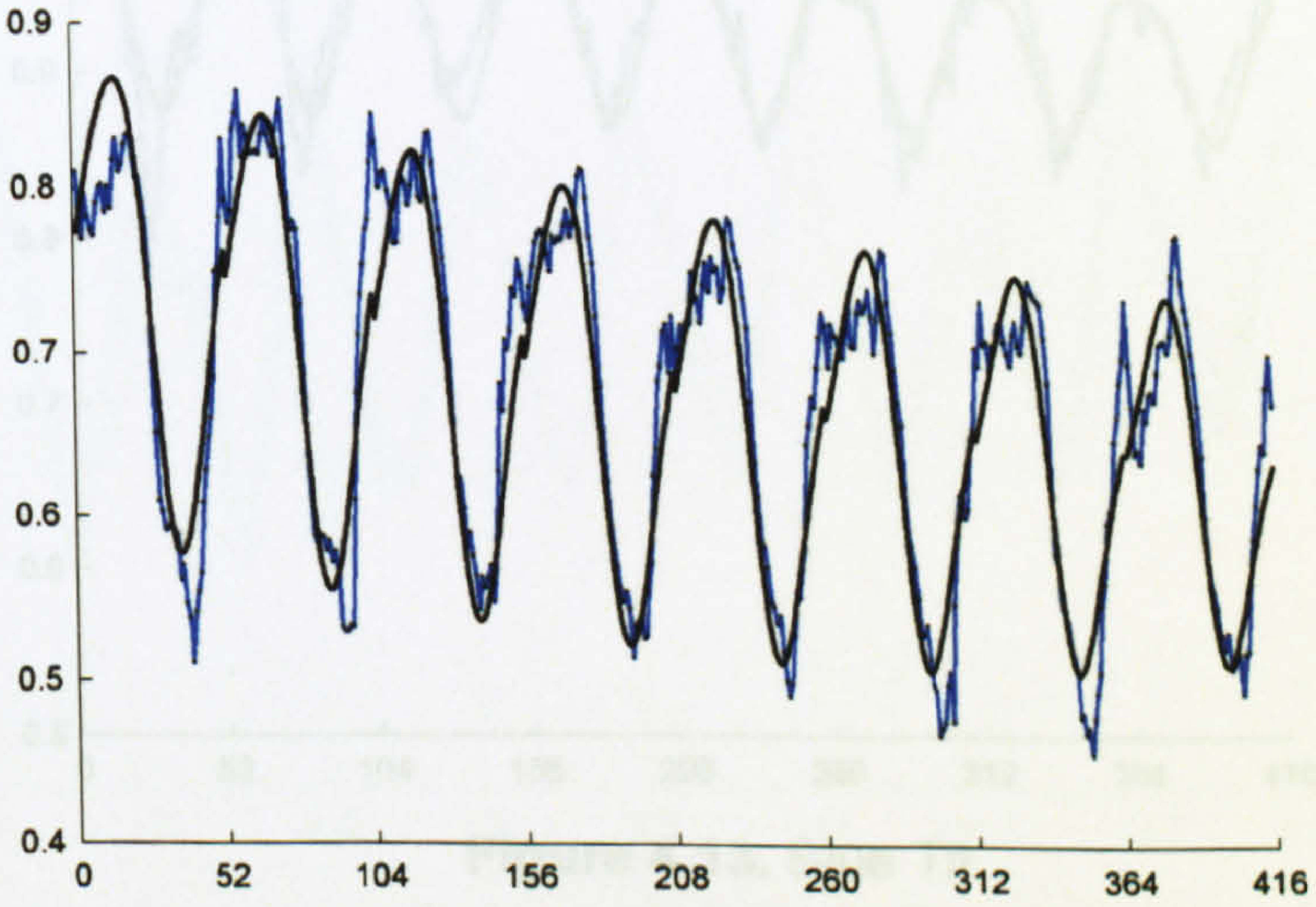

Figure 4.10. Starling

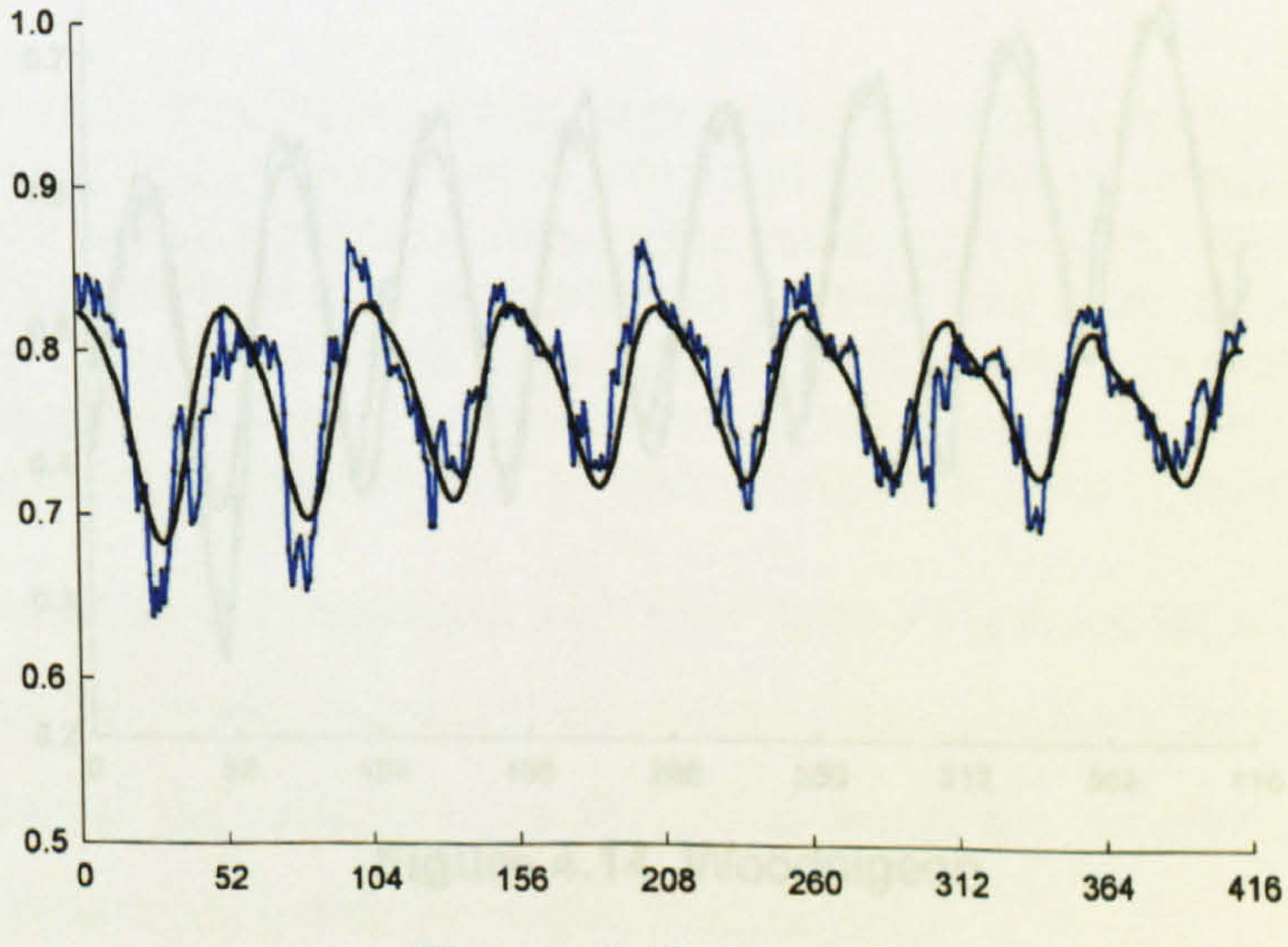

Figure 4.11. Great Tit

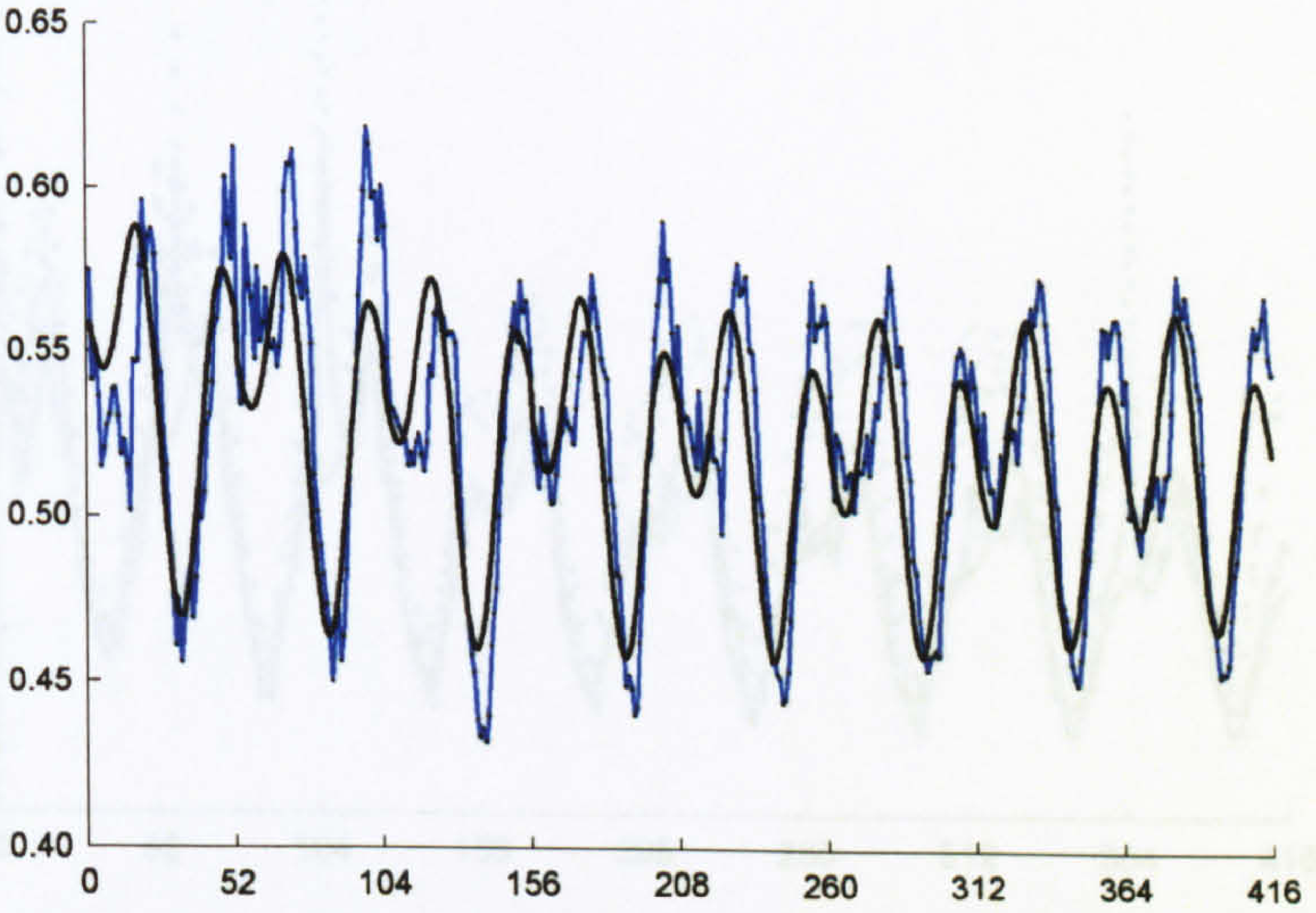

Figure 4.12. Magpie

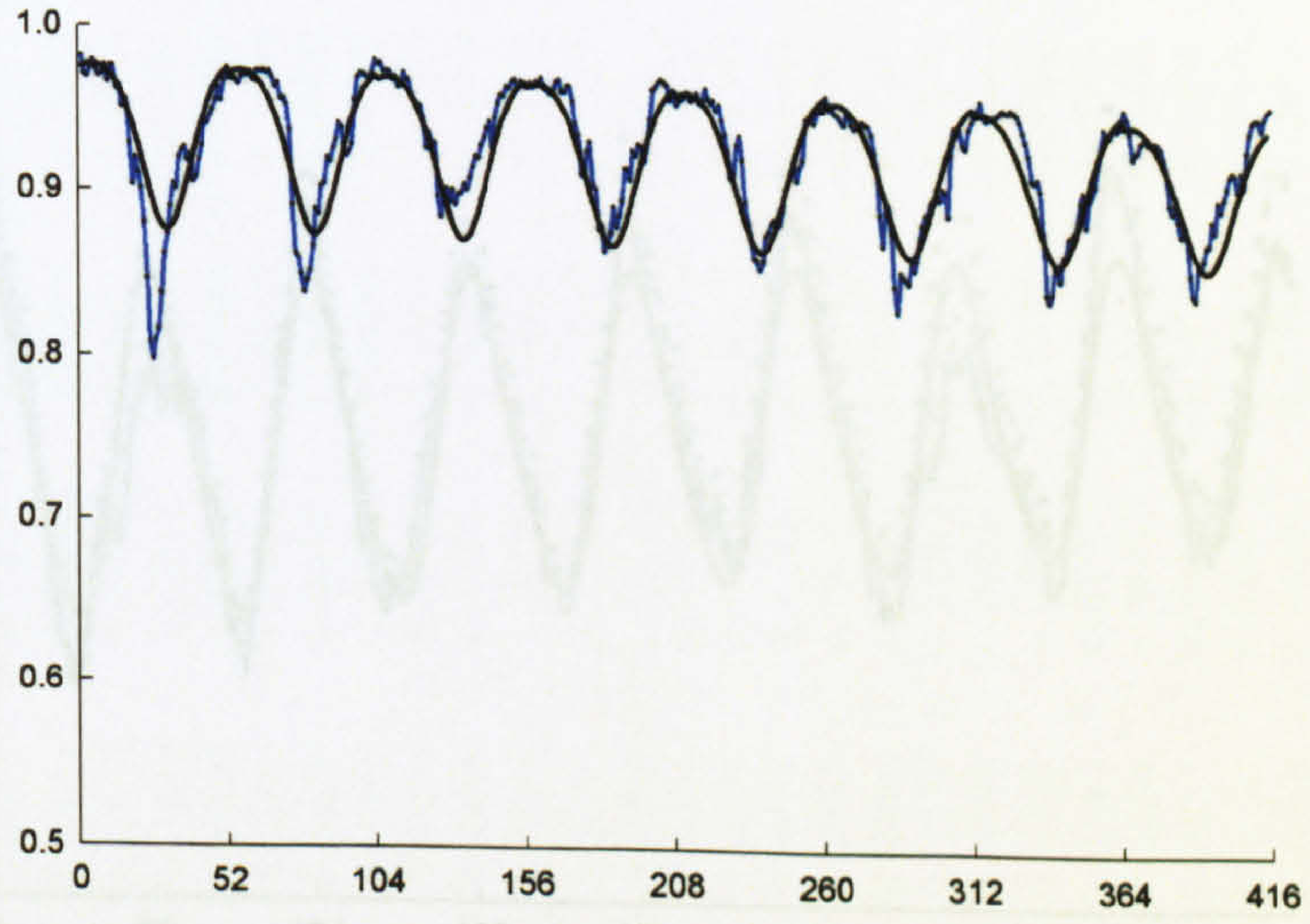

Figure 4.13. Blue Tit

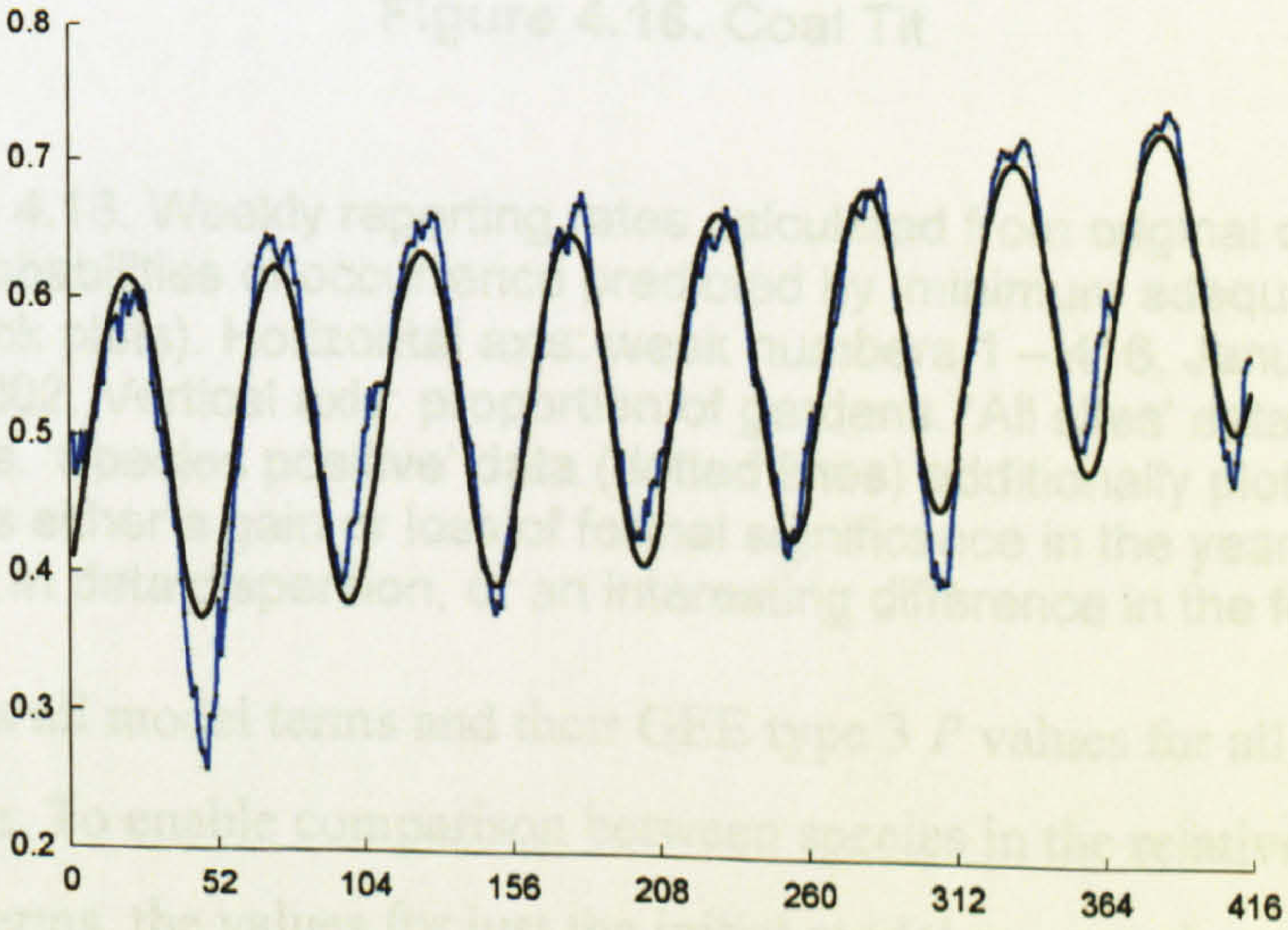

Figure 4.14. Woodpigeon

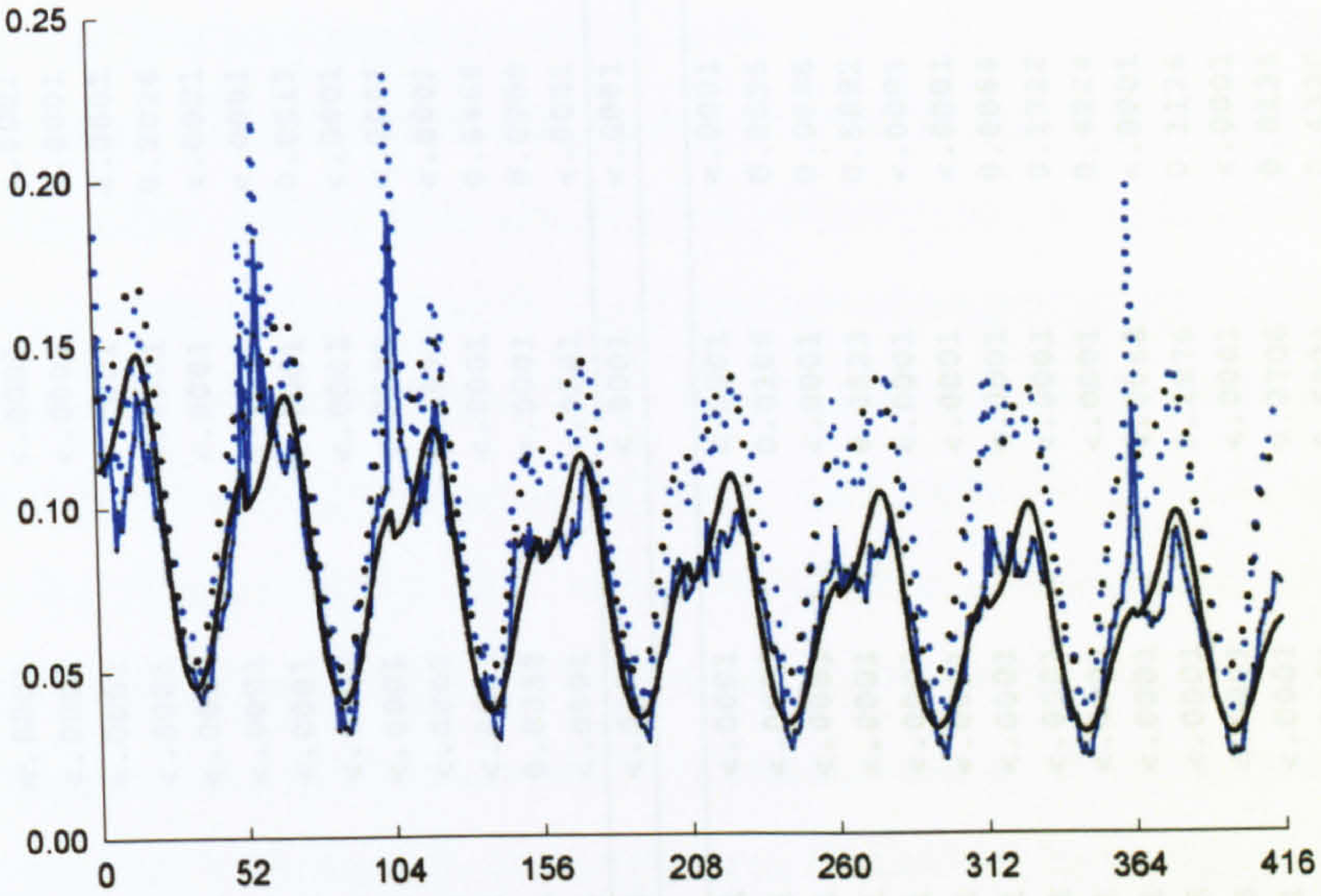

Figure 4.15. Mistle Thrush

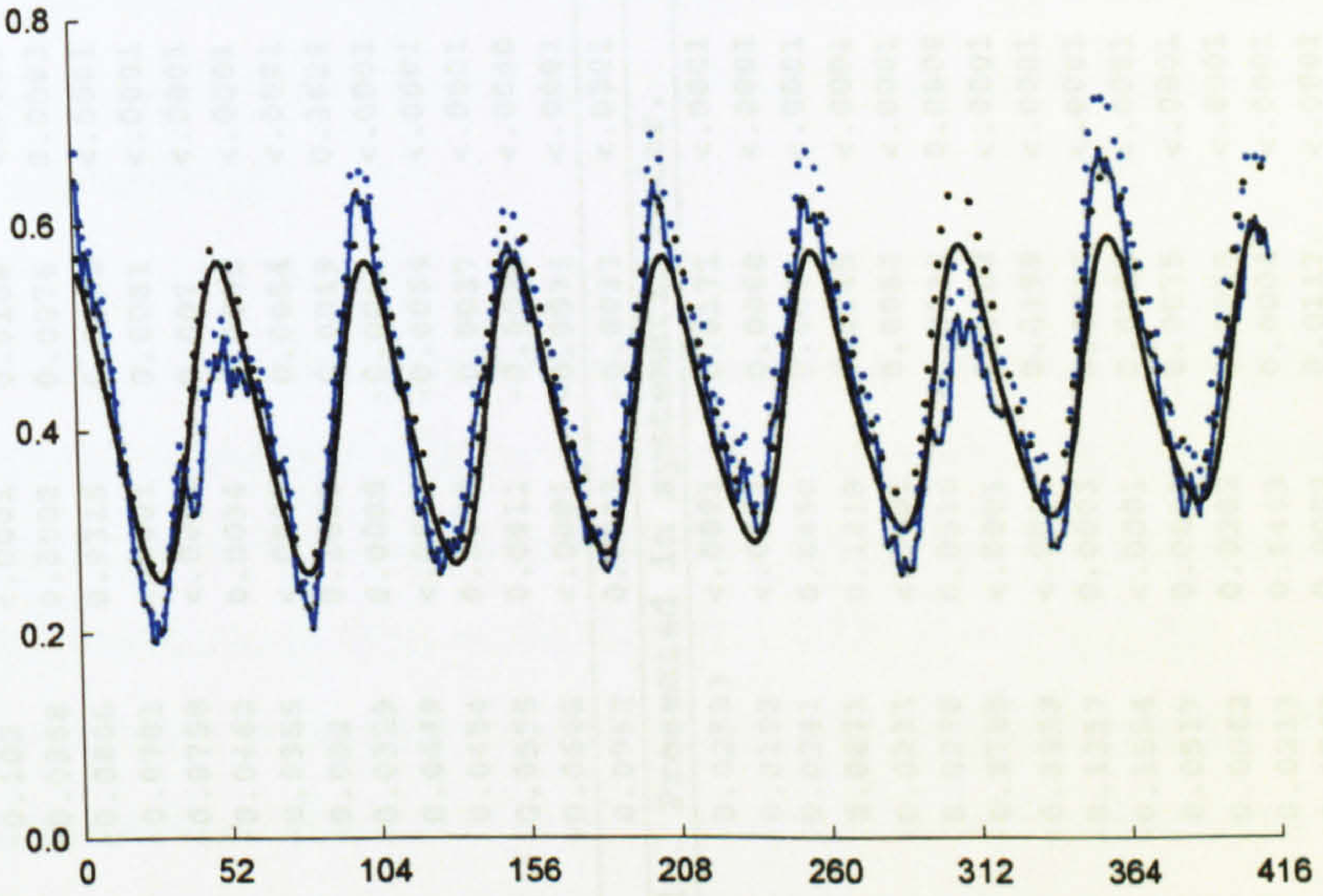

Figure 4.16. Coal Tit

Figures 4.3 – 4.16. Weekly reporting rates calculated from original data ('noisy' blue plots) and probabilities of occurrence predicted by 'minimum adequate' GEE models ('smooth' black plots). Horizontal axis: week numbers 1 – 416, January 1995 to December 2002. Vertical axis: proportion of gardens. 'All sites' data (solid lines) plotted for all species. 'Species positive' data (dotted lines) additionally plotted for species in which there is either a gain or loss of formal significance in the year term or an improvement in data dispersion, or an interesting difference in the form of the two plots.

Table 4.1 lists all model terms and their GEE type 3 *P* values for all 40 species and the 'all sites' data. To enable comparison between species in the relative significance of their model terms, the values for just the initial model run are given, i.e. all terms were included in these models whether significant or not.

Table 4.1. Model Terms and their P values for all sites. All terms included in model whether significant or not. Bold type: significant at $P \leq 0.05$.

Species	Deviance/ DF	Year	Parameter estimate	Year^2	Parameter estimate	cosweek	sinweek	cosweek * sinweek	year * sinweek	year * cosweek
i. Trend unambiguously identified. Presented in ascending order of year parameter estimate, i.e. fastest declining first.										
Turdus philomelos	1.1252	<.0001	-0.24	<.0001	-0.0209	<.0001	<.0001	<.0001	<.0001	<.0001
Passer domesticus	1.0717	<.0001	-0.1818	<.0001	0.0088	<.0001	<.0001	<.0001	<.0001	0.0013
Sturnus vulgaris	1.2500	<.0001	-0.1663	<.0001	0.0093	<.0001	<.0001	<.0001	<.0001	0.0002
Motacilla alba	0.6422	<.0001	-0.1424	<.0001	0.0118	<.0001	<.0001	0.0012	<.0001	<.0001
Prunella modularis	1.1354	<.0001	-0.102	<.0001	0.0108	<.0001	<.0001	<.0001	<.0001	<.0001
Corvus frugilegus	0.5693	<.0001	-0.0988	0.0002	0.0076	0.0003	<.0001	<.0001	<.0001	<.0001
Parus caeruleus	0.5488	0.0002	-0.0806	0.9315	0.0002	<.0001	<.0001	<.0001	<.0001	<.0001
Corvus monedula	1.0381	<.0001	-0.0781	<.0001	0.0081	<.0001	<.0001	<.0001	<.0001	0.2026
Corvus corone/cornix	1.1166	<.0001	-0.0758	<.0001	0.007	<.0001	<.0001	<.0001	<.0001	<.0001
Pica pica	1.3805	0.0006	-0.0462	0.0034	0.0035	<.0001	<.0001	<.0001	<.0001	<.0001
Troglodytes troglodytes	1.3161	0.0025	-0.0355	<.0001	0.0054	<.0001	<.0001	<.0001	<.0001	0.0013
Carduelis chloris	1.1588	0.0286	-0.032	0.1405	0.0019	0.3624	<.0001	<.0001	<.0001	<.0001
Fringilla coelebs	1.1442	0.0259	0.0329	0.0008	-0.0044	<.0001	<.0001	<.0001	<.0001	<.0001
Accipiter nisus	0.6420	0.0049	0.0449	<.0001	-0.0064	<.0001	<.0001	<.0001	0.6892	<.0001
Streptopelia decaocto	1.1246	0.0052	0.0454	0.0092	-0.0037	<.0001	<.0001	<.0001	<.0001	0.6469
Dendrocopos major	0.9914	0.0003	0.0555	0.0411	-0.0028	<.0040	<.0001	0.0338	<.0001	0.0709
Parus major	1.0502	<.0001	-0.0666	<.0001	-0.0071	<.0001	<.0001	<.0001	<.0001	<.0001
Aegithalos caudatus	0.8375	<.0001	0.0962	0.0043	-0.0037	<.0001	<.0001	<.0001	<.0001	<.0001
ii. No trend identified or trend debatable. Presented in systematic order.										
Larus ridibundus	0.2946	<.0001	-0.02593	<.0001	-0.0171	<.0001	<.0001	<.0001	<.0001	<.0001
Columba palumbus	1.3253	0.1492	0.0192	<.0001	0.0068	<.0001	<.0001	<.0001	0.0106	0.2655
Columba livia	0.7003	0.2632	0.0241	0.8450	0.0004	<.0001	<.0001	<.0001	<.0001	0.0886
Strix aluco	0.2691	0.0217	0.0871	0.1818	-0.0045	<.0001	<.0001	<.0001	0.4523	0.5892
Erithacus rubecula	0.8203	0.1119	-0.0231	<.0001	0.0064	<.0001	<.0001	<.0001	<.0001	<.0001
Turdus merula	0.5008	0.1392	0.0278	0.0510	-0.0032	0.0008	<.0001	<.0001	<.0001	<.0001
Turdus pilaris	0.1518	<.0001	-0.2785	<.0001	0.0202	<.0001	<.0001	<.0001	<.0001	0.0064
Turdus iliacus	0.1724	<.0001	-0.3339	<.0001	0.0199	<.0001	<.0001	<.0001	<.0001	0.1722
Turdus viscivorus	0.4900	<.0001	-0.1317	0.0003	0.0066	<.0001	<.0001	<.0001	<.0001	0.4224
Sylvia atricapilla	0.4232	<.0001	-0.1584	<.0001	0.0128	<.0001	<.0001	<.0001	0.0068	<.0001
Regulus regulus	0.3777	0.0291	0.0517	0.0003	-0.0075	<.0001	0.0005	<.0001	0.1876	0.1126
Parus ater	1.3281	0.6259	0.0062	0.0282	0.0025	<.0001	0.0008	<.0001	<.0001	<.0001
Sitta europaea	0.7314	0.2881	0.0213	0.6403	0.0008	<.0001	<.0001	<.0001	0.2706	0.0134
Certhia familiaris	0.1776	<.0001	-0.1547	0.0002	0.0117	<.0001	<.0001	<.0001	0.6924	0.4326
Garrulus glandarius	0.7200	0.6698	0.0077	0.3480	-0.0015	<.0001	0.0139	<.0001	0.1887	0.0257
Passer montanus	0.3687	0.0223	0.0785	0.2889	-0.0033	0.2036	<.0001	<.0001	<.0001	0.5976
Fringilla montifringilla	0.1257	<.0001	0.1695	<.0001	-0.0247	<.0001	<.0001	<.0001	0.0582	0.1953
Carduelis carduelis	0.9890	0.1811	0.0208	<.0001	0.014	<.0001	<.0001	<.0001	0.0812	<.0001
Carduelis spinus	0.4412	0.0115	-0.0502	0.0747	0.0033	<.0001	<.0001	<.0001	<.0001	<.0001
Pyrrhula pyrrhula	0.4342	<.0001	-0.1258	<.0001	0.0136	<.0001	<.0001	<.0001	<.0001	0.0048
Emberiza citrinella	0.2124	0.0063	-0.1034	0.3534	0.0032	0.0009	<.0001	0.5504	0.8295	0.0035
Emberiza schoeniclus	0.0803	0.0005	-0.1910	0.0644	0.0093	<.0001	<.0001	0.0200	0.3642	0.7923

SAS Procedure GENMOD does not provide GEE fit statistics (SAS Institute Inc. 2003), nonetheless the deviance statistics from the initial maximum likelihood models divided by degrees of freedom are presented in table 1 as a 'rule of thumb' indicator of relative data dispersion. This figure should be approximately equal to 1 (Der & Everitt 2002; SAS Institute Inc. 2003); from practical experience, values between 0.5 and 2.0 suggest dispersion is reasonably controlled and provide a pragmatic assessment of model appropriateness when combined with visual inspection of predicted probability plots and residuals if necessary. For the 'all sites' data, only 14 of the 40 species had deviance/DF figures outside this range; five of these (Black-headed Gull, Fieldfare, Redwing, Brambling and Siskin) are winter visitors with particularly sharp and sudden reporting rate peaks that are clearly less amenable to sine/cosine modelling. Tawny Owl, Goldcrest, Treecreeper, Tree Sparrow, Bullfinch, Yellowhammer and Reed Bunting are low reporting rate species (generally < 0.1), while Mistle Thrush and Blackcap have fairly low general reporting rates with some irregular peaks; nonetheless the data for these two species are only marginally underdispersed (deviance/DF = 0.49 and 0.43 respectively).

The magnitudes and directions of the GEE parameter estimates for the terms year and year^2 (table 4.1.) indicate whether the models have identified significant overall trends. From table 1, 32 of the 40 species modelled using data from all sites have a statistically significant year term in their models (type 3 GEE $P_r > \chi^2 \leq 0.05$). Of the eight remaining, four have significant year^2 terms and the year^2 term for Blackbird is only marginally non-significant ($P = 0.051$). For only three species, Feral Pigeon (figure 4.7), Nuthatch and Jay has this modelling method clearly failed to identify significant year-on-year change across all sites over the sampling period. These three species have uniformly low reporting rates (≈ 0.1).

For 18 species (table 4.1, section i.) the trends are unambiguous, that is, data dispersion is clearly within an acceptable range and type 3 GEE scores for year are significant. The three species most clearly identified as having negative trends are Song Thrush (figure 4.8), House Sparrow (figure 4.9) and Starling (figure 4.10). These trends are visually apparent from the reporting rate plots, that for Song Thrush showing a recent upturn which is reflected in the high positive parameter estimate for year^2. Positive trends are visually apparent in the three species with the most positive year terms, Great Spotted Woodpecker, Great Tit and Long-tailed Tit, that for Great Tit (figure 4.11) possibly more due to progressive flattening of intra-year reporting rate variation. The parameter estimate for year^2 for Great Tit is considerably more negative compared to the other two and indeed some decrease in the rate of change is suggested by the plot. Pied Wagtail and Dunnock have relatively high positive year^2 parameter estimates as well as negative year terms; their reporting rate trends are mitigated by apparent recovery towards the end of the survey period.

Negative year trends for four corvids, Rook, Jackdaw, Crow and Magpie (figure 4.12) are somewhat surprising given anecdotally reported increases in garden use; their plots support the suggestion of a slightly downturning overall trend although the year^2 parameter estimates are all positive albeit relatively small. A slight downward trend for Blue Tit (figure 4.13) is apparent from the plot but the dispersion statistic is relatively poor perhaps due to the progressive flattening of the periodicity in this species. The reporting rate trajectory for Wren reflects a known population decline and recovery, as discussed in Cannon (2000); an overall trend for this species over this timescale is probably meaningless. The suggested negative trend for Greenfinch might be accounted for by a similar flattening of the reporting rate periodicity as in Blue Tit (the year^2 term is exceptionally non-significant in both species, perhaps suggesting some similarity in data form). The *P* value for year is not impressive by the standards of this model; the same can be said about Chaffinch for which a positive overall trend is suggested.

A number of species have trends that are clearly apparent to the eye from their reporting rate plots but which are not reflected in the *P* values for both year and year^2 terms. Perhaps the most notable are Woodpigeon (figure 4.14, positive), Coal Tit (positive), Goldfinch (positive) and Mistle Thrush (figure 4.15, negative). Year and year^2 parameter estimates for these species are shown in table 4.1 section ii. Mistle Thrush was excluded from table 4.1 section i. due to a relatively poor dispersion statistic. However, the plot suggests this may result from a number of irregular reporting rate spikes. If these are disregarded the significant and relatively large negative parameter estimate for the year term probably reflects an authentic downward trend. The accelerating reporting rate increase for Goldfinch is reflected in the highly significant and relatively large positive parameter estimate for year^2 but two anomalous reporting rate peaks, one high (spring 1996), one low (spring 2002) might explain the inability of the model to resolve a significant year term. The summer reporting rate minima for Woodpigeon show inter-year variation (figure 4.14). This may be compromising the ability of the model to reflect the clearly-apparent upward trend although again a highly significant year^2 term partly redeems this. Poor *P* values for both year and year^2 (the latter formally significant but unimpressive in the context of this model) in Coal Tit are disappointing given an apparent upward trend, however both the winter maxima and summer minima for this species are notably variable from year to year.

Table 4.2. Effect of removing any sites where a species has never occurred from the modelled data set on the data dispersion statistic and on the GEE model *P* values and parameter estimates for terms year and year^2.

Species	'all sites' data set					'species positive' data set				
	D/DF	Year	P est	Year^2	P est	D/DF	Year	P est	Year^2	P est
i. Species gaining significance										
Columba palumbus	1.29	0.1492	0.0192	<0.0001	0.0069	1.30	0.006	0.0371	<0.0001	0.0067
Columba livia	0.70	0.2632	0.0241	0.8450	0.0004	1.06	0.0003	0.0828	0.7035	-0.0008
Parus ater	1.33	0.6259	0.0062	0.0282	0.0025	1.33	0.0068	0.0351	0.1617	0.0016
Sitta europaea	0.73	0.2881	0.0213	0.6403	0.0008	1.18	0.0001	0.0831	0.4602	-0.0014
Garrulus glandarius	0.72	0.6698	0.0077	0.3480	-0.0015	0.95	0.0025	0.0548	0.0766	-0.0029
Carduelis carduelis	0.99	0.1811	0.0208	<0.0001	0.014	1.04	0.0322	0.0332	<0.0001	0.0146
ii. Species losing significance										
Corvus monedula	1.24	<0.0001	-0.0781	<0.0001	0.0081	1.24	0.0771	-0.0301	<0.0001	0.0075
Carduelis chloris	1.14	0.0286	-0.0320	0.1405	0.0019	1.14	0.1029	-0.0240	0.0977	0.0022
Carduelis spinus	0.44	0.0115	-0.0502	0.0747	0.0033	0.56	0.7384	0.0065	0.2215	0.0022
iii. Species with notably improved data dispersion										
Emberiza citrinella	0.21	0.0063	-0.1034	0.3534	0.0032	0.58	0.4236	-0.0301	0.5052	0.0024
Emberiza schoeniclus	0.08	0.0005	-0.1910	0.0644	0.0093	0.35	0.2006	-0.0684	0.1641	0.0071
Strix aluco	0.27	0.0217	0.0871	0.1818	-0.0045	0.65	<0.0001	0.1553	0.0674	-0.0062
Turdus viscivorus	0.49	<0.0001	-0.1317	0.0003	0.0066	0.63	<0.0001	-0.0877	0.0002	0.0069
Passer montanus	0.37	0.0223	0.0785	0.2889	-0.0033	0.91	0.0046	0.1065	0.4686	-0.0025
Pyrrhula pyrrhula	0.43	<0.0001	-0.1258	<0.0001	0.0136	0.58	<0.0001	-0.0940	<0.0001	0.0146

As can be seen from table 4.2 section i, all four of the species having clearly visible trends in their raw data but failing to trend unambiguously in the 'all sites' models acquire either significant year terms (Woodpigeon, Coal Tit, Goldfinch) or an acceptable dispersion statistic (Mistle Thrush) when modelled using only 'species positive' data. Significant upward trends are also acquired by the only three species for which the model previously failed to identify any significant trend (Feral Pigeon figure 4.7, Nuthatch and Jay). Conversely, for Jackdaw, Greenfinch and Siskin the year terms lose formal significance when the models are applied to the 'species positive' data set. For Siskin, the replacement of a significant negative year term in the 'all sites' data with a small (although highly non-significant) positive year term in the 'species positive' data might be predicted from comparing the plots (figure 4.6). In addition to Mistle Thrush, five other low reporting rate species acquire a more respectable dispersion statistic (table 4.2 section iii) although that for Reed Bunting remains unacceptably low. Formal significance of the year terms for Tawny Owl, Tree Sparrow and Bullfinch does not change although the *P* values greatly improve.

Figures 4.17 – 4.24. Mean values of predicted GBW reporting rates over weeks 14-26, plotted with corresponding Great Britain BBS Indices, years 1995 – 2002 (2001 missing) for eight species with significant and/or interesting correlations. Winter GBW means additionally plotted for Blackbird (Fig. 4.22)

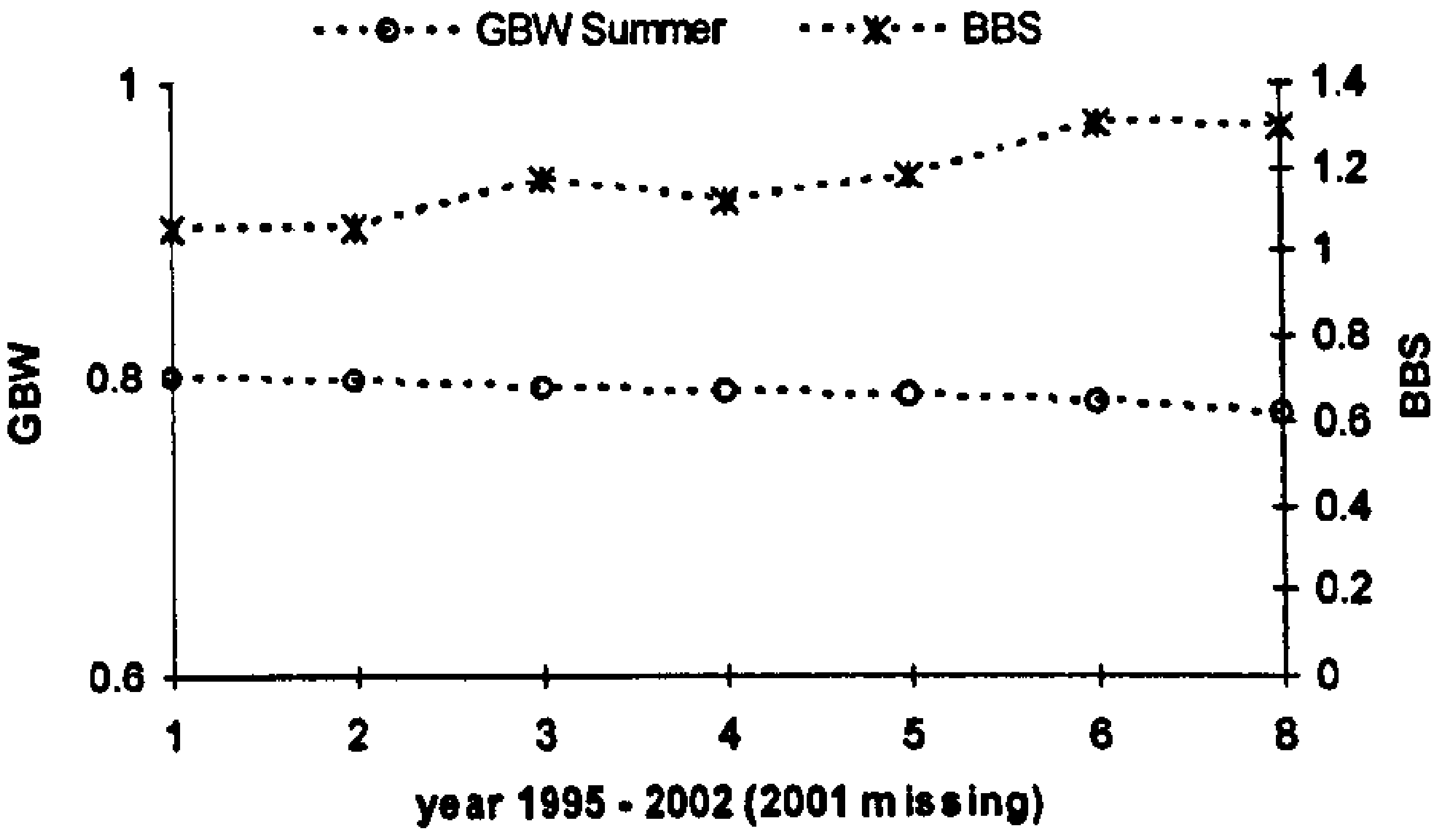

Figure 4.17. Greenfinch

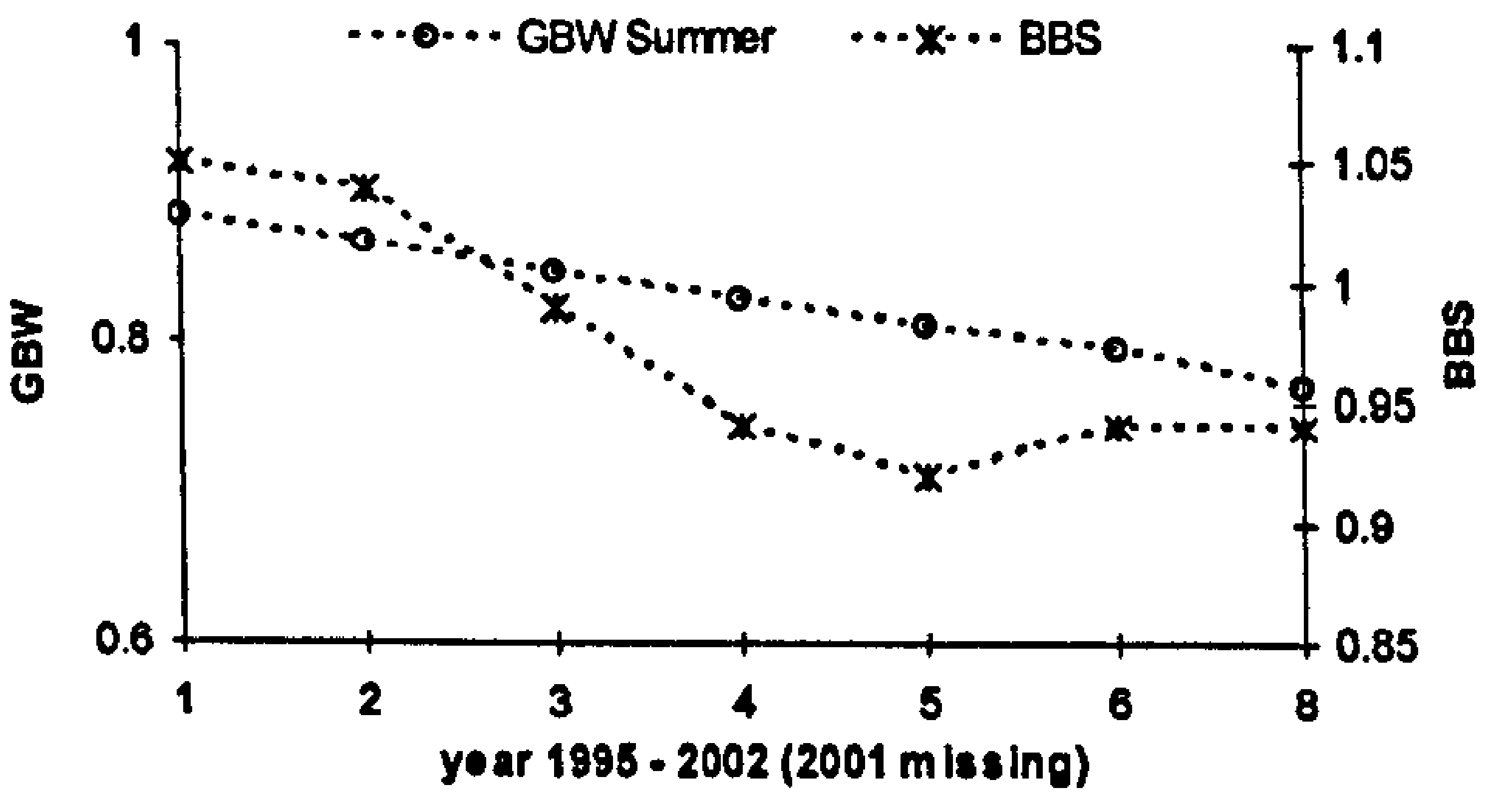

Figure 4.18. House Sparrow

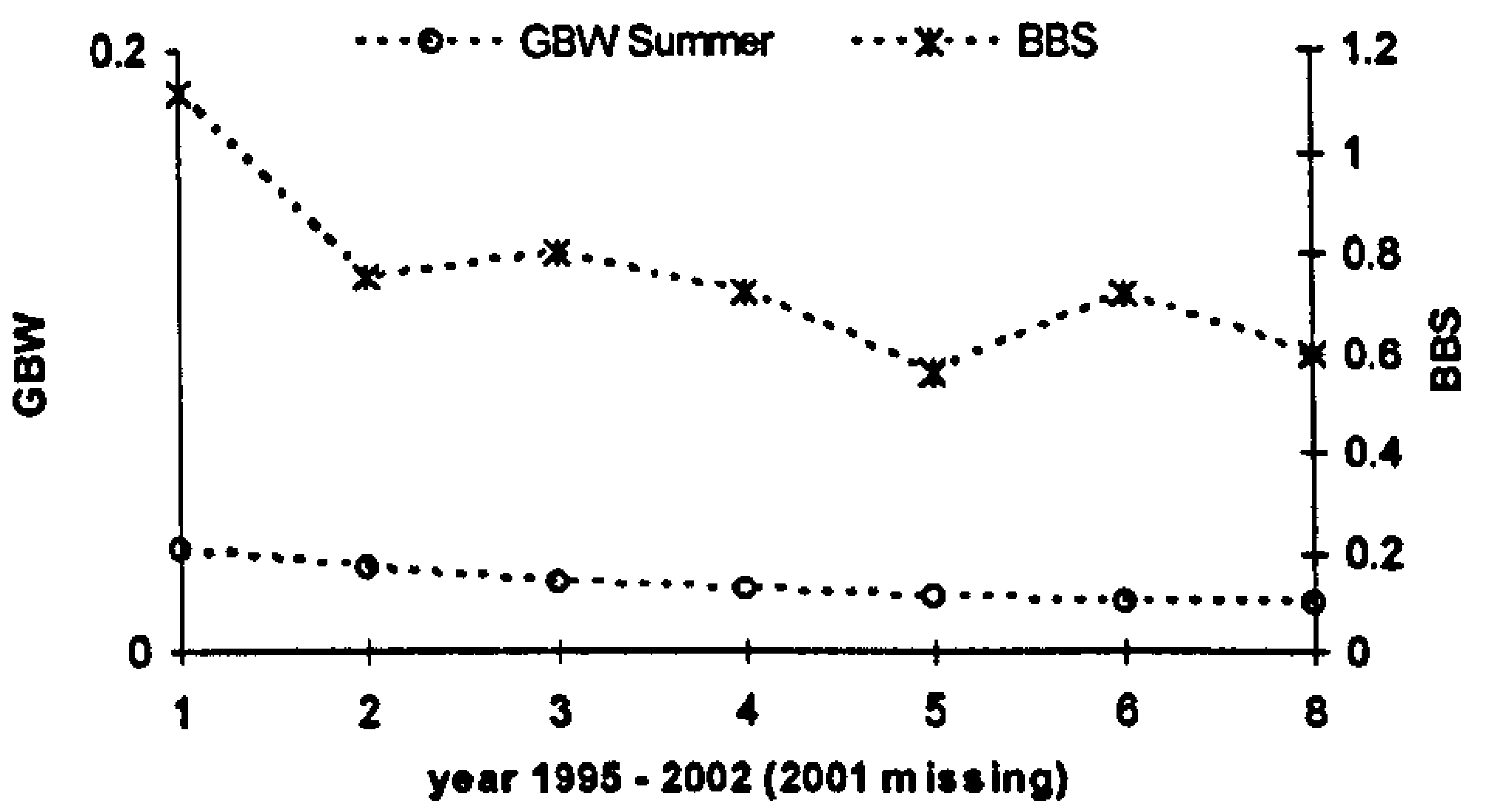

Figure 4.19. Black-headed Gull

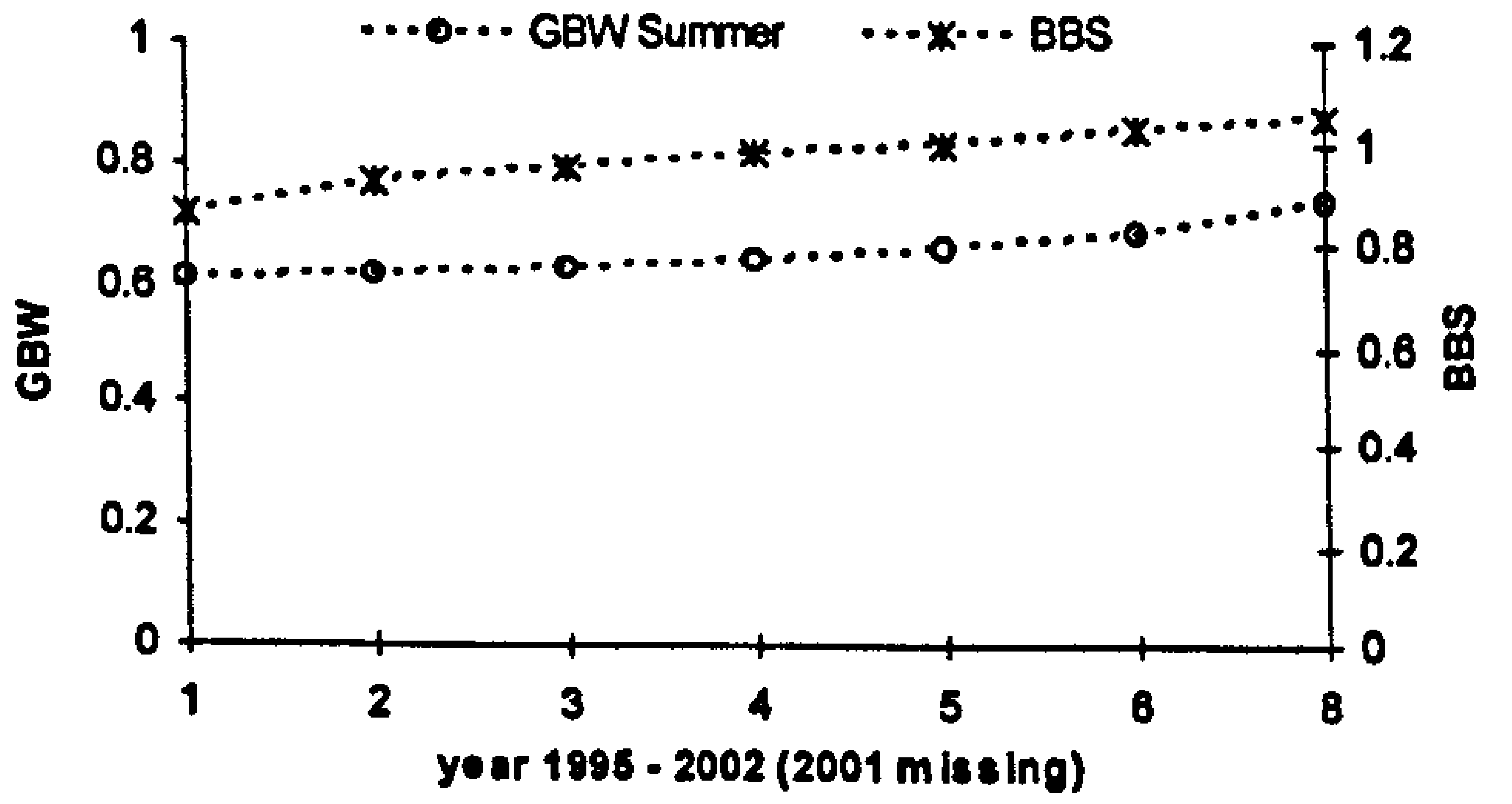

Figure 4.20. Woodpigeon

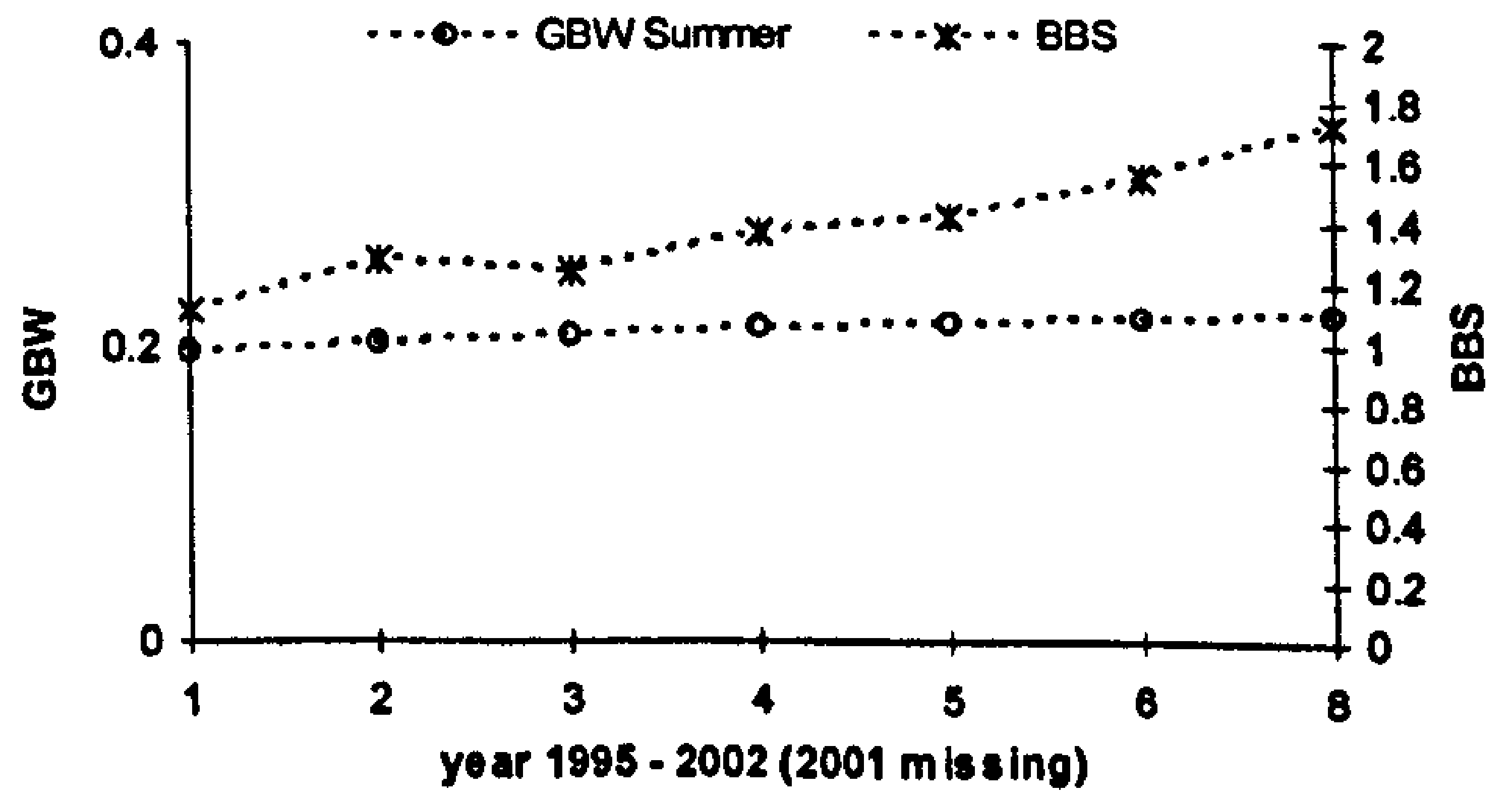

Figure 4.21. Great Spotted Woodpecker

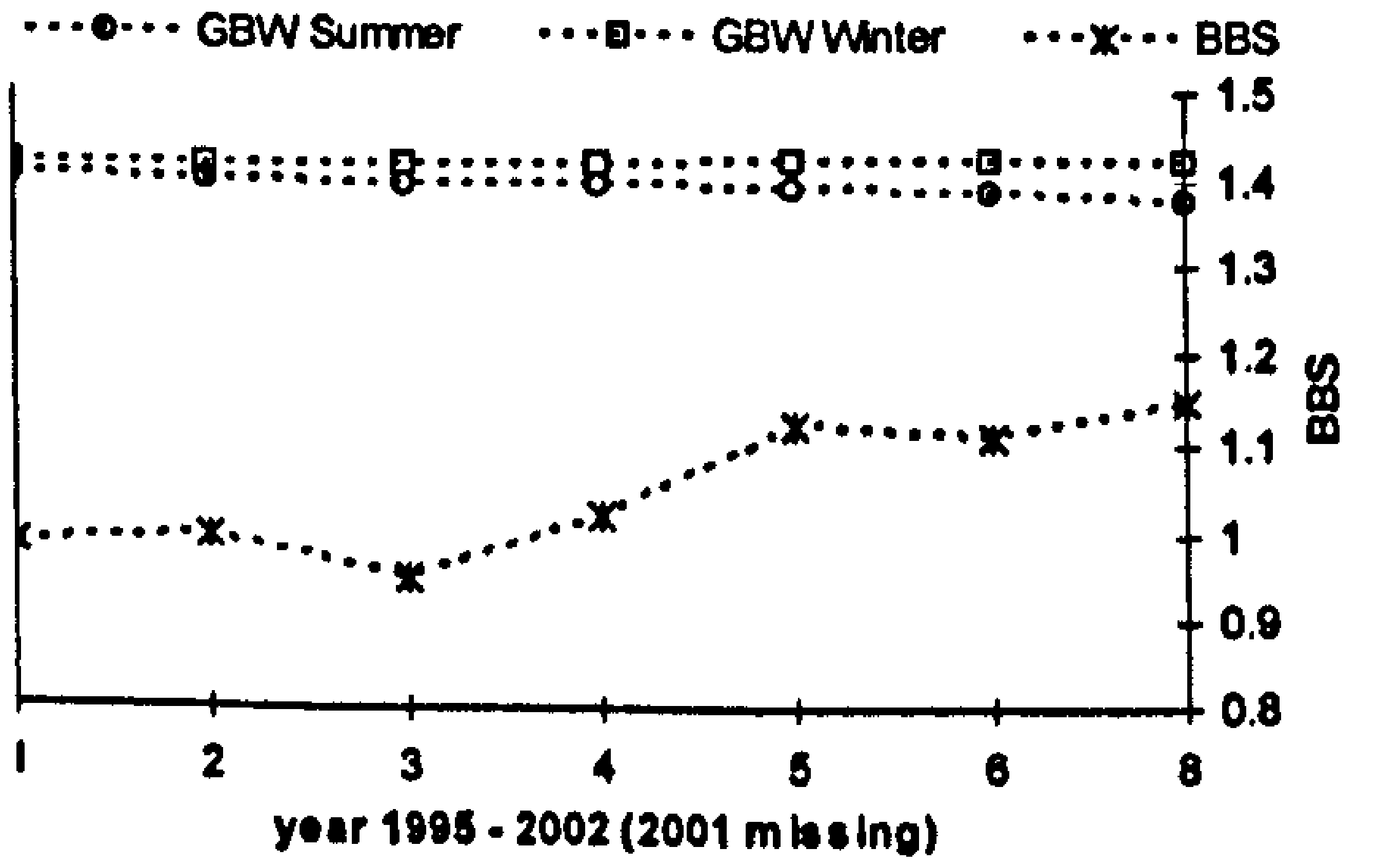

Figure 4.22. Blackbird

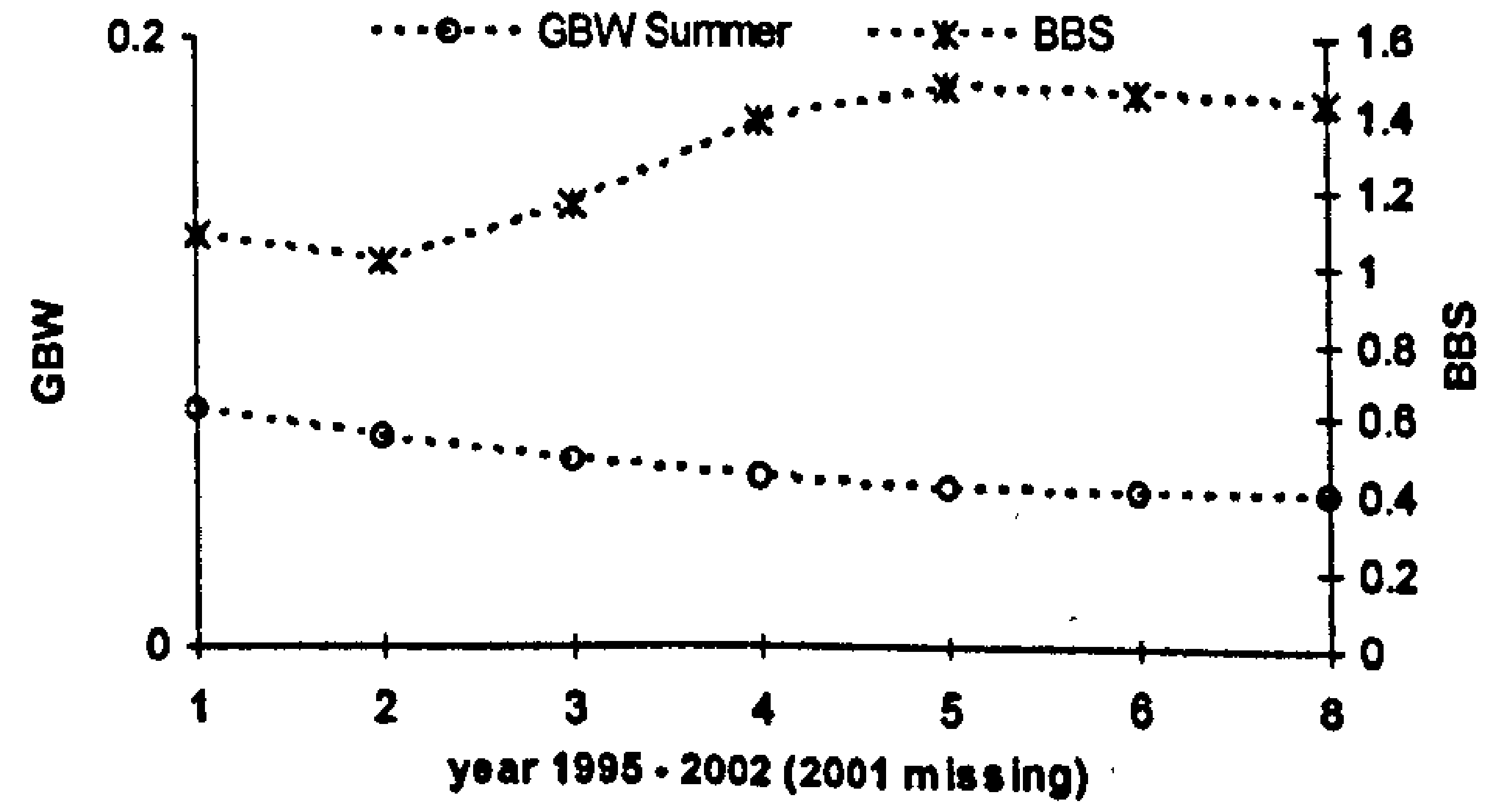

Figure 4.23. Blackcap

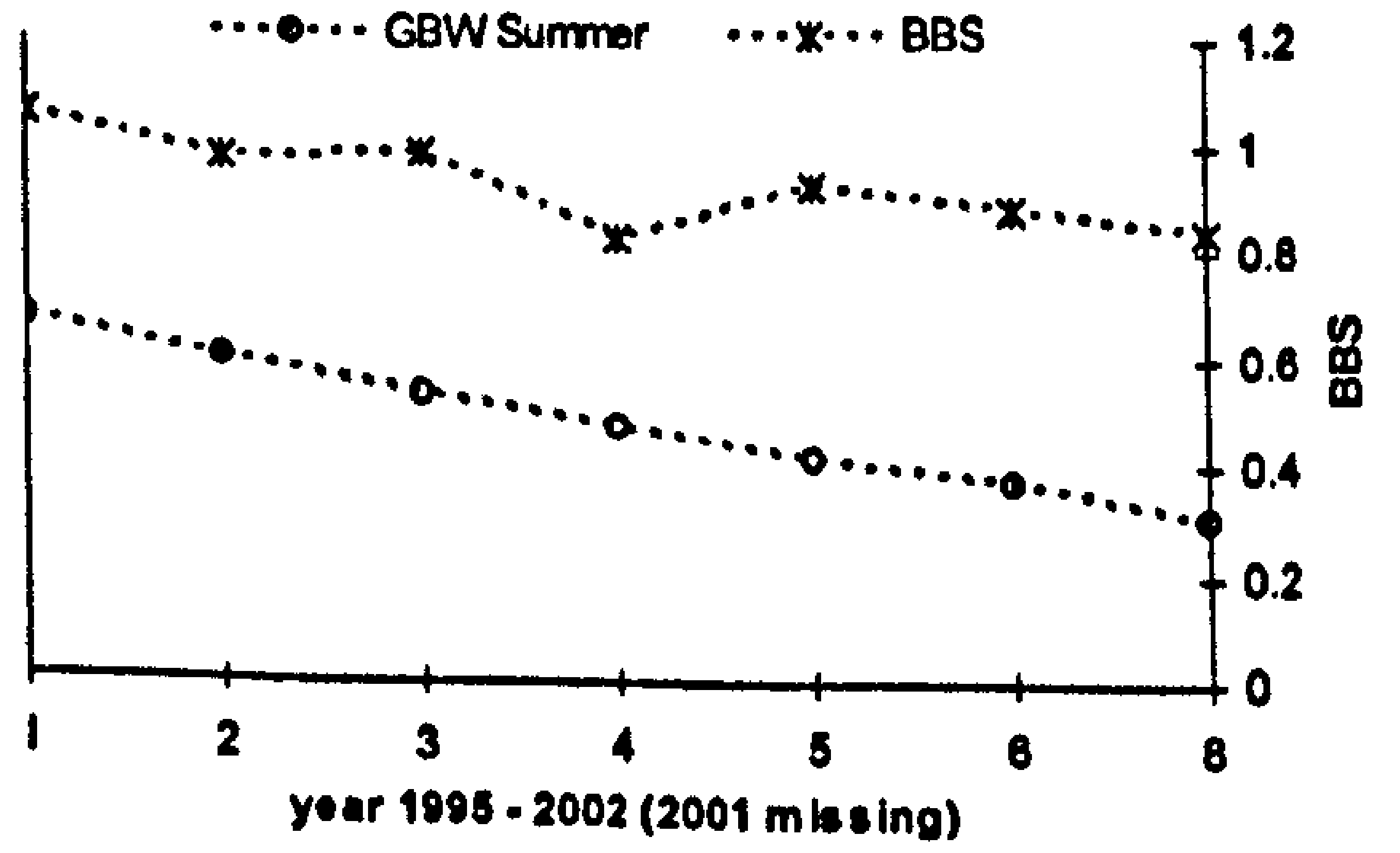

Figure 4.24. Starling

In seven of the 37 species for which BBS indices are available, their values correlate significantly with the GBW mean predicted reporting rates over the same period (table 4.3 and figures 4.17 – 4.24). Woodpigeon (figure 4.20) and Great Spotted Woodpecker (figure 4.21) have very strong positive correlations and rising trends, Black-headed Gull (figure 4.19) and House Sparrow (figure 4.18) have strong positive correlations and falling trends. In Greenfinch (figure 4.17), Blackbird (figure 4.22) and Blackcap (figure 4.23), rising BBS trends are negatively correlated with falling trends in GBW, although relatively poor data dispersion and irregularity of winter peaks cast some doubt on the modelled GBW means for Blackcap. BBS indices for all these species show similarly strong correlations with winter GBW predicted means although the correlation for Blackbird reverses, becoming negative. Crow and Jackdaw also show significant negative correlation between winter GBW means and rising BBS trends but their breeding season correlations are non-significant, that for Jackdaw strikingly so. For Starling, all three correlations are positive and marginally non-significant, both BBS and GBW figures are clearly decreasing. Correlations for Yellowhammer are also marginally non-significant and consistent. Robin has a significant positive winter$_{-1}$ correlation (rising trend) while Tawny Owl has a significant positive winter$_{+1}$ correlation, although the clear opposition of the overall GBW (rising) and BBS (declining) trends suggests the latter can be explained by the fall in BBS index having occurred in the most recent two years only. The year with the biggest fall (2002) is ignored in the winter$_{+1}$ calculation; prior to 2000 there was a rising trend in BBS as in GBW. If notional BBS and GBW values for the missing BBS year (2001) are interpolated by simple averaging, the correlation loses significance (r_s=0.393, p=0.383).

When sites at which species never occur were removed ('species positive' data sets), results for the seven species with the strongest GBW/BBS correlations were largely unchanged except that for Blackcap the winter$_{-1}$ correlation became non-significant. Siskin acquires very strong significant correlations in the 'species positive' data (table 4.4), the rising BBS trend correlating positively with GBW breeding season predicted means in gardens favoured by the species despite an overall negative GBW trend in the 'all sites' data. Figure 4.6 shows the breeding season reporting rate in the 'species positive' gardens creeping up. The correlations are strongly negative with both winter GBW means, but the way the model appears to have smoothed this species' irregular, weather-dependent winter peaks into a steady declining trend may be misleading.

Table 4.3. Correlations (Spearman's rank) between BBS Indices (GB) and GBW mean reporting predicted rates for weeks 14-26 (breeding), weeks 1-13 same calendar year (winter$_{-1}$) and weeks 1-13 following calendar year (winter$_{+1}$), data from all sites. % difference between last year and first year values of GBW means and GB BBS Indices for the period are also given, UK BBS trends provided for reference. Bold type: significant at $P \leq 0.05$.

Species	BBS/GBW breeding		BBS/GBW winter$_{-1}$		BBS/GBW winter$_{+1}$		% change in GBW means weeks 14-26	% change in GBW means weeks 1-13	% change GB BBS 1995 - 2002	UK BBS status 1994 - 2002
	r_s	P	r_s	P	r_s	P				
i. positive correlations										
Columba palumbus	**1**	**<.0001**	**1.00000**	**<.0001**	**1.00000**	**<.0001**	20.39	25.28	22.09	+5.0
Dendrocopus major	**0.96429**	**0.0005**	**0.96429**	**0.0005**	**0.94286**	**0.0048**	12.15	11.56	53.57	+71.5
Larus ridibundus	**0.82886**	**0.0212**	**0.82886**	**0.0212**	**0.84067**	**0.0361**	-53.24	-60.14	-46.43	-33.2
Passer domesticus	**0.81537**	**0.0254**	**0.81537**	**0.0254**	**0.89865**	**0.0149**	-13.00	-15.58	-10.48	-7.3
Erithacus rubecula	0.57143	0.1802	**0.92857**	**0.0025**	0.54286	0.2657	7.30	0.78	4.50	+16.1
Strix aluco	0.17857	0.7017	0.17857	0.7017	**0.88571**	**0.0188**	32.69	32.43	-11.11	-35.5
Sturnus vulgaris	0.75	0.0522	0.75000	0.0522	0.77143	0.0724	-15.22	-17.51	-20.75	-13
Emberiza citrinella	0.72075	0.0676	0.72075	0.0676	0.77143	0.0724	-32.47	-42.94	-8.51	-13.4
Accipiter nisus	0.70921	0.0743	-0.43644	0.3276	-0.63775	0.1731	1.79	-15.37	-2.30	-13.2
ii. negative correlations										
Carduelis chloris	**-0.91896**	**0.0034**	**-0.91896**	**0.0034**	**-0.92763**	**0.0077**	-3.14	-7.27	21.70	+30.8
Turdus merula	**-0.85714**	**0.0137**	**0.85714**	**0.0137**	0.77143	0.0724	-0.81	0.14	16.16	+16.1
Sylvia atricapilla	**-0.82143**	**0.0234**	**-0.89286**	**0.0068**	-0.77143	0.0724	-35.14	-20.14	32.41	+46.2
Corvus corone	-0.68471	0.0897	**-0.95499**	**0.0008**	**-0.81168**	**0.0499**	-6.06	-11.39	16.16	+15.1
Corvus monedula	-0.07143	0.8790	**-0.92857**	**0.0025**	**-0.82857**	**0.0416**	4.24	-8.59	8.41	+12.0
Regulus regulus	-0.45047	0.3104	-0.45047	0.3104	**-0.92763**	**0.0077**	-9.29	-9.13	15.17	+64.9
iii. non-significant and poor correlation										
Passer montanus	0.64286	0.1194	0.64286	0.1194	0.42857	0.3965	22.84	21.59	44.33	+55.1
Parus major	0.59462	0.1591	-0.45047	0.3104	-0.77143	0.0724	2.23	-2.37	13.59	+18.7
Carduelis carduelis	0.54554	0.2053	0.54554	0.2053	0.26482	0.6121	118.76	149.38	21.65	+18.2
Garrulus glandarius	0.52254	0.2289	-0.52254	0.2289	-0.23191	0.6584	2.84	-2.49	46.15	+16.3
Certhia familiaris	0.5	0.2532	0.50000	0.2532	-0.08571	0.8717	-28.39	-28.10	-5.74	+18.7
Pyrrhula pyrrhula	0.44475	0.3174	0.55594	0.1950	0.52179	0.2883	-2.38	-11.20	-8.54	-26.2
Streptopelia decaocto	0.43644	0.3276	0.43644	0.3276	0.23540	0.6534	0.52	0.40	20.39	+25.8
Troglodytes troglodytes	0.35714	0.4316	0.00000	1.0000	0.77143	0.0724	4.24	0.13	-1.74	+13.7
Aegithalos caudatus	0.21622	0.6414	0.21622	0.6414	0.49281	0.3206	42.22	56.21	-17.70	-2.7
Parus caeruleus	0.17857	0.7017	0.17857	0.7017	0.37143	0.4685	-3.98	-3.63	3.85	+8.8
Carduelis spinus	0.14286	0.7599	0.14286	0.7599	-0.02857	0.9572	-6.87	-34.70	7.89	-18
Prunella modularis	0.09009	0.8477	-0.61264	0.1436	-0.28989	0.5774	-1.68	-4.63	7.77	+12.5
Corvus frugilegus	0.09009	0.8477	0.48651	0.2682	0.17393	0.7417	-12.95	-27.68	-5.94	-0.3
Motacilla alba	-0.07143	0.8790	-0.10714	0.8192	0.08571	0.8717	-19.48	-29.59	-3.91	+23.4
Emberiza schoeniclus	-0.10714	0.8192	-0.10714	0.8192	0.08571	0.8717	-53.64	-53.35	-3.92	+3.1
Fringilla coelebs	-0.18019	0.699	-0.41443	0.3553	-0.37143	0.4685	-0.99	-4.39	7.22	+5.3
Parus ater	-0.21822	0.6383	0.41825	0.3504	-0.52179	0.2883	12.84	-0.37	18.45	+28.4
Pica pica	-0.30632	0.5040	0.01802	0.9694	-0.57977	0.2278	-3.70	-8.10	-3.85	+2.4
Sitta europaea	-0.34236	0.4523	0.34236	0.4523	-0.05798	0.9131	-5.06	4.72	34.58	+43.6
Turdus viscivorus	-0.37062	0.4131	-0.37062	0.4131	-0.63775	0.1731	-32.94	-39.63	0.00	+0.8
Columba livia	-0.39641	0.3786	-0.39641	0.3786	-0.77143	0.0724	-3.61	-4.18	0.00	-6.3
Turdus philomelos	-0.60714	0.1482	-0.42857	0.3374	0.02857	0.9572	-27.57	-22.42	13.00	+13.4

Table 4.4. Changes in GBW/BBS correlations when sites at which species never occurred were removed from data ('species positive' data set). Correlations acquiring or losing significance are shown in *italics*. Correlations changing sign are underlined.

Species	BBS/GBW wks 14 - 26		BBS/GBW winter$_{-1}$		BBS/GBW winter$_{+1}$	
	r_s	P	r_s	P	r_s	P
i.species gaining significance						
Carduelis spinus	***0.90094***	***0.0056***	**-0.90094**	**0.00056**	**-0.94286**	**0.0048**
Parus major	***0.81084***	***0.0269***	-0.10911	0.8175	-0.48571	0.3287
Streptopelia decaocto	***0.80013***	***0.0307***	0.70921	0.0743	***0.85331***	***0.0307***
Regulus regulus	***0.81084***	***0.0269***	***0.81084***	***0.0269***	*0.55078*	*0.2574*
Corvus monedula	***0.85714***	***0.0137***	**0.82143**	**0.0234**	**0.94286**	**0.0048**
ii. species losing significance						
Sylvia atricapilla	***-0.89286***	***0.0068***	-0.32143	0.4821	0.25714	0.6228
Larus ridibundus	*0.70273*	*0.0782*	**0.82886**	**0.0212**	**0.84067**	**0.0361**
Corvus corone/cornix	0.18019	0.699	*-0.45047*	*0.3104*	*0.08697*	*0.9699*

For Jackdaw, the 'species positive' breeding season GBW/BBS correlation becomes highly significant and positive, in contrast to the negative 'all sites' correlation; both winter correlations also change sign to become highly significant and positive with respect to the rising BBS trend. Both winter correlations for Crow (significant in the 'all sites' data) become poor and highly non-significant. The winter$_{+1}$ correlation for Goldcrest loses significance when only 'species positive' sites are used but breeding and winter$_{+1}$ correlations become significant (positive, rising trend), which makes sense considering the significant positive year term in the model (albeit with poor dispersion). Finally, in their 'species positive' data sets Great Tit and Collared Dove acquire significant positive breeding season correlations with rising BBS trends.

To provide a simple indicative comparison of overall variation, percentage differences between 1995 and 2002 in the 13-week 'winter' and 'breeding' GBW predicted reporting rate means were calculated and are tabulated in table 4.3 together with simple arithmetic percentage differences between 1995 and 2002 in BBS indices for Great Britain. Table 4.3 also shows the percentage changes in BBS index for the UK as a whole between 1994 and 2002 (from Raven et al. 2003) which are model-derived and significance-tested rather than simply arithmetical.

Interaction terms (year * sinweek, year * cosweek) were included in the model in the hope of detecting significant timing shifts in the seasonal reporting rate cycles. In only four species were both these model terms non-significant (Tawny Owl, Goldcrest, Brambling and Reed Bunting), in a further 13 species one of these two interaction terms is non-significant. It is hard to see any systematic relationships between model term significance and plotted reporting rates. For example, in Pied Wagtail there is clear variation between the timing of the sharp and irregular reporting rate peaks and the smoothed peaks of the predicted reporting rate plot, however in Dunnock (figure 4.5) and Robin the peaks are broad and there is little obvious variation in the phase relationship of the actual and modelled data plots.

4.4. Conclusions

The results suggest that the modelling method can resolve underlying trends in these highly cyclical data, despite the dominance of the sine and cosine terms, which for most species produce GEE parameter estimates an order of magnitude greater than those for the year and interaction terms. However, there are some discrepancies between the timing of modelled occurrence probability peaks and reporting rate peaks in the raw data (e.g. Blue Tit, House Sparrow). Logistic regression models might be expected to detect statistical significance for even quite weak trends in such a large data set, but in some cases visually-apparent trends in raw data do not produce correspondingly significant model terms (e.g. Coal Tit figure 4.16). It seems this modelling method may require further refinement adequately to capture trends in species whose reporting rates are significantly irregular or irruptive.

There is also the issue of assessing fit. For example, Reed Bunting shows a clearly apparent decreasing trend in the raw data and although this is reflected as expected in a significant negative year term in the model, the dispersion statistic is outside normal limits of acceptability. Although the GEE technique allows for temporal autocorrelation, spatial autocorrelation is also a theoretical issue but at the time of writing no generally available modelling method that allowed for this in binary data was available. Given the eight-year timescale and the wide distribution of sites on a national scale (figure 4.2.), broad-scale long-term trends should greatly outweigh local spatial autocorrelation effects in these data. Adding further complication to the modelling would be practically unfeasible; as it is, data from a total of 16,172 different sites were included in data sets having typically between 2.3 and 2.5 million observations; calculating GEE models with autoregression across 416 weeks for datasets of this size was extremely computationally intensive. The high sensitivity of the model to small interactions leaves it unable meaningfully to assess inter-year changes in the timing of garden use. Inspection of the GBW data suggests that such changes may be emerging in some species and will be worthy of further investigation. However, figure 4.9 shows that for House Sparrow the model fails to keep pace with the peak in actual reporting rates, which is becoming later each year, and has trouble tracking the small post-breeding reporting rate peak despite the excellent dispersion statistic (1.07).

With a very large sample size and excellent geographical coverage, Garden BirdWatch is effectively monitoring the specific target habitat, private residential gardens. One point frequently raised in discussion of volunteer garden surveys is that virtually all Garden BirdWatch volunteers provide supplementary food. Given that supplementary food is extremely widespread and frequently superabundant in British gardens and that survey data from Sheffield (Chapter 8) suggest that around one third of British households provide food for birds, 'gardens with supplementary food' should be monitored as an important habitat in their own right. Furthermore, most British gardens are smaller than the normal territory (and considerably smaller than the winter feeding range) of most species considered here. A mobile bird exploiting supplementary food in one garden will also be exploiting the two unfed gardens either side, hence presence/absence data from fed gardens is likely to be representative of the British garden habitat as a whole, certainly as far as the 40 commoner species covered by Garden BirdWatch are concerned. There have been some changes in the timing and types of food provided over the period considered (Toms 2003) and it is possible that these are affecting reporting rates. For example, the reduction in amplitude of the seasonal cycles noted in several species might be partly due to a shift from winter-only to year-round provisioning. If the relative proportions of various garden types in the survey changed as participation increased over the period considered, this might affect reporting rates for some species but there is no evidence of this and the recruiting methods and target audience have remained unchanged.

The reporting rate data document a period of almost universal change in garden usage rate in most of the commoner species that exploit British gardens regularly, and the mathematical models have successfully captured significant trends for several important species. Of the 18 species with trends clearly identified by the model, the three with the most negative year term parameter estimates are 'red-listed' as of high conservation concern (Song Thrush, House Sparrow, Starling), that with the fifth most negative (Dunnock) is 'amber listed' as of medium concern (Gregory et al. 2002). Five are designated 'pest' species of economic importance (Rook, Jackdaw, Crow, Magpie and Collared Dove) (DEFRA 2004b); for all of these the model has successfully identified significant year trends, all negative except for Collared Dove which is positive as would be expected from the >25% national population increase over this period. Crow, Magpie and Jackdaw, in contrast, all have generally increasing populations so the negative trends in the garden reporting rates are interesting and conflict with anecdotal evidence of a general increase in corvids' use of residential gardens. The models failed to identify significant trends across all sites in four 'red-' (Tree Sparrow, Bullfinch, Yellowhammer and Reed Bunting) and five 'amber-listed' (Black-headed Gull, Redwing, Fieldfare, Mistle Thrush and Goldcrest) species. None of these species are typical garden residents, being either seasonal visitors or primarily associated with other types of habitat. Three 'pests' also fail to show a significant trend across all sites although all three (Woodpigeon, Feral Pigeon and Jay) do have significant and positive year terms in the 'species positive' gardens.

The presence and detectability of underlying trends in the GBW data enable examination of whether trends in this habitat differ from those in general populations in direction or timing, perhaps due to gardens acting as a refuges or to temporal resource partitioning. Of the species with significant BBS/GBW correlations, positive correlations on rising trends (Woodpigeon, Great Spotted Woodpecker) suggest that increasing populations are colonising gardens while those on falling trends (House Sparrow, Starling) suggest that garden reporting rates can reflect known serious declines in species of conservation concern. Other species have negative correlations, notably Greenfinch and, perhaps surprisingly for a well-established garden-breeding species, Blackbird (although the GBW decline for the latter is very slight, suggesting this correlation should be treated with caution). Negative winter correlations in Jackdaw, Crow and Goldcrest support a conclusion that some species are using gardens differently from others. That Greenfinch (negative correlation) and House Sparrow (positive correlation) are using gardens in very different ways is supported by the large timing difference between their reporting rate peaks.

For some species, garden usage may well reflect breeding populations whereas for others, it may primarily reflect winter feeding behaviour. A previous study found significant correlations between average percentages of winter garden feeders visited and US BBS indices across 13 states for nine North American species (Wells et al.

1998) but temporal correlations across a seven year period were less successful, significant only for Carolina Wren and House Sparrow, whereas we have found significant correlations for 15 species over 8 years. The detection of significant trends and the demonstration of so many correlations with trends in the general population over a relatively short timescale show that Garden BirdWatch has great potential as a monitoring tool for a habitat that is important in its own right and not adequately covered by other monitoring schemes. It provides a wealth of data that would not be affordable or practicable to collect by any other means and is ongoing, so the value and information content of the data can only increase.

5. Comparison of urban and non-urban trends in garden usage

Abstract

Urban, suburban and rural garden reporting rate trends over eight years (1995-2002) were compared using weekly records of common wild bird species from private gardens across Great Britain and modelled separately using trigonometric logistic regression. Significant differences were found between the three garden types in their inter-year trends in 13 species. Discriminant function analysis with subjective garden classifications as the training set systematically classified the sites according to relative urbanisation of their surrounding land cover according to satellite imaging. Overall, urban bird reporting rates are changing less than non-urban but in a generally similar manner. Where there is change it is generally negative although several species, including some of conservation interest, show recent upturns in their non-urban garden reporting rate trends. There were significant differences in inter-year linear trends between the three garden classes for 13 species of which five had significant trends in both urban and rural gardens; three of these are listed as of conservation concern, the other two are 'pest' species, underlining the importance of monitoring urban garden birds.

5.1. Introduction

In this chapter, trends in the use of private residential gardens within urban, suburban and rural environments by wild birds are separated and those of urban and non-urban gardens compared. While both the importance of private gardens in general as wild bird habitat (Chapter 4) and the increasing conservation relevance of urban habitats (Chapter 1) are becoming more widely accepted, few attempts have been made to discriminate between the relative contributions of gardens in urban areas and those in other landscape settings. This is an important issue generally, given ongoing urbanisation, and specifically in the U.K. given the government's plans for future house building. Up to 3.8 million extra households are argued to be needed in England alone by 2021 (ODPM 2000a). The pressure on available land (particularly if impacts on previously undeveloped 'green field' sites are to be minimised) means that the gardens of new housing will be smaller than those of many older dwellings. Guidance on housing recommends increasing densities from the 'normal' 20-25 to a perhaps more typically 'urban' 30-50 dwellings ha^{-1} (ODPM 2000b), and portions of many existing gardens (particularly larger ones) are likely to be built over, due to pressure for 'backland' development (London Biodiversity Partnership 2001). Consequently, an increasing proportion of the important habitat resource represented by residential gardens is likely to become 'urban' in character. Given the marked effects of urbanisation on avian species richness and abundance (e.g. Crooks et al. 2004), this can be expected to affect its avifauna. For example, Chamberlain et al. (2004) showed that garden occurrence probabilities for 22 of the 40 species considered in this chapter were significantly associated with an urban-rural local habitat gradient.

5.2. Methods

As in Chapter 4, this analysis used weekly records of the presence or absence of common wild birds in gardens across Britain during the period 1995 – 2002 from the British Trust for Ornithology/CJ WildBird Foods Ltd Garden BirdWatch (GBW) project (Cannon 2000; Toms 2003) GBW participants are asked to classify their gardens as *urban*, *suburban* or *rural* according to a simple subjective protocol, as follows: "*Urban* means densely built-up areas and town centres with very few natural or near-natural bird feeding sites. *Suburban* means inhabited areas near countryside or with large gardens, municipal parks or recreational areas. *Rural* refers to areas away from towns, with just a few scattered houses, farms or other isolated buildings". Although these distinctions appear straightforward, practical experience of administering the project since 1995 (pers obs) revealed that they confused a proportion of volunteers and that the character of a garden as perceived by its owner and the character of the avifauna 'available' to that garden as a consequence of the type of land cover dominating the surrounding area did not always match well. In particular, the proportion of gardens designated by their owners as *urban* appeared to be inappropriately small, given the prevalence of urbanisation in the British landscape, probably due to the impreciseness of the project's definition of 'suburban' and perhaps also due to a preference among volunteers to think of their homes as non-urban. Therefore, a more objective classification method was sought.

The Centre for Ecology and Hydrology (CEH) Land Cover Map 2000 (LCM2000) is a thematic classification of satellite image data (CEH 2001; Fuller et al. 2002), which provides a means of resolving this difficulty by assigning garden locations to land cover classes more objectively. The 1 km summary dataset summarises the original 25 m raster data within a 1 km grid and according to 10 aggregate land cover classes and 27 subclasses, of which two 'suburban/rural development' (c24) and 'continuous urban' (c25) are distinguished within the aggregate class 'built up areas and gardens'. Each garden in the GBW dataset was assigned to the appropriate 1 km square with its associated values (0 – 100%) for each of the 27 land cover subclasses. Some of these land cover variables, such as saltmarsh, were unlikely to play a significant role in discriminating between urban and non-urban 1km squares. A subset of the LCM2000 land cover variables that contributed significantly to discriminating among the *a priori* garden types was therefore pre-selected by performing a stepwise backwards elimination discriminant analysis using PROC STEPDISC in SAS (v8.02) (SAS Institute Inc. 1998). The significance level for a variable to stay in the analysis was 0.15 (SAS default). Then, to re-classify the sites according to these selected variables, Discriminant Function Analysis (DFA) using PROC DISCRIM in SAS (Der & Everitt 2002) was applied, selecting the CROSSVALIDATE option in which each observation in the dataset is classified using a discriminant function derived from all other observations in the dataset, i.e. the 'training' and 'test' samples are the same (SAS Institute Inc. 1998). The garden types assigned by the volunteers were the *a priori* classification ('training set') in the DFA, which used all the land cover subclasses that had been identified as significant discriminators by the discriminant analysis. Prior to the DFA, Kolmogorov-Smirnov tests for normality in SAS PROC UNIVARIATE were applied to the LCM2000 subclass values to determine whether parametric or non-parametric DFA should be used.

Weekly reporting rates for each of the 40 species and 416 weeks were then calculated and modelled exactly as in Chapter 4 but in this case for the DFA-classified *urban*, *suburban* and *rural* garden data separately. Prior to modelling the reporting rates for the three samples, *urban*, *suburban*, and *rural* separately, the same model was run using the entire data set (referred to below as the *allsites* models) but with the additional inclusion of the interaction term *gardenclass * year*, in order to determine whether differences in the inter-year trends between the three reclassified samples were formally significant.

5.3. Results & Discussion

Discriminant analysis identified 16 land cover variables that contributed significantly to discriminating between sites ($P_r > F < 0.15$) with respect to their *a priori* garden type classifications and eight non-significantly discriminating variables (table 5.1). The values of all the land cover variables were normally distributed across all grid squares (Kolmogorov-Smirnov tests, $P<0.01$) so parametric DFA was used. This reclassified 14.22% of the gardens that were *a priori* designated *rural*, 41.28% of *suburban* and 48.93% of *urban*, increasing the number of gardens in the *urban* sample from 791 to 2074. The *rural* sample increased from 5683 to 7260 gardens, while the *suburban* sample decreased from 9501 gardens to 6641.

Tables 5.2 and 5.3 show the deviance / degrees of freedom (as a measure of relative model fit) and the type 3 P values for the *gardenclass*year* interaction term in the *allsites* models, together with deviance / degrees of freedom values and the parameter estimates of the *year* and $year^2$ terms in the three models *rural*, *suburban*, and *urban*. Significances of these model effects (from type 3 P values) are indicated by bold type and asterisks. In the *allsites* model, 13 species had both model deviance / degrees of freedom within an acceptable range ($0.5 < D/DF < 1.5$) and a significant type 3 P value for the interaction term; they were Sparrowhawk, Collared Dove, Woodpigeon, Great Spotted Woodpecker, Dunnock, Song Thrush, Coal Tit, Jackdaw, Carrion / Hooded Crow, House Sparrow, Goldfinch, Siskin and Bullfinch (table 5.2). Figure 5.1 depicts the differences between linear trends in the two endpoint garden classes, *urban* and *rural*, by comparing on a scatterplot of the model *year* term parameter estimates for just the *urban* and *rural* garden samples; their magnitudes and signs indicating relative slope and direction respectively of any linear inter-year reporting rate trend.

For five of the above 13 species, *year* terms were not significant in either *rural* and *urban* models, while for another five, Song Thrush and House Sparrow (red listed), Dunnock (amber listed), Crow and Jackdaw (both 'pest' species); they were significant in both. In total, eleven species had significant *year* terms in all three habitat types; the five noted above and another six that had no significant interaction term in the *allsites* models, Black-headed Gull, Pied Wagtail, Fieldfare, Redwing, Blackcap and Starling. In all 11 of these species, all the *year* terms are negative but mitigated by positive $year^2$ terms (not significant in Redwing or Blackcap). All 11 are located in the 'negative rural, negative urban' quadrant of figure 5.1, based on the signs of their *year* term parameter estimates, and of the five with a significant *allsites* interaction term, only Dunnock has a less negative trend in *urban* than in *rural*. In fact, where significant inter-year linear trends were detected they were overwhelmingly negative; from tables 5.2 and 5.3, the only significant positive *year* terms were in *rural* Long-tailed Tit, Tree Sparrow and Brambling and *suburban* Goldfinch, Feral Pigeon, Great Tit and Brambling; there were no significant positive *year* terms in the *urban* garden sample.

Table 5.1. Land cover subclasses and their contributions to discrimination between the *a priori* garden types. Codes *cnn* are CEH LCM2000 land cover subclass designations

i. Variables Retained

Variable	Partial r^2	F	Pr > F
c03 Littoral Rock	0.0003	2.33	0.0975
c10 Open dwarf shrub heath	0.0025	19.97	<.0001
c12 Broad-leaved / mixed woodland	0.003	23.91	<.0001
c13 Coniferous woodland	0.0051	40.83	<.0001
c14 Improved grassland	0.0128	103.49	<.0001
c15 Neutral grass	0.0013	10.06	<.0001
c16 Setaside grass	0.0003	2.4	0.0909
c17 Bracken	0.0005	3.79	0.0225
c18 Calcareous grass	0.0021	16.42	<.0001
c19 Acid grassland	0.0026	20.97	<.0001
c20 Fen, marsh, swamp	0.0009	6.9	0.001
c21 Arable cereals	0.0124	99.98	<.0001
c22 Arable horticulture	0.0083	66.9	<.0001
c23 Arable non-rotational	0.0028	22.33	<.0001
c24 Suburban/rural development	0.0124	100.24	<.0001
c25 Continuous urban	0.0157	127.56	<.0001

ii. Variables removed (in order of removal)

Variable	Partial r^2	F	Pr > F
c02 Water (inland)	0	0	0.9968
c05 Saltmarsh	0	0.09	0.9172
c06 Supra-littoral rock	0	0.19	0.8269
c04 Littoral sediment	0.0001	0.65	0.5216
c07 Supra-littoral sediment	0.0001	0.89	0.4127
c09 Dense dwarf shrub heath	0.0001	1.04	0.3541
c08 Bog (deep peat)	0.0001	1.15	0.3169
c01 Sea / Estuary	0.0001	1.1	0.3341

Table 5.2. Summary of model results for the 13 species having a significant *garden class* * *year* interaction term in the *allsites* models, deviance /degrees of freedom (D/DF) bold type if within acceptable range ($0.5 < D/DF < 1.5$). Significance of *year* and *year*^{2} terms in *rural*, *suburban* and *urban* models denoted by bold type and asterisks, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0005$ where P = type 3 $p_r > \chi^2$. Species presented in ascending order of *year* term parameter estimate in *urban* models i.e fastest urban linear decline first, fastest urban linear increase last.

Model:	*allsites*		*rural*			*suburban*			*urban*		
Species	D/DF	$P_{garden\ class * year}$	D/DF	year estimate	year2 estimate	D/DF	year estimate	year2 estimate	D/DF	year estimate	year2 estimate
Turdus philomelos	**1.1202**	**<0.0001**	**1.193**	**-0.2273*****	**0.0217*****	**1.093**	**-0.2498*****	**0.0214*****	**0.9402**	**-0.321*****	**0.0216*****
Passer domesticus	**1.0746**	**<0.0001**	**1.0737**	**-0.156*****	**0.0089*****	**1.0785**	**-0.176*****	**0.006***	**1.0627**	**-0.2598*****	**0.0116***
Prunella modularis	**1.1037**	**0.0420**	**0.9977**	**-0.2003*****	**0.0223*****	**1.1467**	**-0.0783****	**0.0099*****	**1.3292**	**-0.1622*****	**0.0152*****
Corvus monedula	**0.9986**	**0.0155**	**1.1932**	**-0.1066*****	**0.0123*****	**0.9089**	**-0.068***	**0.007****	**0.6052**	**-0.1539***	0.0097
Corvus corone/cornix	**1.1216**	**0.0287**	**1.1108**	**-0.0831****	**0.0091*****	**1.1328**	**-0.1015*****	**0.0096*****	**1.1198**	**-0.1134***	0.0072
Streptopelia decaocto	**1.1155**	**0.0073**	**1.1316**	0.052	-0.0025	**1.0573**	0.0409	-0.0045	**1.2645**	-0.0755	0.006
Pyrrhula pyrrhula	0.4327	**0.0001**	0.4767	**-0.1985*****	**0.0181*****	0.4314	**-0.1118****	**0.0159*****	0.2747	-0.0477	0.0093
Carduelis carduelis	0.9850	**0.0028**	**1.0508**	**-0.0515***	**0.0201*****	**0.9692**	**0.0762****	**0.0111*****	**0.7649**	-0.0134	**0.018****
Columba palumbus	**1.3145**	**0.0052**	**1.3456**	0.0021	**0.0081*****	**1.288**	-0.0065	**0.0118*****	**1.2849**	0.0008	**0.0075*****
Parus ater	**1.3183**	**0.0011**	**1.3331**	-0.0292	**0.0079*****	**1.3245**	0.0044	0.0029	**1.2326**	0.0148	-0.0015
Accipiter nisus	**0.6390**	**0.0045**	**0.7454**	0.0139	-0.0032	**0.5736**	0.0478	**-0.005***	0.4824	0.0216	-0.0091
Dendrocopos major	**0.9577**	**0.0199**	**1.198**	0.0443	0.0007	**0.7796**	0.0035	0.0001	**0.713**	0.0742	-0.0065
Carduelis spinus	0.4344	**0.0007**	**0.5238**	-0.0589	0.0052	0.3889	**-0.1133*****	**0.0073***	0.2518	0.1237	**-0.0172***

Table 5.3. Summary model results for 27 species having either non-significant *garden class* * *year* interaction term and/or deviance / degrees of freedom (D/DF) outside acceptable range (0.5 < D/DF < 1.5, bold type if compliant) in *allsites* models. Significance of *year* and $year^2$ terms in *rural*, *suburban* and *urban* models denoted by bold type and asterisks, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0005$ where P = type 3 $p_r > \chi^2$. Species presented in systematic order.

Model:	allsites		rural			suburban			urban		
Species	D/DF	P garden class * year	Deviance/DF	year estimate	year2 estimate	Deviance/DF	year estimate	year2 estimate	Deviance/DF	year estimate	year2 estimate
Larus ridibundus	0.2983	0.9613	0.2137	**-0.2778*** **	**0.0199*** **	0.3835	**-0.2747*** **	**0.0187*** **	0.302	**-0.3529*** **	**0.0256*** **
Columba livia	0.6418	0.3014	0.3587	0.0098	0	0.7845	**0.081* **	-0.0044	1.167	0.0405	0.0002
Strix aluco	0.2621	**0.0199**	0.401	0.0729	-0.0017	0.155	0.0695	-0.0078	0.1372	-0.1819	0.0146
Motacilla alba	**0.5953**	0.1202	0.8847	**-0.1189*** **	**0.0095*** **	0.3898	**-0.0999*** **	**0.0058*** **	0.2368	**-0.3028*** **	**0.0259*** **
Troglodytes troglodytes	**1.2982**	0.3214	1.3719	-0.016	**0.0038* **	1.2445	**-0.0736*** **	**0.0095*** **	1.2069	**-0.159*** **	**0.0161*** **
Erithacus rubecula	**0.7958**	0.9346	0.6414	-0.0383	**0.0082*** **	0.8812	**-0.0438* **	**0.0089*** **	1.0525	-0.0781	**0.0126** **
Turdus merula	0.4876	0.1144	0.46	-0.0446	0.0048	0.4717	0.0401	-0.0032	0.6428	-0.0409	0.0008
Turdus pilaris	0.1448	0.9594	0.2297	**-0.229*** **	**0.0161*** **	0.0798	**-0.4878*** **	**0.0373*** **	0.0636	**-0.4714*** **	**0.0275** **
Turdus iliacus	0.1729	**0.0026**	0.1942	**-0.3539*** **	**0.0272*** **	0.1527	**-0.3368*** **	**0.0138*** **	0.162	**-0.1771** **	-0.0035
Turdus viscivorus	0.4846	0.0994	0.6095	**-0.1005*** **	0.0044	0.3903	**-0.2135*** **	**0.0129*** **	0.3624	-0.0581	-0.0015
Sylvia atricapilla	0.4234	0.7103	0.4103	**-0.1737*** **	**0.0149*** **	0.4365	**-0.1451*** **	**0.0116*** **	0.3973	**-0.1337* **	0.0102
Regulus regulus	0.3809	0.7520	0.4123	0.022	-0.0032	0.3609	0.0254	-0.0038	0.3315	0.0845	**-0.0124* **
Aegithalos caudatus	**0.8471**	0.1517	0.8727	**0.1242*** **	**-0.0058** **	0.8401	0.0433	0.002	0.7742	-0.0022	0.0075
Parus caeruleus	**0.5317**	0.7735	0.4689	**-0.0935* **	0.0025	0.5726	**-0.1461*** **	**0.0074* **	0.6137	-0.109	0.0041
Parus major	**1.0166**	0.0335	0.818	0.0124	-0.0031	1.1613	**0.0496* **	-0.004	1.2218	0.0545	-0.0036
Sitta europaea	**0.7187**	0.2998	0.8812	-0.0029	0.0044	0.639	-0.0111	0.0035	0.4065	-0.0256	0.0038
Certhia familiaris	0.1741	0.2230	0.2629	**-0.1691*** **	**0.0142*** **	0.1135	**-0.1747* **	**0.0136* **	0.0661	-0.1794	0.0066
Garrulus glandarius	**0.7307**	0.5676	0.7102	0.0098	-0.0012	0.7353	-0.0268	0.0018	0.7868	-0.0399	0.002
Pica pica	**1.3746**	0.1718	1.3811	**-0.0611** **	**0.005* **	1.367	**-0.0603** **	**0.0052** **	1.3779	0.0351	-0.002
Corvus frugilegus	**0.5388**	0.1641	0.7495	**-0.1227*** **	**0.0088** **	0.403	-0.0246	0.0015	0.2526	-0.1599	0.0103
Sturnus vulgaris	**1.2439**	0.1953	1.2988	**-0.1363*** **	**0.0072*** **	1.1856	**-0.1724*** **	**0.0085*** **	1.2427	**-0.2107*** **	**0.0148*** **
Passer montanus	0.3508	0.7672	0.4948	**0.1117* **	-0.0069	0.2392	0.0613	-0.0021	0.2247	-0.0683	0.0072
Fringilla coelebs	**1.0459**	0.5529	0.7836	**-0.0735** **	**0.0054* **	1.2316	0.0296	-0.003	1.3379	0.0183	-0.0026
Fringilla montifringilla	0.1262	0.9527	0.1437	**0.1267* **	**-0.0181** **	0.123	**0.2047*** **	**-0.03*** **	0.0723	0.2893	-0.0338
Carduelis chloris	**1.1156**	0.7663	0.9542	-0.0511	0.0044	1.2106	**-0.0717** **	**0.0069*** **	1.3651	**-0.0845* **	**0.0074* **
Emberiza citrinella	0.1933	0.1222	0.3421	**-0.1012* **	0.0025	0.0827	**-0.2196* **	0.0143	0.0467	0.0071	-0.0269
Emberiza schoeniclus	0.0775	0.4379	0.0851	-0.1137	-0.0044	0.0779	**-0.2908** **	**0.0184* **	0.0468	-0.1767	0.0154

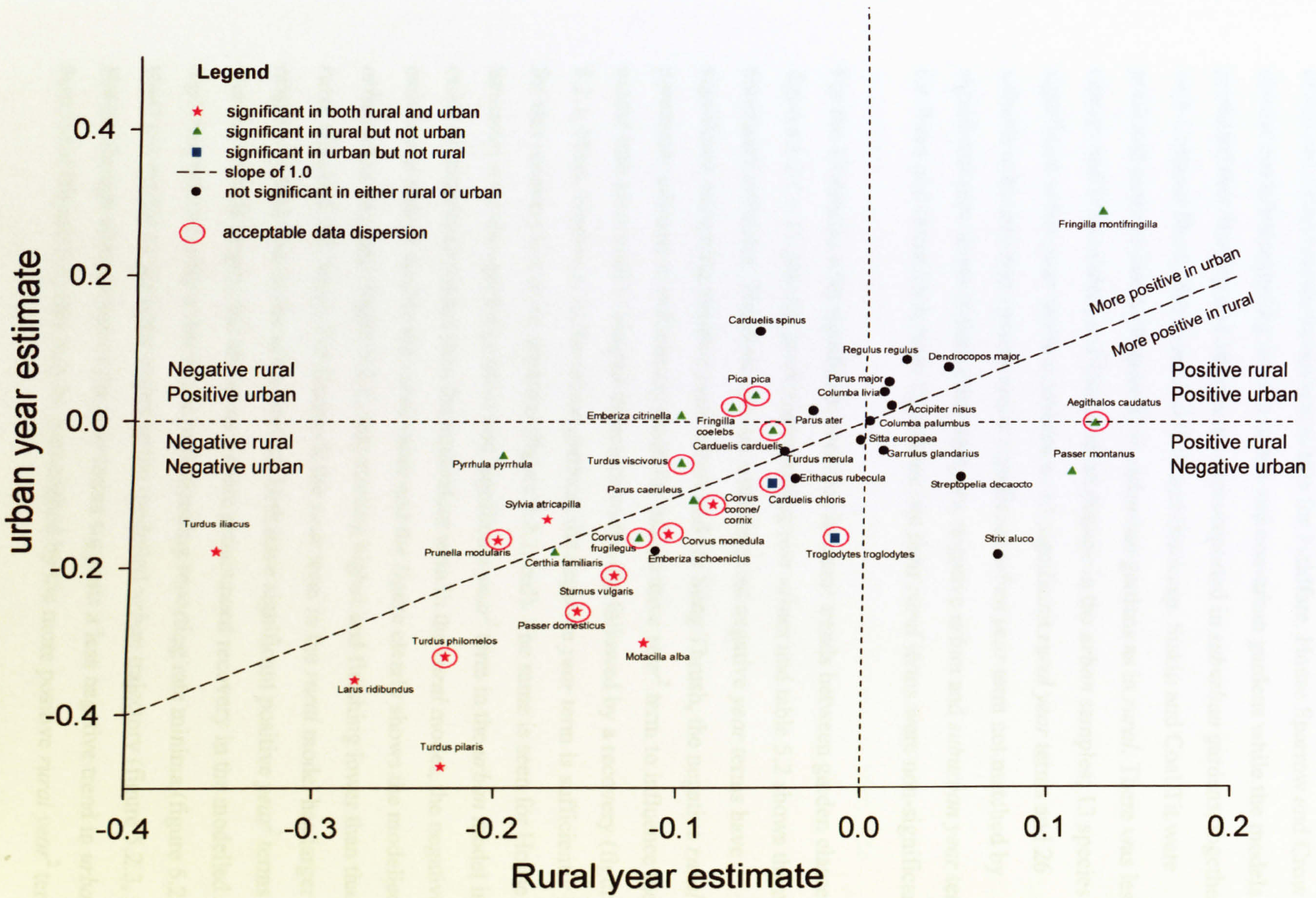

Figure 5.1. *Urban year* term parameter estimates against *rural year* term parameter estimates, from models. Legend refers to *year* model terms.

Generally, modelled reporting rates were higher in *rural* gardens than *urban* or *suburban* (28 species), but *urban* gardens had highest rates for Feral Pigeon and, more surprisingly, Woodpigeon, Jay and Redwing, for which the highest reporting rates are *urban* and lowest *rural*; the reverse is true for Fieldfare. House Sparrow and Crow had similar modelled reporting rates in *urban* and non-urban gardens while the models predicted that Starling and Magpie are most-reported in *suburban* gardens, together with Collared Dove, Black-headed Gull and Blackcap. Siskin and Coal Tit were predicted more or less as frequently in *suburban* gardens as in *rural*. There was less change and little evidence of independent change in the *urban* samples; 13 species had significant *urban year* terms compared to 23 significant *rural year* terms and 26 *suburban*. In only two species was a significant *urban year* term not matched by significant *year* terms in both other samples; negative *urban* and *suburban year* terms for Wren and Greenfinch were significant but their *rural* terms were non-significant

For the 13 species with significant variation in linear trends between garden classes, figures 5.2.1 – 13 plot the predicted reporting rate values and table 5.2 shows the model parameter estimates. The three species with the most negative *year* terms have significant mitigating positive $year^2$ terms and for Song Thrush, the negative *rural year* parameter estimate is sufficiently small for this positive $year^2$ term to influence the model into an overall U-shaped trajectory with a dip followed by a recovery (figure 5.2.1, blue). However, in the *urban* gardens, the negative *year* term is sufficiently large for this recovery not to be apparent (figure 5.2.1, red). The same is seen for House Sparrow; even though the positive and significant $year^2$ term in the *urban* model is an order of magnitude higher than the equivalent term in the *rural* model, the negative *year* estimate is almost double the *rural* value and the figure clearly shows the modelled *urban* reporting rate (figure 5.2.2, red) starting higher and finishing lower than that for *rural* (figure 5.2.2, blue). For Dunnock the *year* term in the *rural* model has larger magnitude than that in the *urban* model; both have significant positive $year^2$ terms but that for *rural* is larger; this shows as a more pronounced recovery in the modelled *rural* reporting rate, notably a rise in the post-breeding reporting rate minima (figure 5.2.3 blue) not visible to the same extent in the modelled *urban* trajectory (figure 5.2.3, red). Hence, though comparison of the *year* terms suggests a less negative trend in *urban* than *rural* (figure 5.1) this may be outweighed by the more positive *rural* $year^2$ term.

The *urban* $year^2$ model term for Jackdaw is not significant; this is apparent from the plot in which the modelled *urban* reporting rate shows a steady linear decline (figure 5.2.4, red) but the *rural* model shows a quadratic recovery becoming an overall increase (figure 5.2.4, blue). Similarly, the modelled *urban* trend for Crow spp. is clearly negative and linear (figure 5.2.5, red) whereas in the *rural* model the negative linear trend is slower and mitigated by a significant positive $year^2$ term (figure 5.2.5, blue). Significant negative *year* and positive $year^2$ terms are apparent in the modelled reporting rate plots for Bullfinch; the initial decline of the rural model (figure 5.2.7, blue) is steeper than that in the *suburban* model (figure 5.2.7, pink). Neither *urban* model term is significant for this species but the flat plot (as opposed to the falling *rural* and *suburban* trajectories) shows a rising tendency although the reporting rate is very low overall which probably accounts for the lack of significance. Goldfinch shows extreme periodicity and uniformly rising trends dominated by significant $year^2$ terms although the *urban* model (figure 5.2.8, red) lacks a significant *year* term. The difference in linear trends indicated by the *allsites* model is probably due to a reversal in sign of the *year* terms between *rural* (negative) and *suburban* (positive). The same explanation may apply to Woodpigeon, although the sign difference is reversed and the *year* terms are non-significant; despite the difference between garden types indicated by the *allsites* model, modelled reporting rates for all three garden classes show a uniform positive trend (figure 5.2.9), driven again by significant positive $year^2$ terms.

Coal Tit has a significant positive $year^2$ term in *rural* (figure 5.2.10, blue) but no other terms are significant despite the slight overall upward trend suggested by the plots. The only significant term for Sparrowhawk is a negative $year^2$ term in *suburban*; this is surprising as the urban modelled reporting rate (figure 5.2.11, red) clearly diverges negatively from that for *suburban* (figure 5.2.11, pink); however, the urban reporting rate is very low, which probably prevents the model from resolving any formally significant trend. For Collared Dove and Great Spotted Woodpecker, the *allsites* model indicates a significant difference in linear trend between the three garden classes but none of the three single class models produce either significant *year* or $year^2$ terms. The modelled urban reporting rate for Collared Dove (figure 5.2.6, red) diverges negatively and that for *rural* Great Spotted Woodpecker (figure 5.2.12, blue) diverges positively but for both these species the actual values of seasonal maxima and minima in the raw data (black plots) are quite variable; this may prevent the models from resolving formally significant terms without longer runs of data.

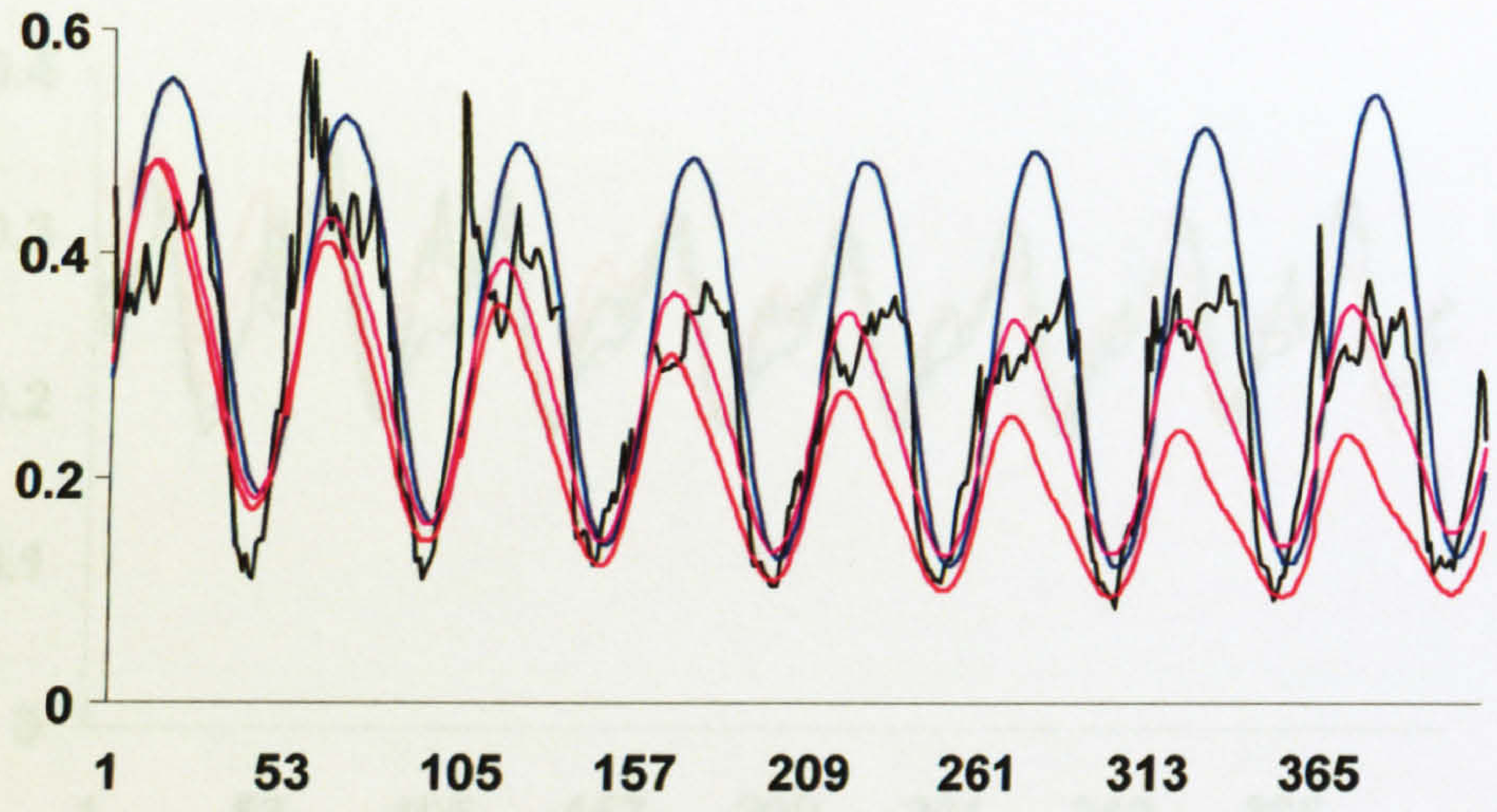

Figure 5.2.1. Song Thrush

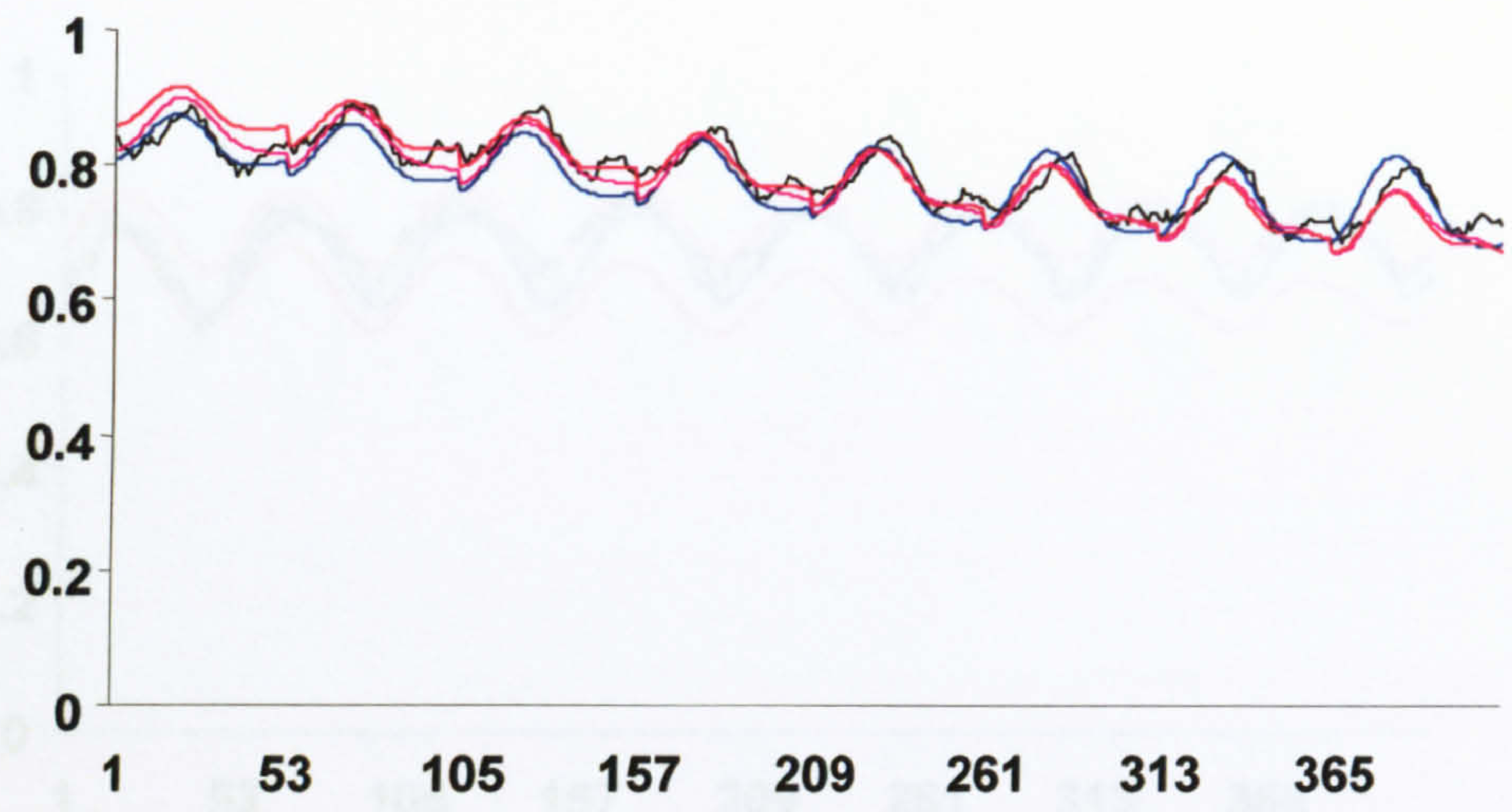

Figure 5.2.2. House Sparrow

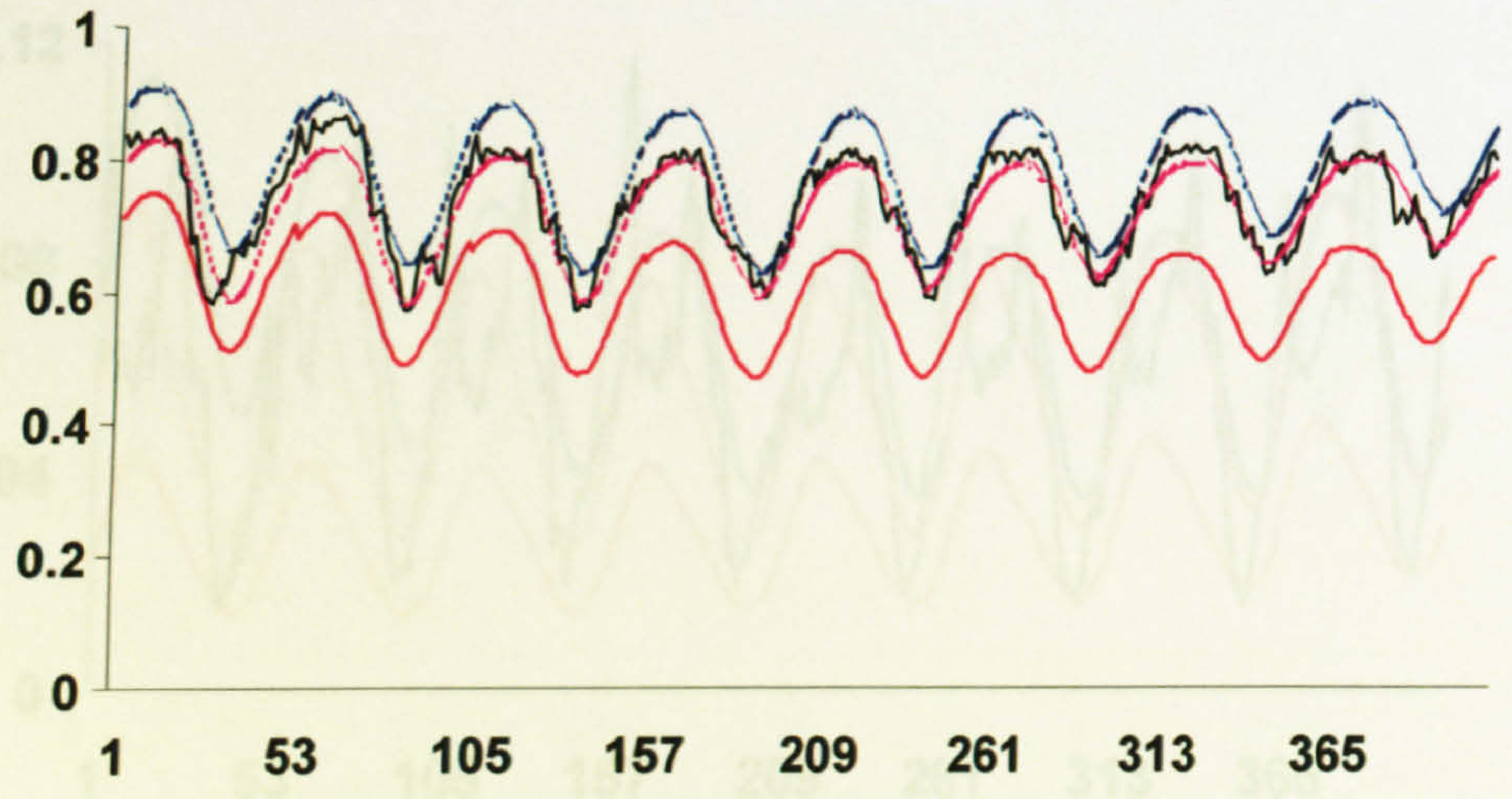

Figure 5.2.3. Dunnock

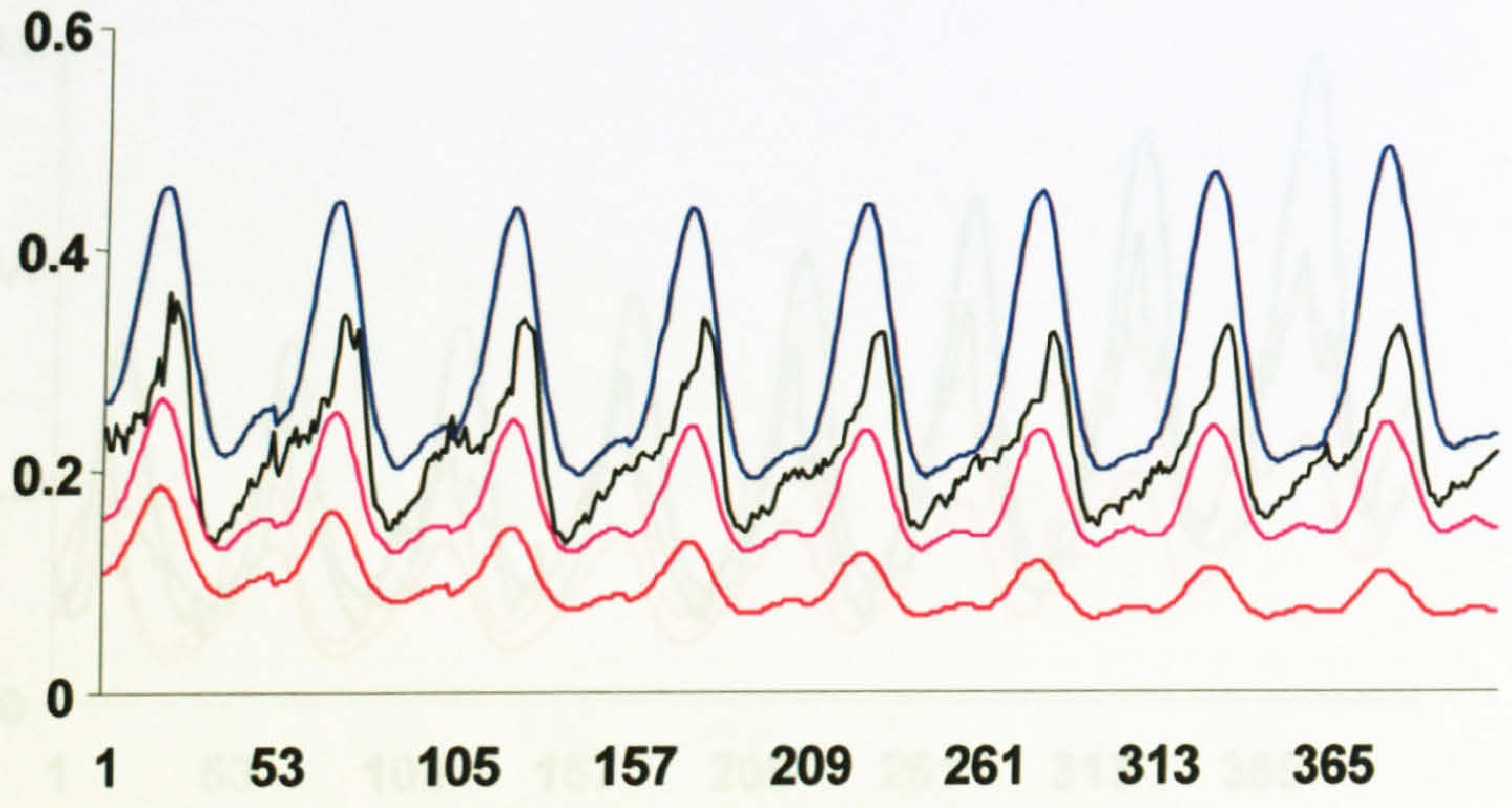

Figure 5.2.4. Jackdaw

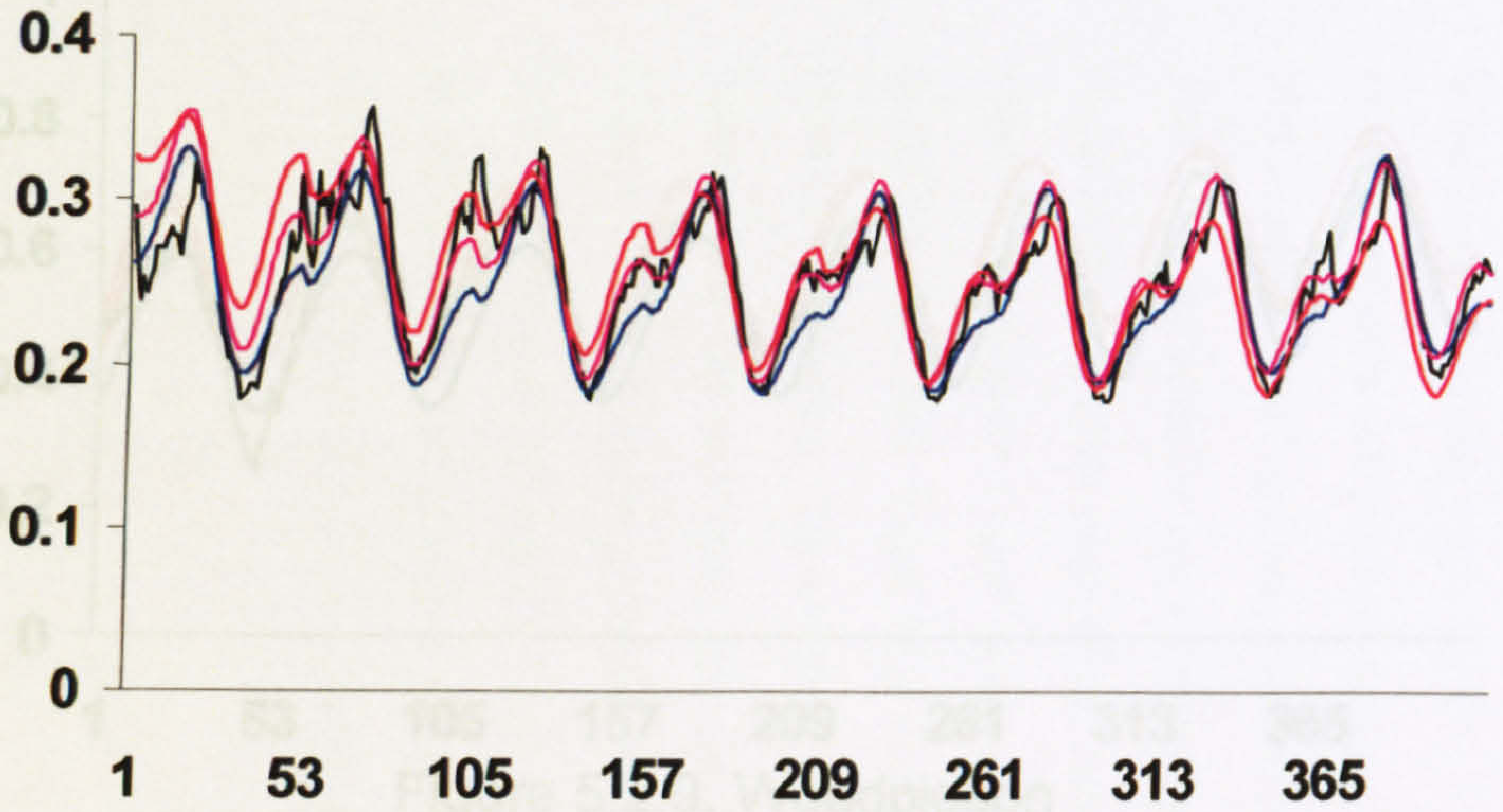

Figure 5.2.5. Carrion / Hooded Crow

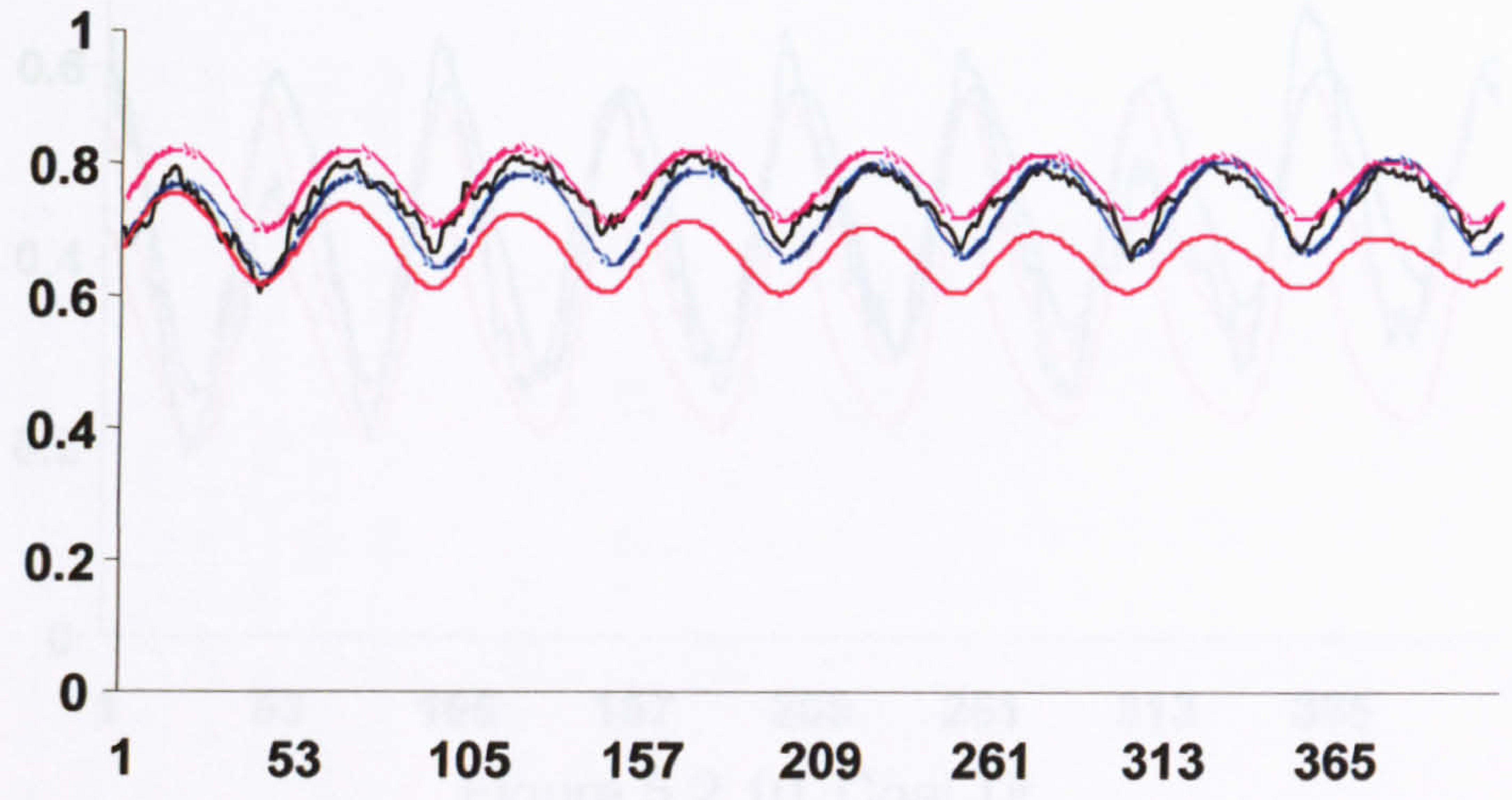

Figure 5.2.6. Collared Dove

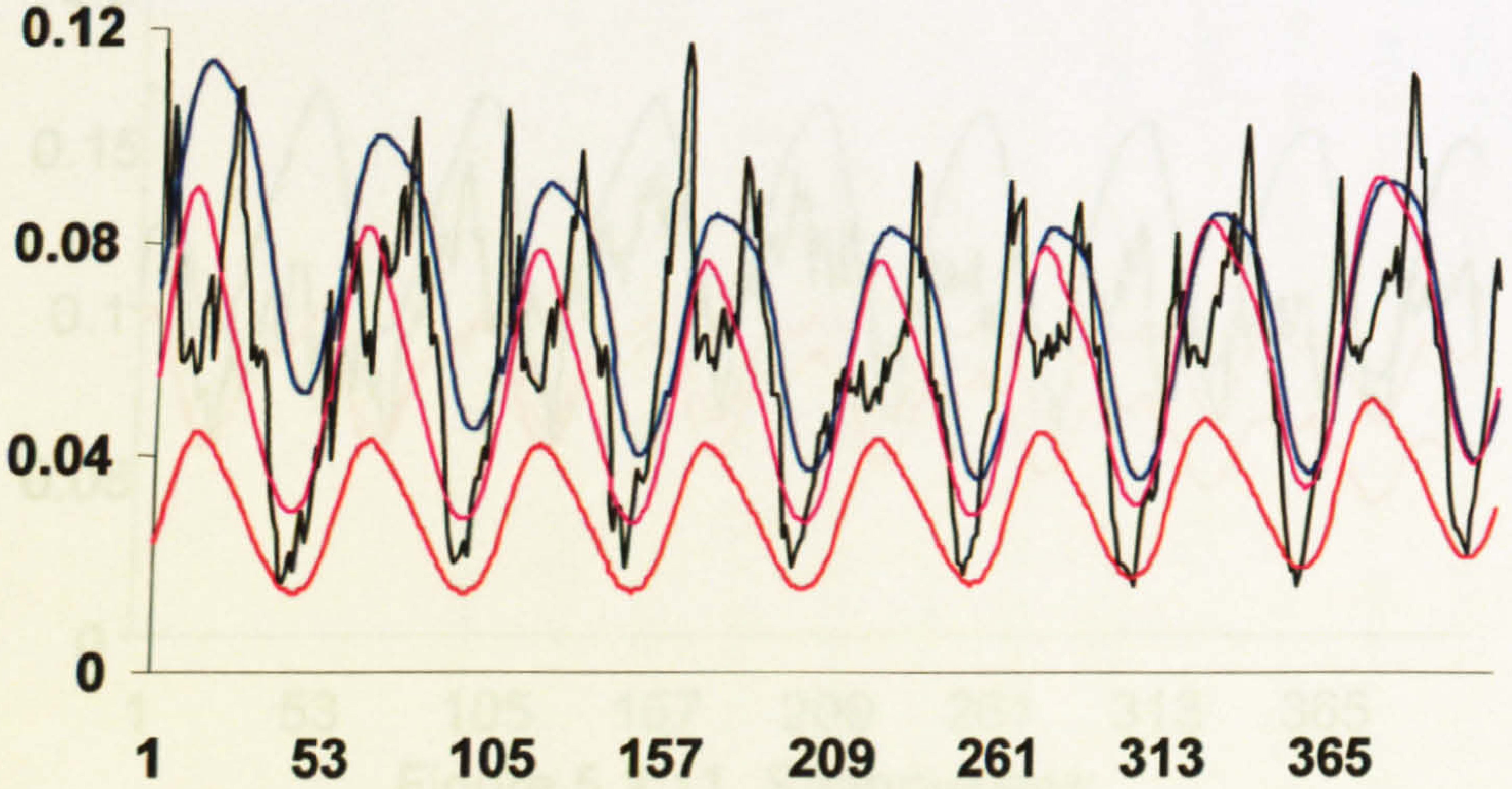

Figure 5.2.7. Bullfinch

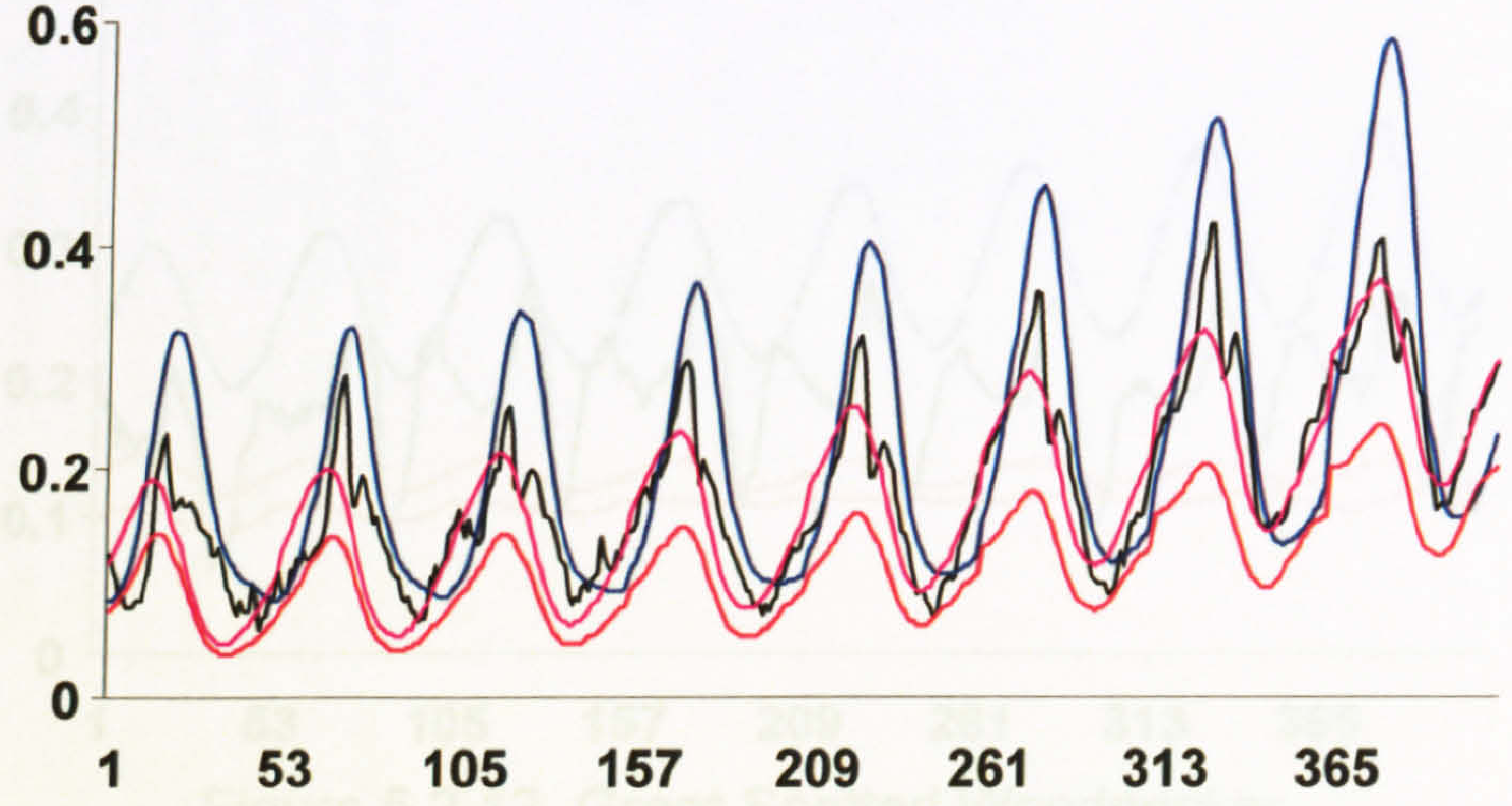

Figure 5.2.8. Goldfinch

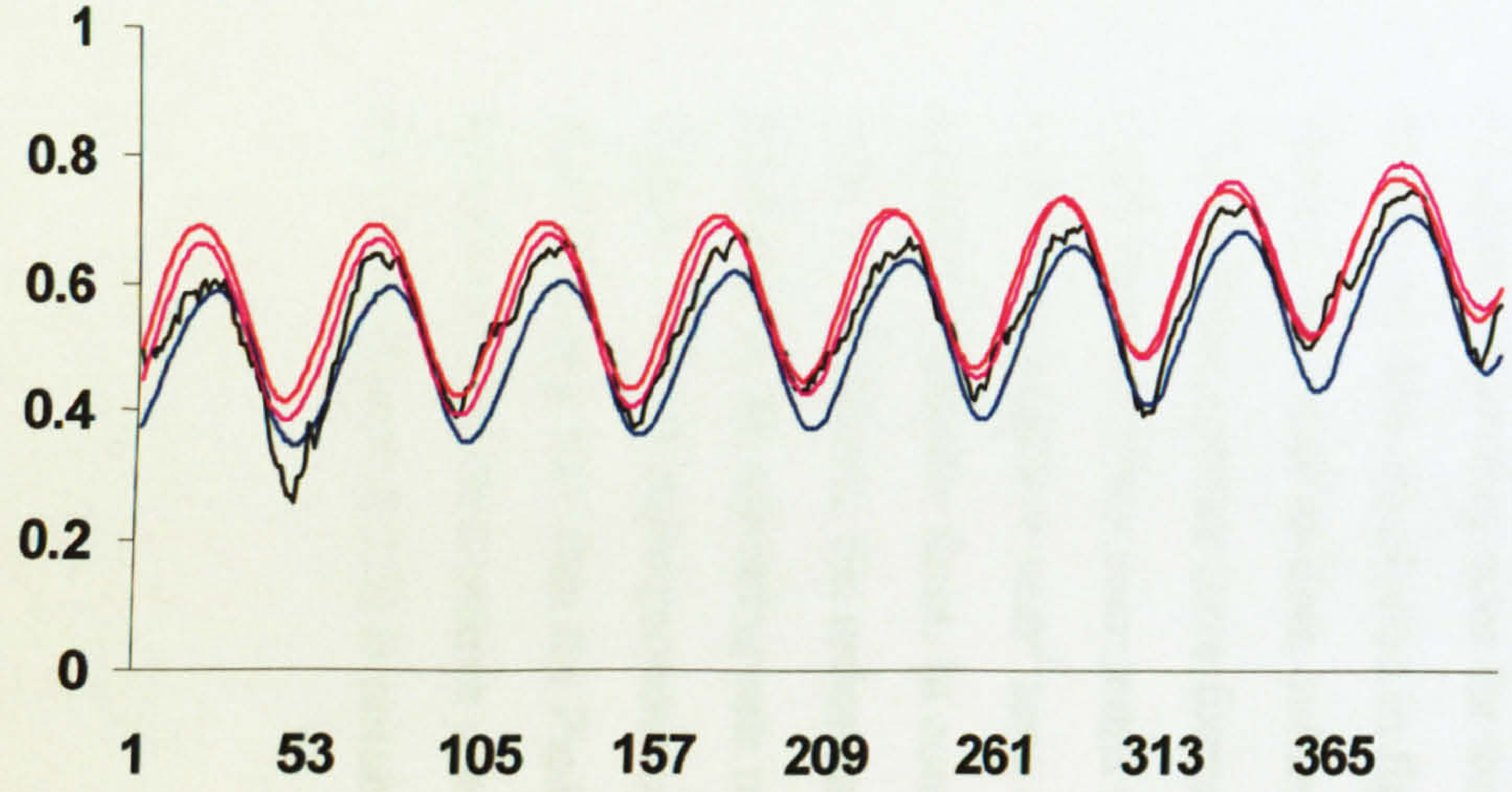

Figure 5.2.9. Woodpigeon

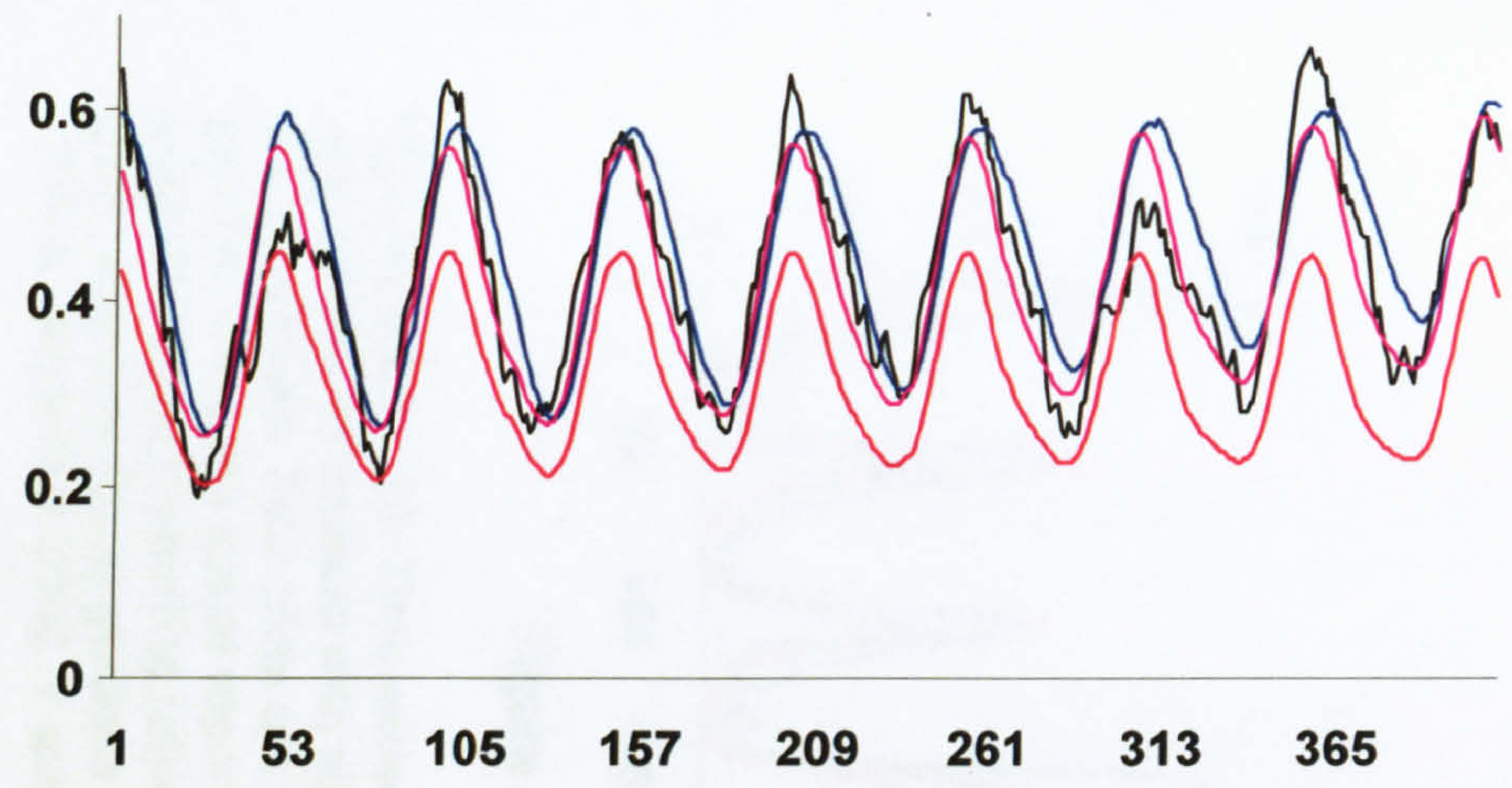

Figure 5.2.10. Coal Tit

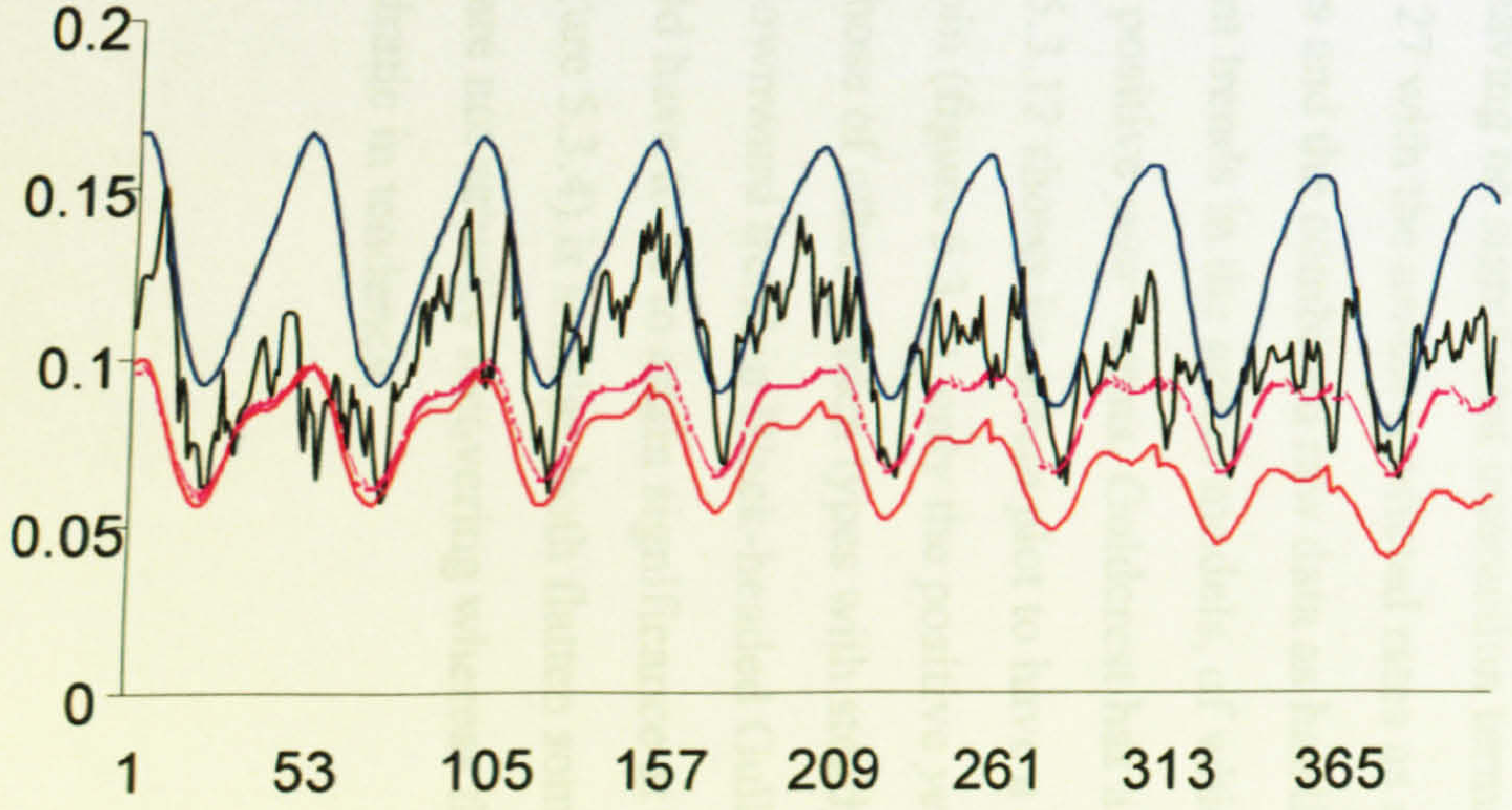

Figure 5.2.11. Sparrowhawk

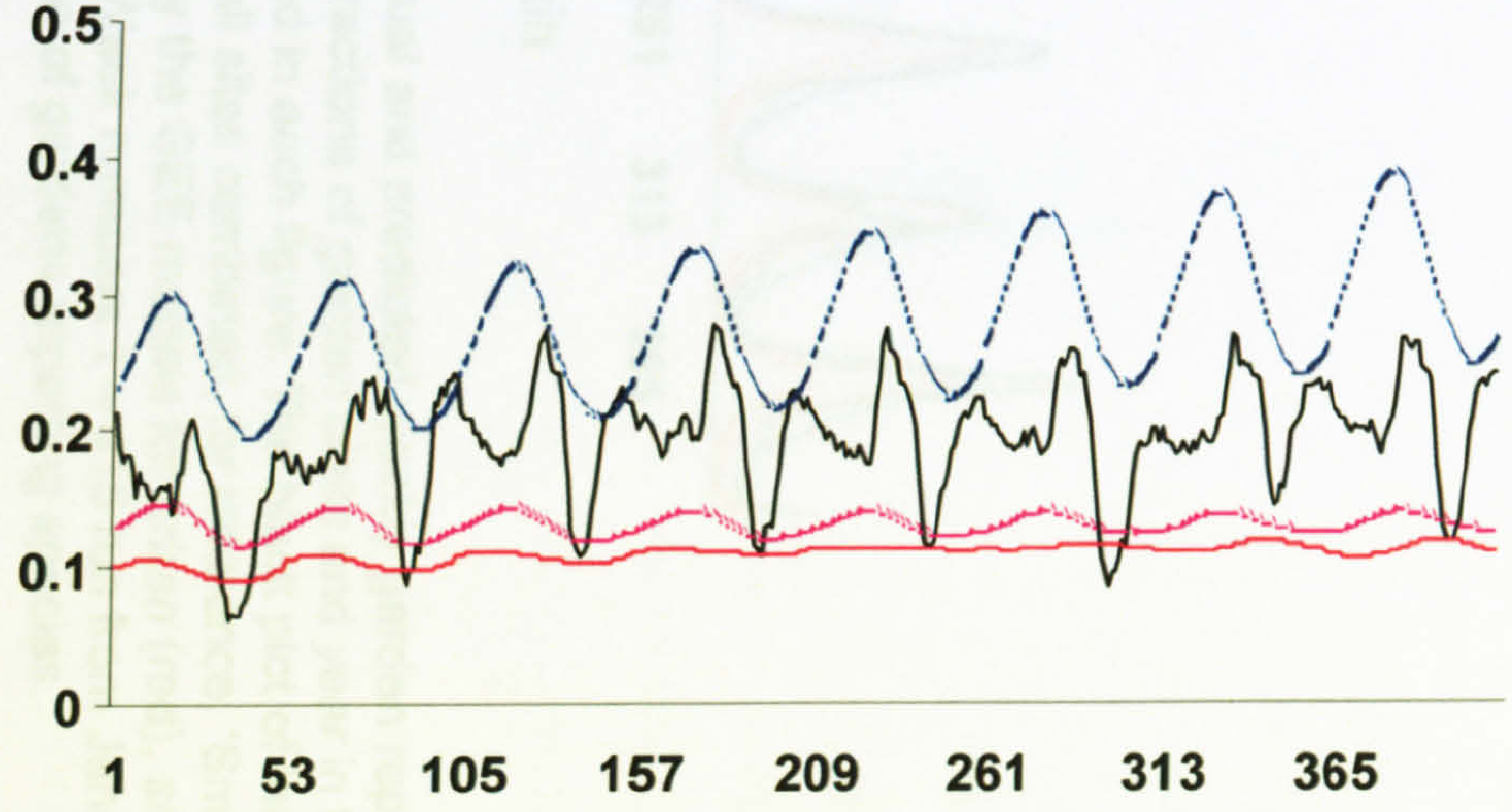

Figure 5.2.12. Great Spotted Woodpecker

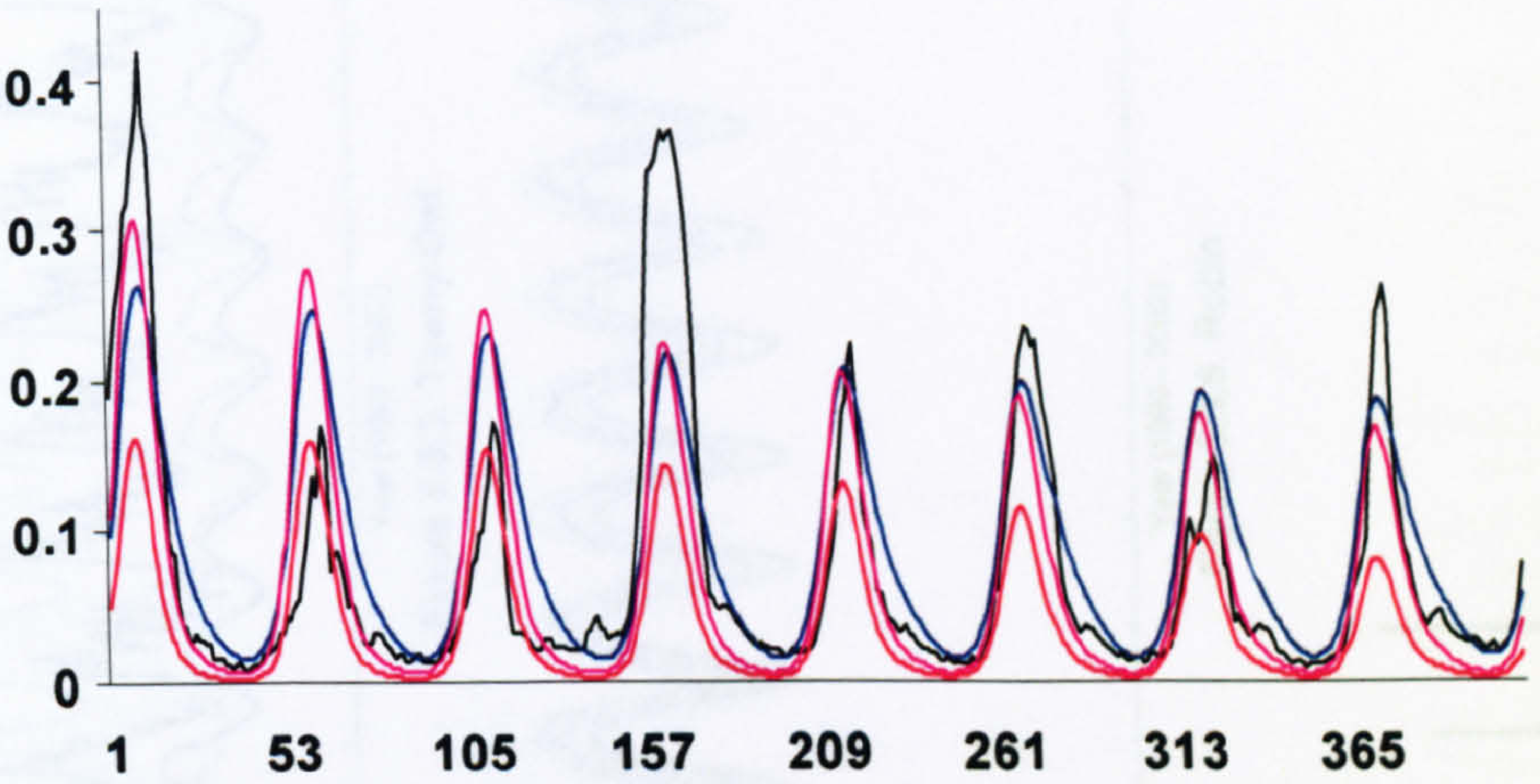

Figure 5.2.13. Siskin

Figures 5.2.1 – 13. Time series plots of actual and predicted weekly garden reporting rates for the 13 species with significant interactions of *garden class* and *year* in the *allsites* models. Four plots are superimposed in each figure. The black plot of 'noisy' appearance is the actual reporting rate for all sites combined, for reference. 'Smoothed' plots are weekly reporting rates predicted by the GEE models for *urban* (red), *suburban* (pink) and *rural* (blue) gardens separately. Week numbers 1 – 416 run from January 1995 to December 2002. *Y* axis is proportion of gardens reporting species.

Modelled reporting rates for the 27 species having no significant interaction terms in the *allsites* models are plotted in figures 5.3.1 – 27 with the *urban* predicted rates as solid black lines, *rural* as dots, *suburban* as dashes and the combined raw data as hairlines. Ten of these species have formally significant trends in the *urban* models, of which eight have negative *year* terms mitigated by positive $year^2$ terms. Goldcrest has a significant negative $year^2$ term only; figure 5.3.12 shows its *urban* plot to have a negative quadratic form. In contrast, for Robin (figure 5.3.6), only the positive $year^2$ term is significant; the *urban* model tracks those of other garden types with steady increases in the reporting rate minima The downward trend in Black-headed Gull (figure 5.3.1) is quite pronounced, as it would have to be to attain significance at this low reporting rate; that for Pied Wagtail (figure 5.3.4) is similar; both flatten somewhat as indicated by the positive $year^2$ terms but are not actually recovering whereas the plot for Wren (figure 5.3.5) is notably more quadratic in tendency.

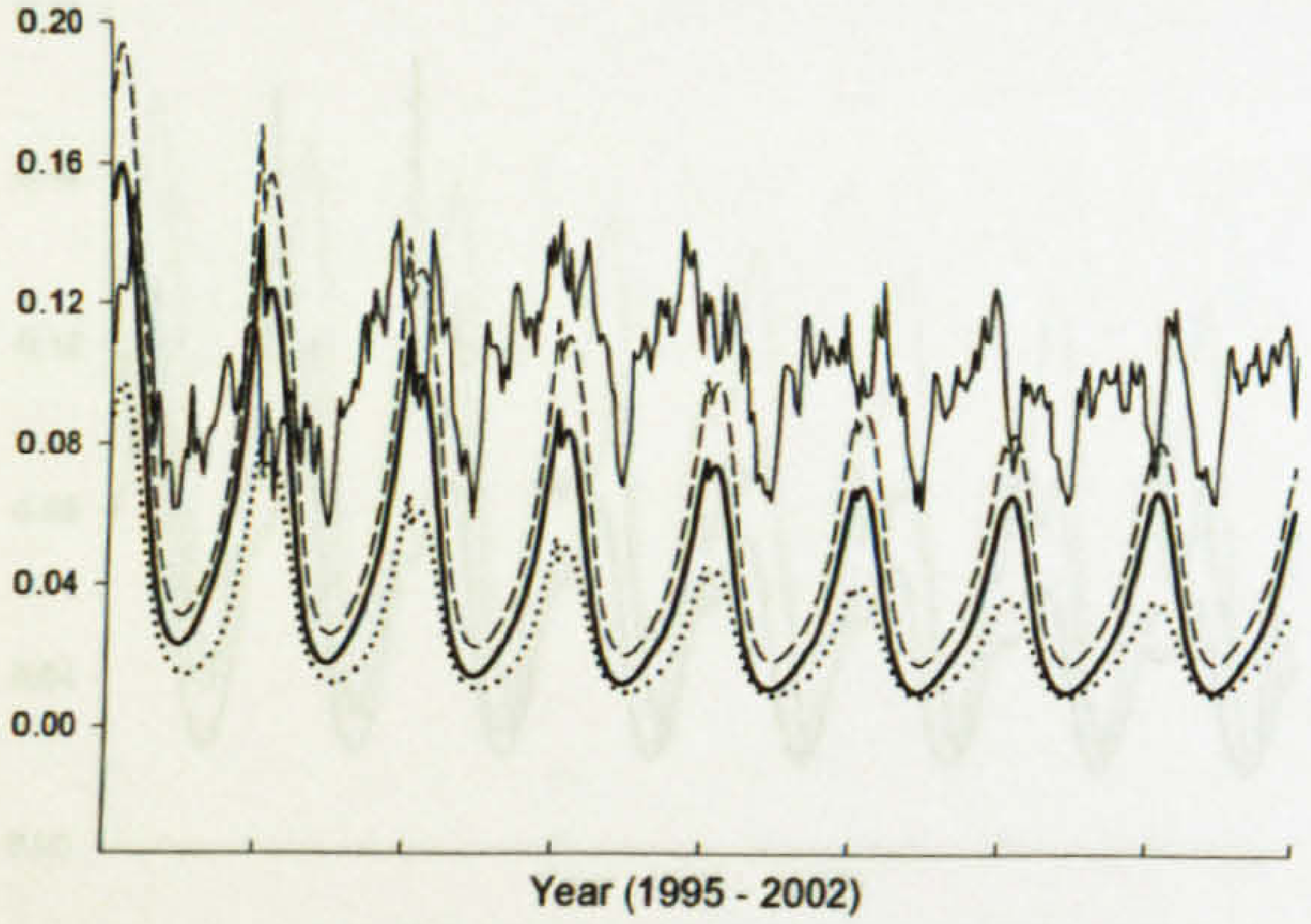

Figure 5.3.1. Black-headed Gull

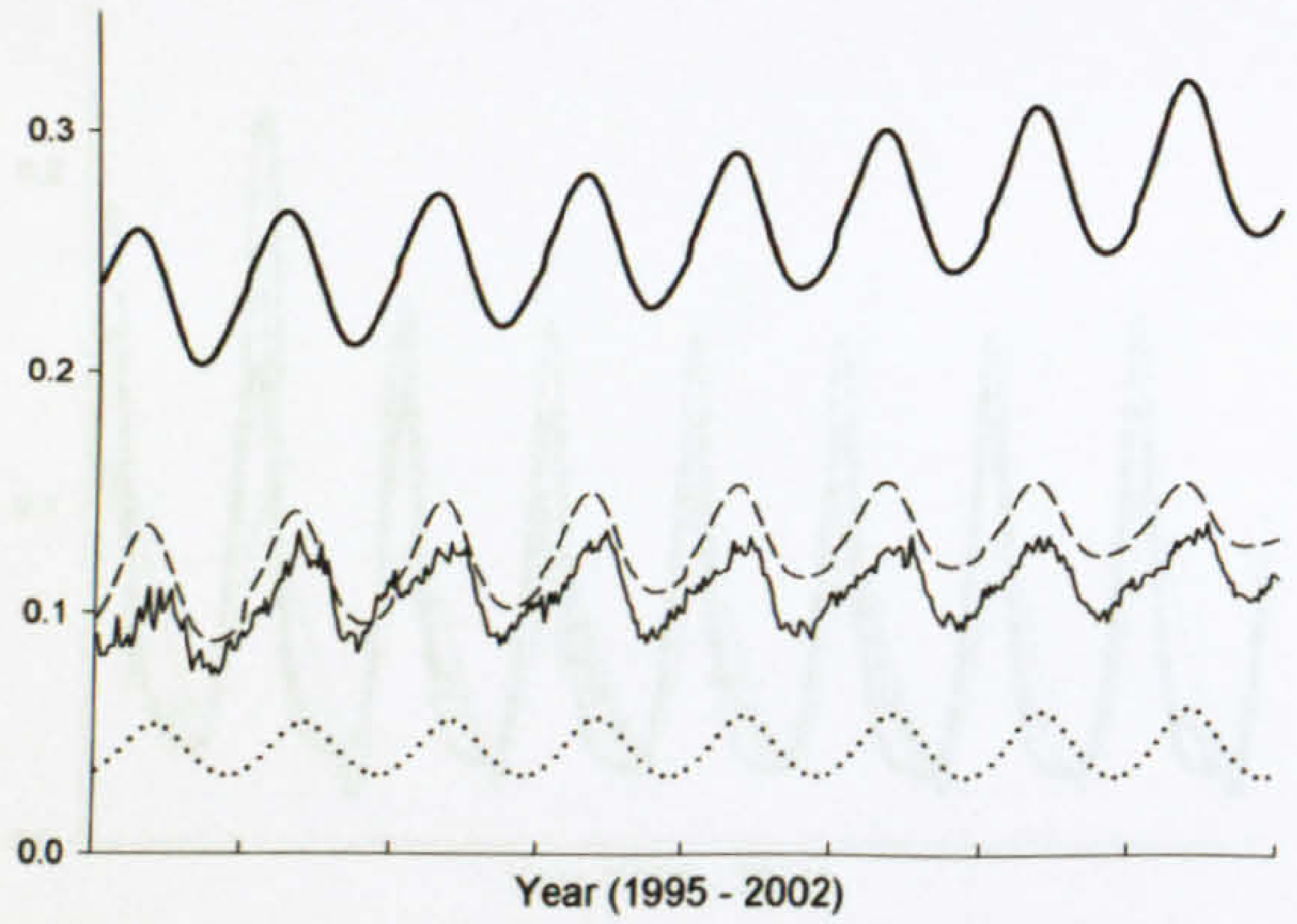

Figure 5.3.2. Feral Pigeon

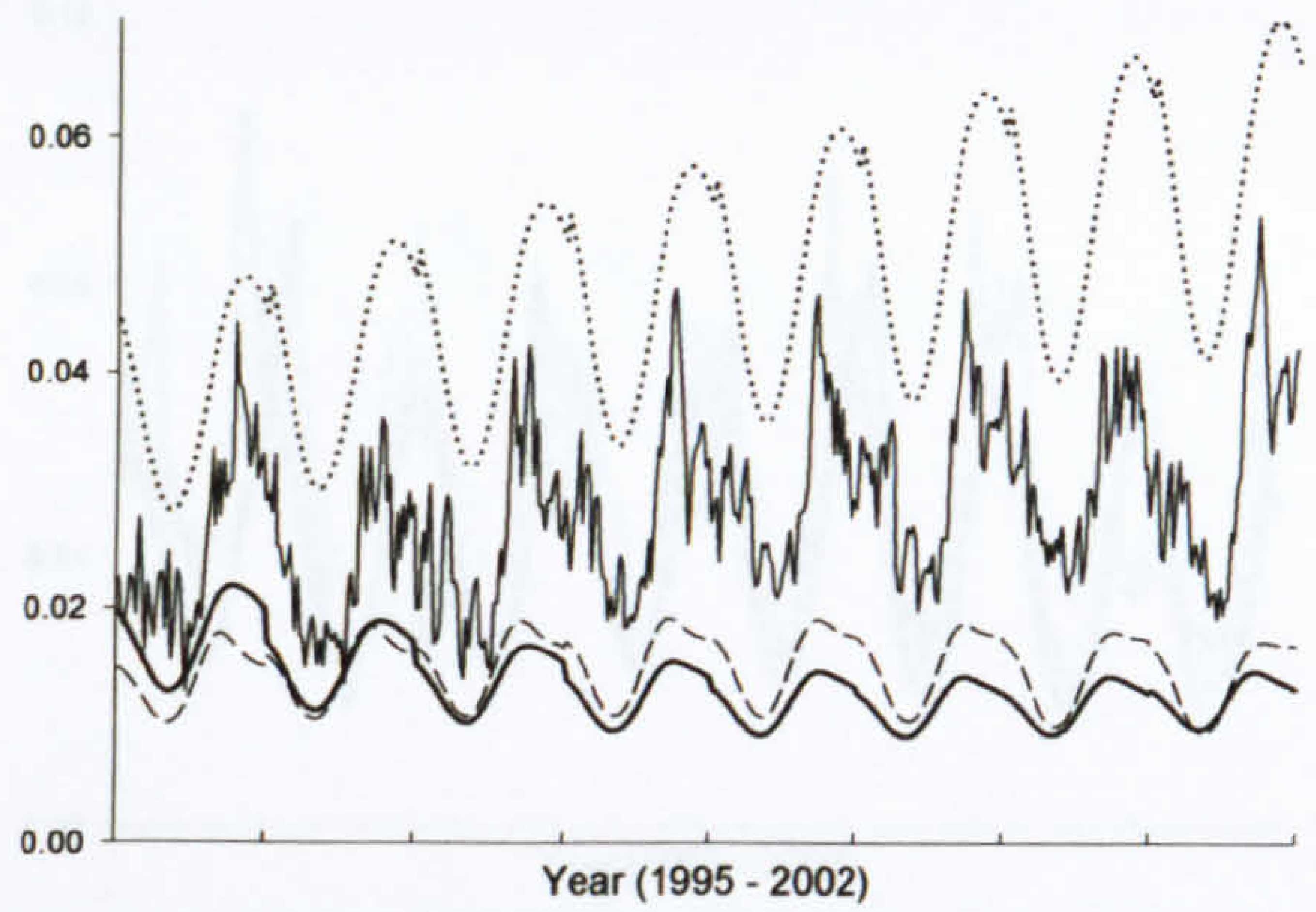

Figure 5.3.3. Tawny Owl

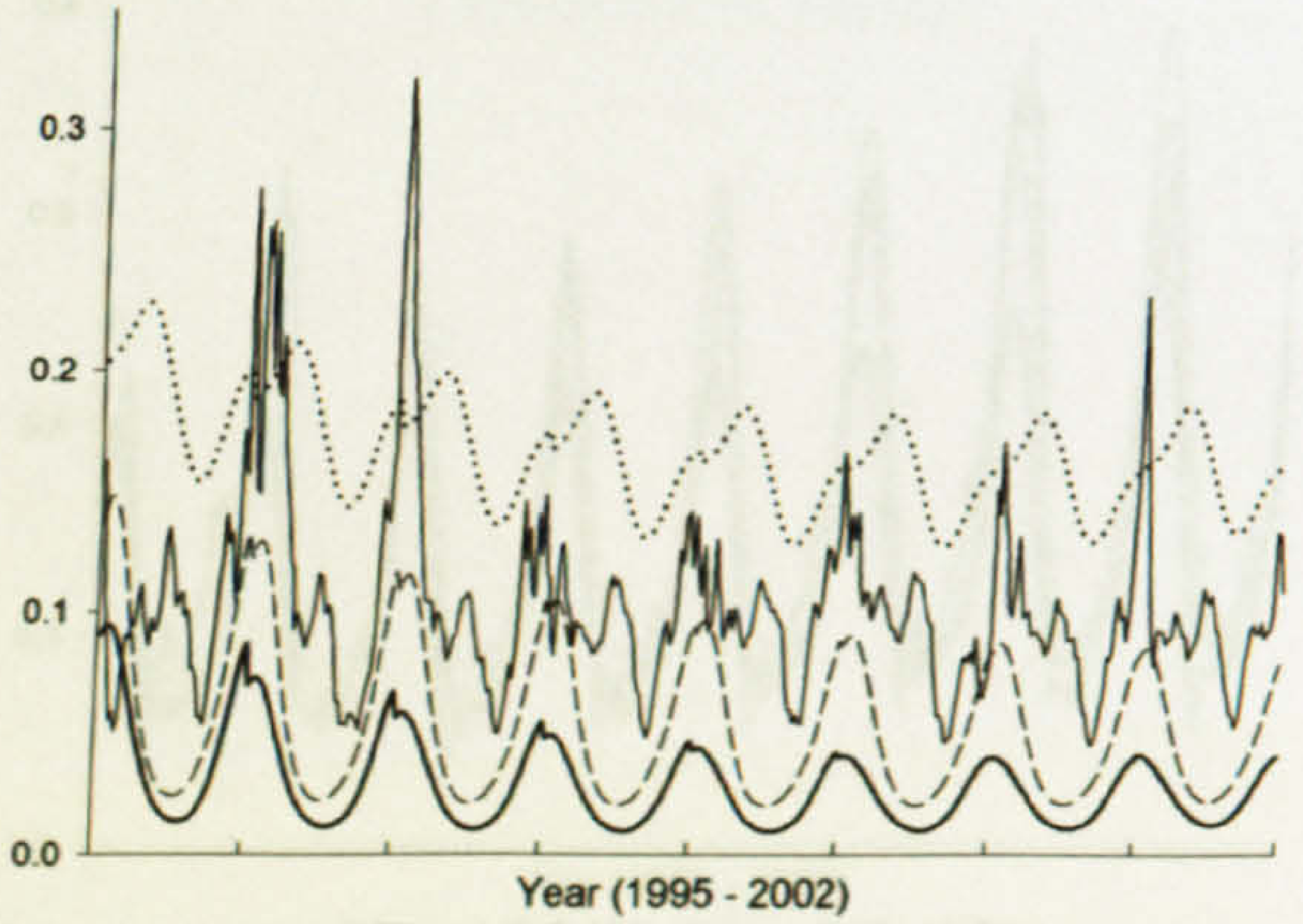

Figure 5.3.4. Pied Wagtail

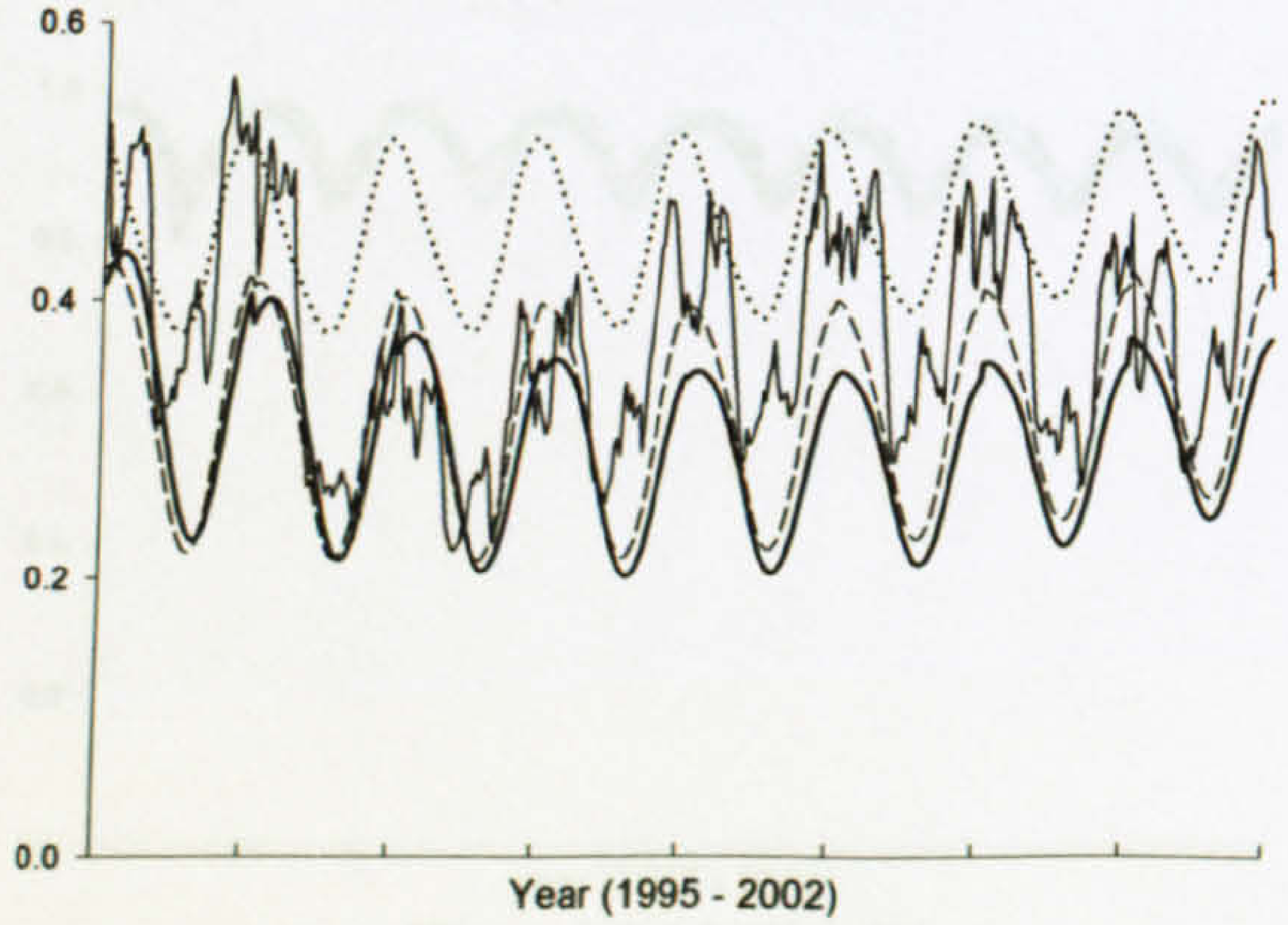

Figure 5.3.5. Wren

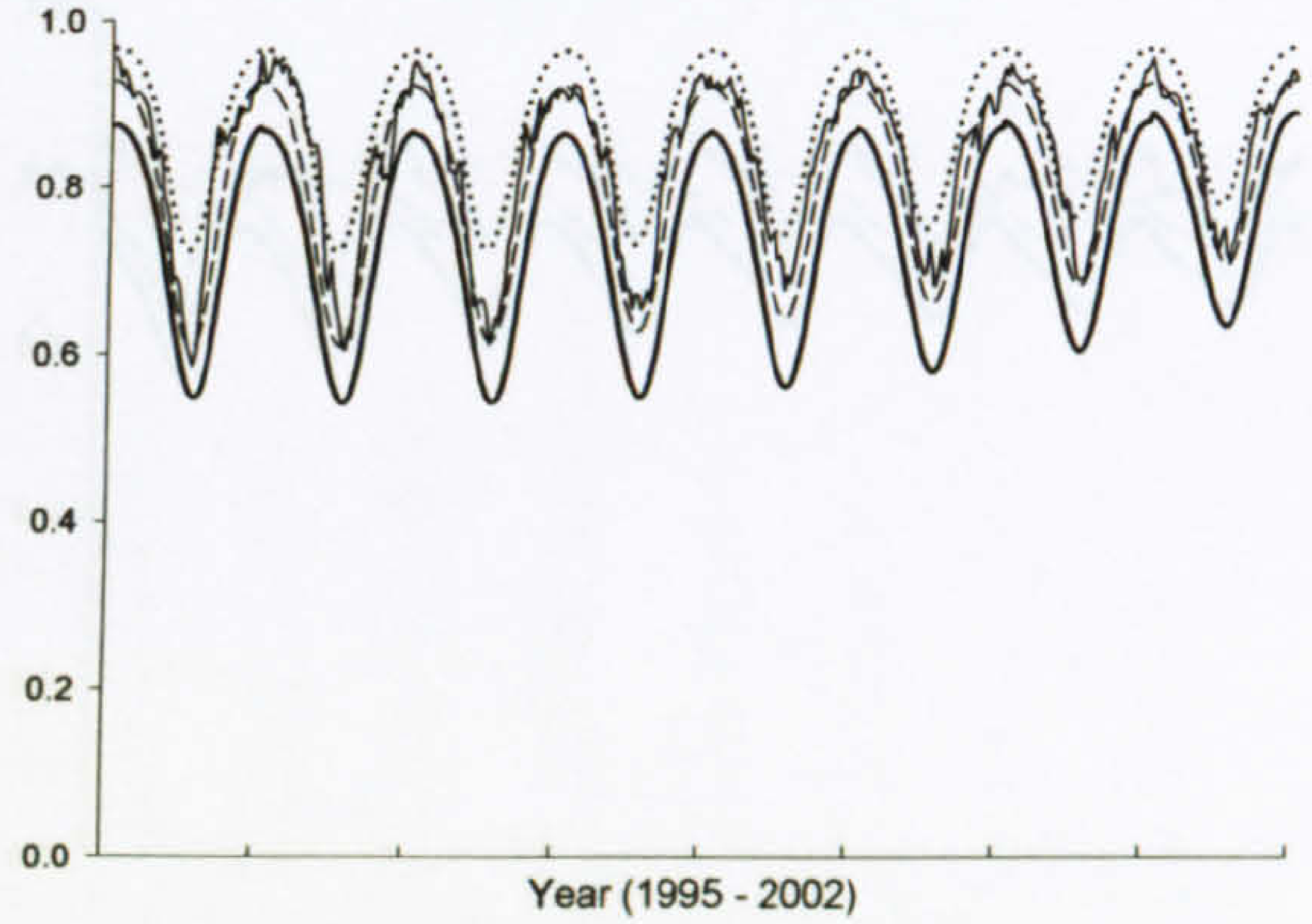

Figure 5.3.6. Robin

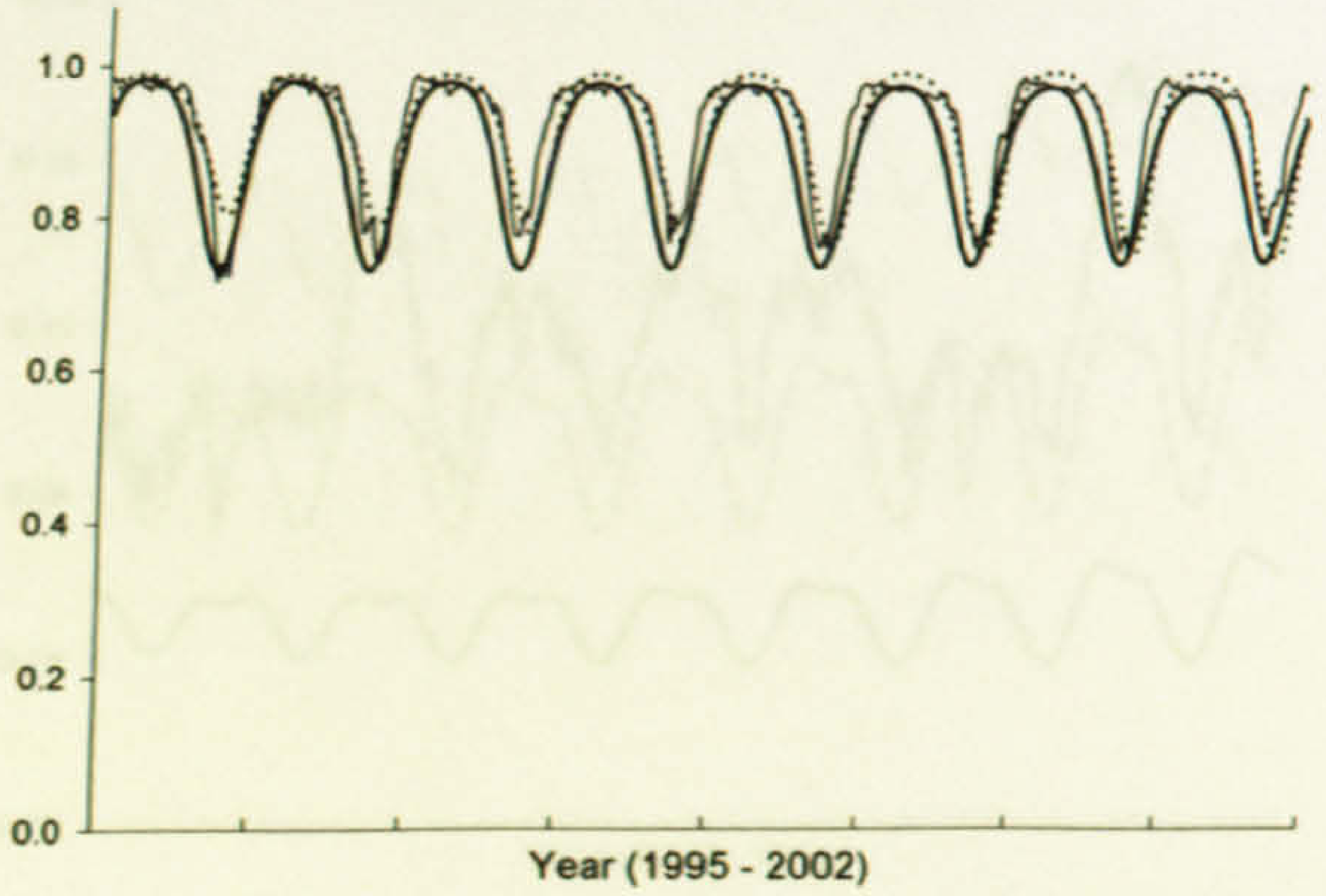

Figure 5.3.7. Blackbird

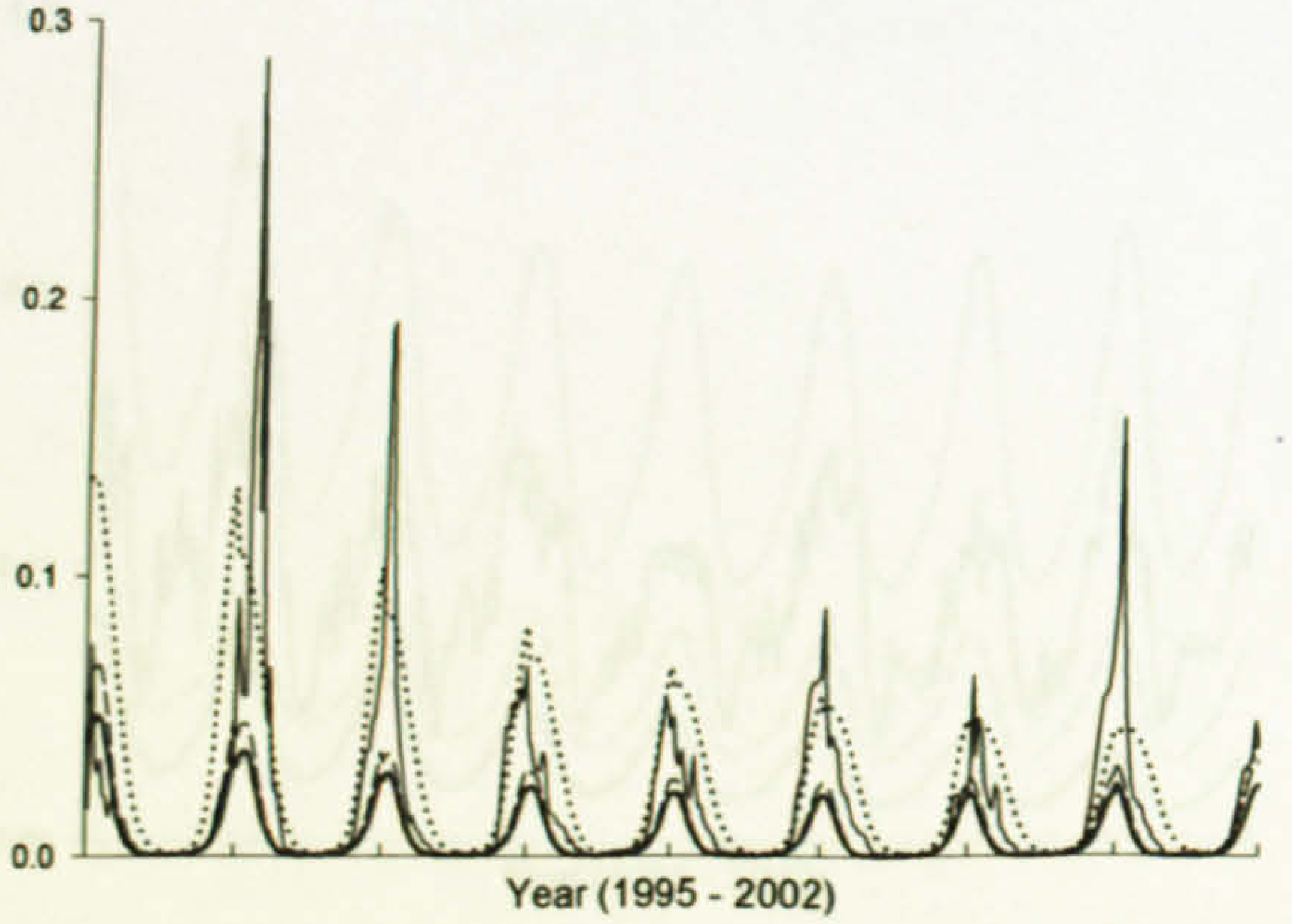

Figure 5.3.8. Fieldfare

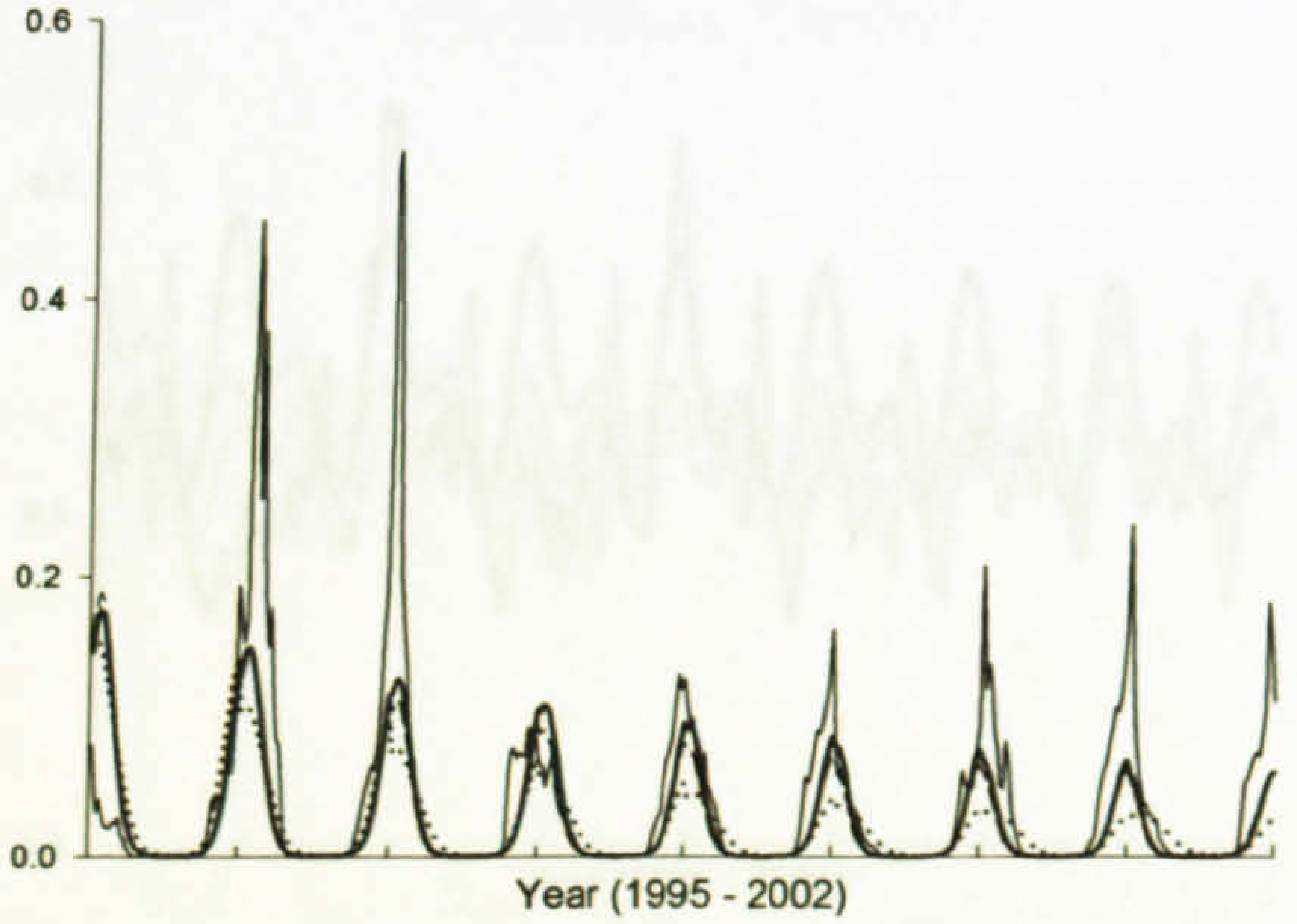

Figure 5.3.9. Redwing

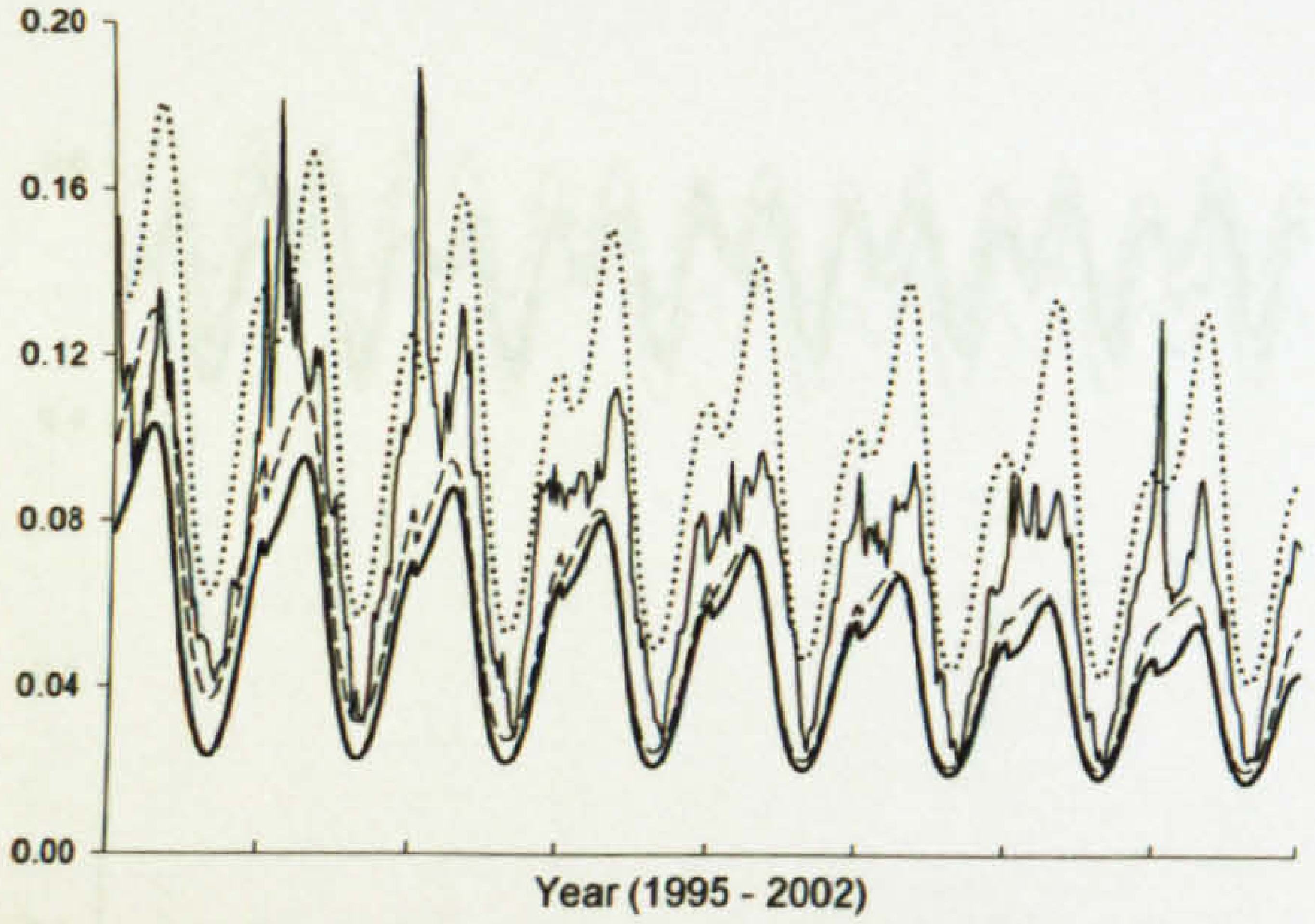

Figure 5.3.10. Mistle Thrush

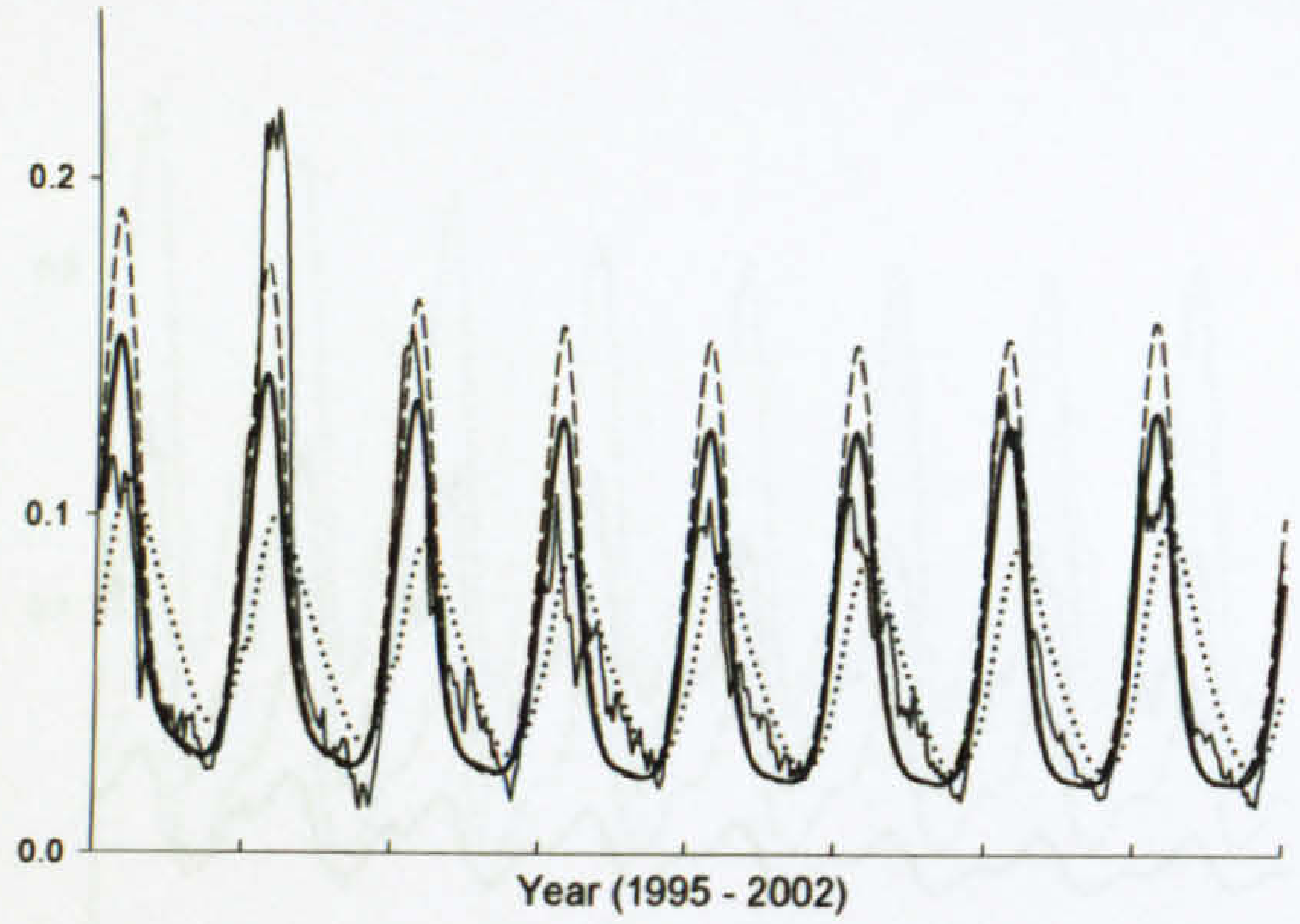

Figure 5.3.11. Blackcap

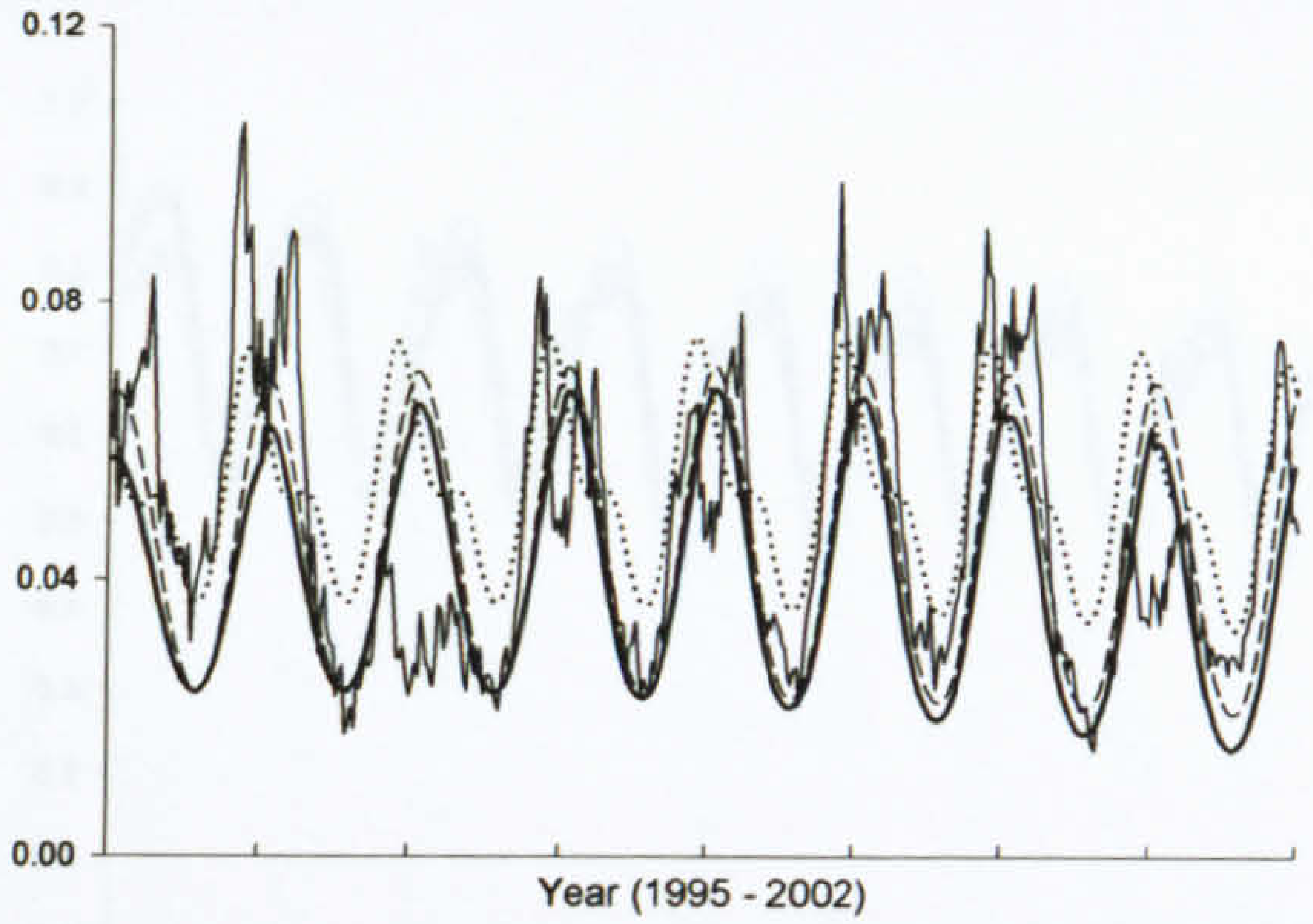

Figure 5.3.12. Goldcrest

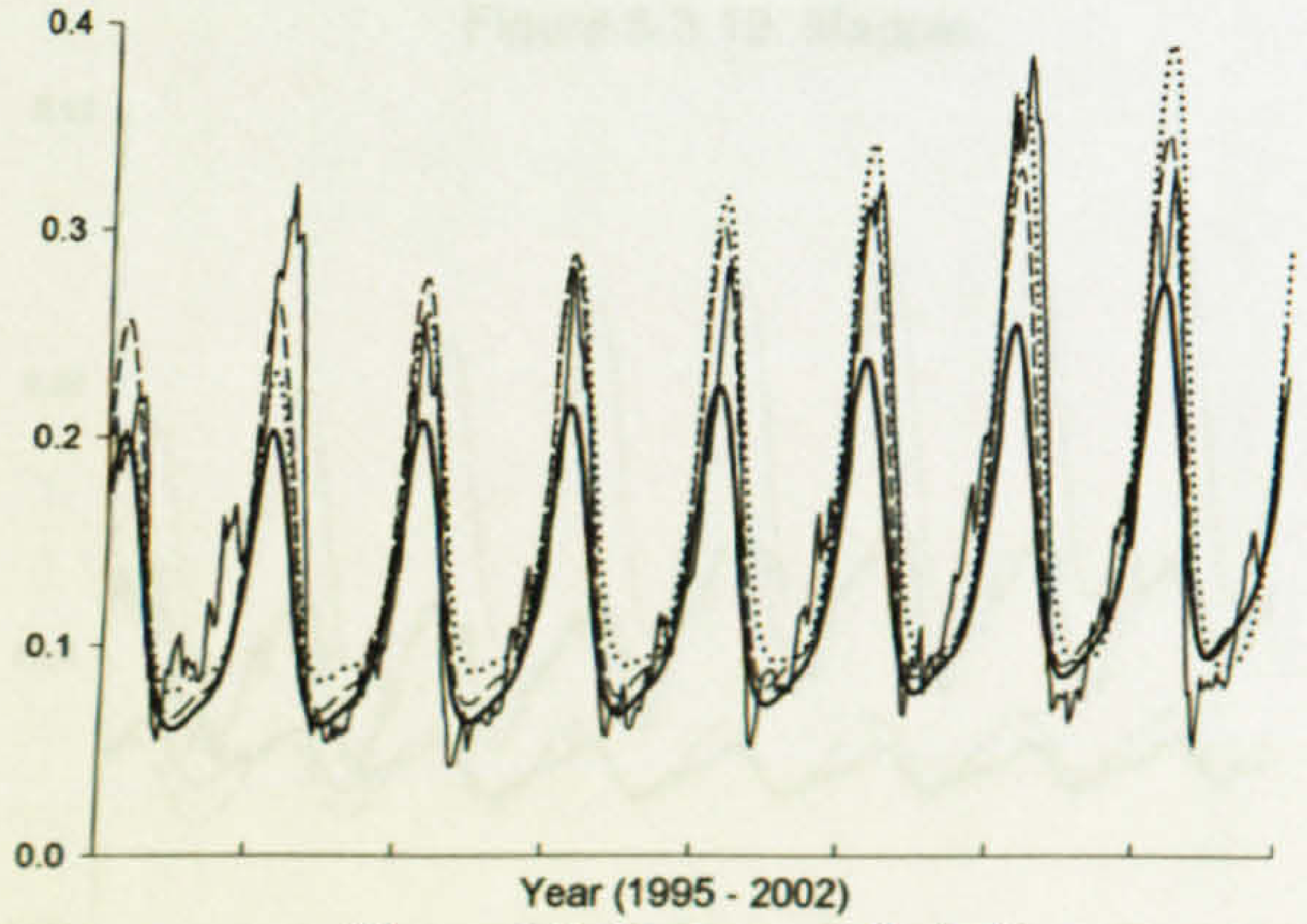

Figure 5.3.13. Long-tailed Tit

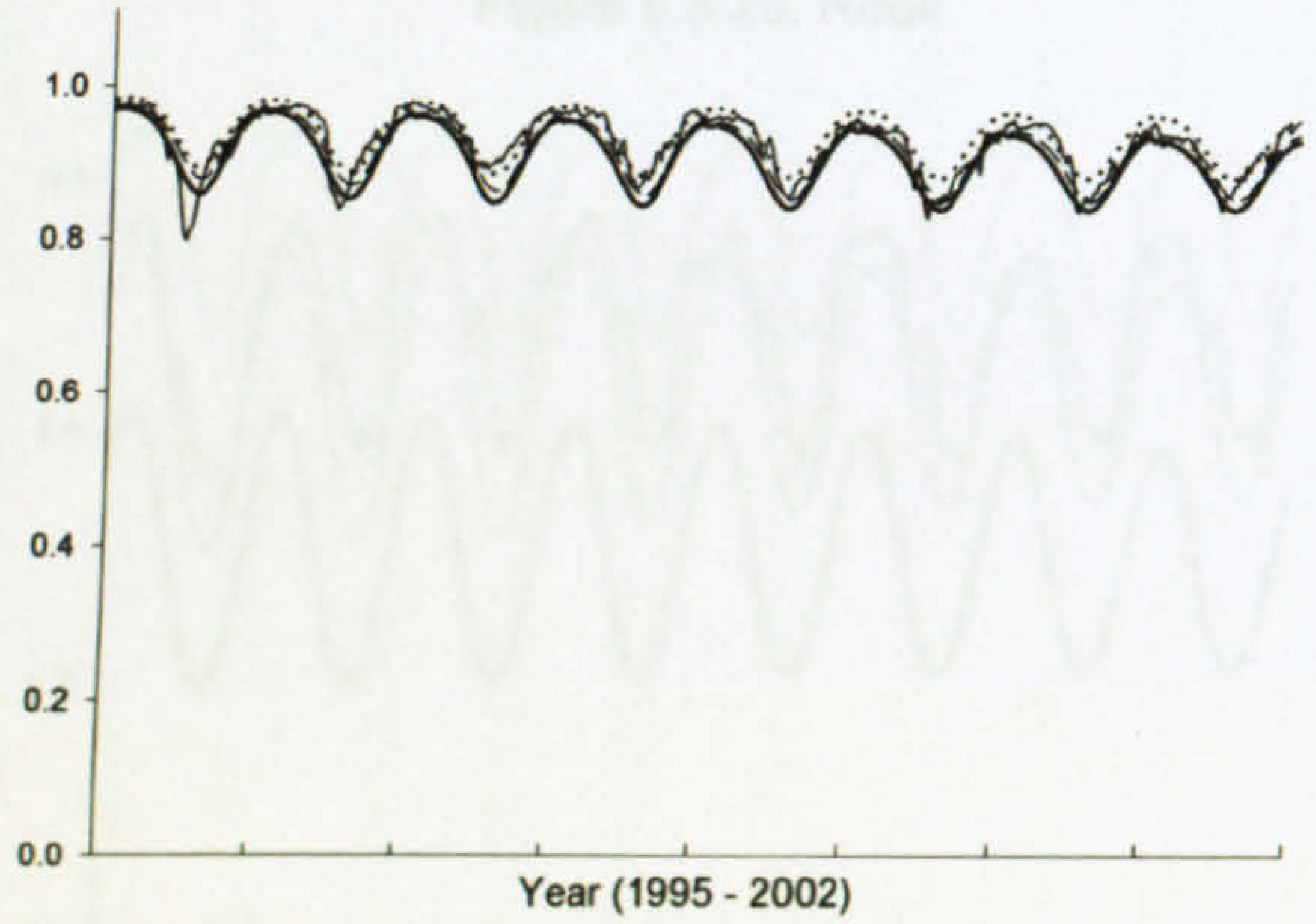

Figure 5.3.14. Blue Tit

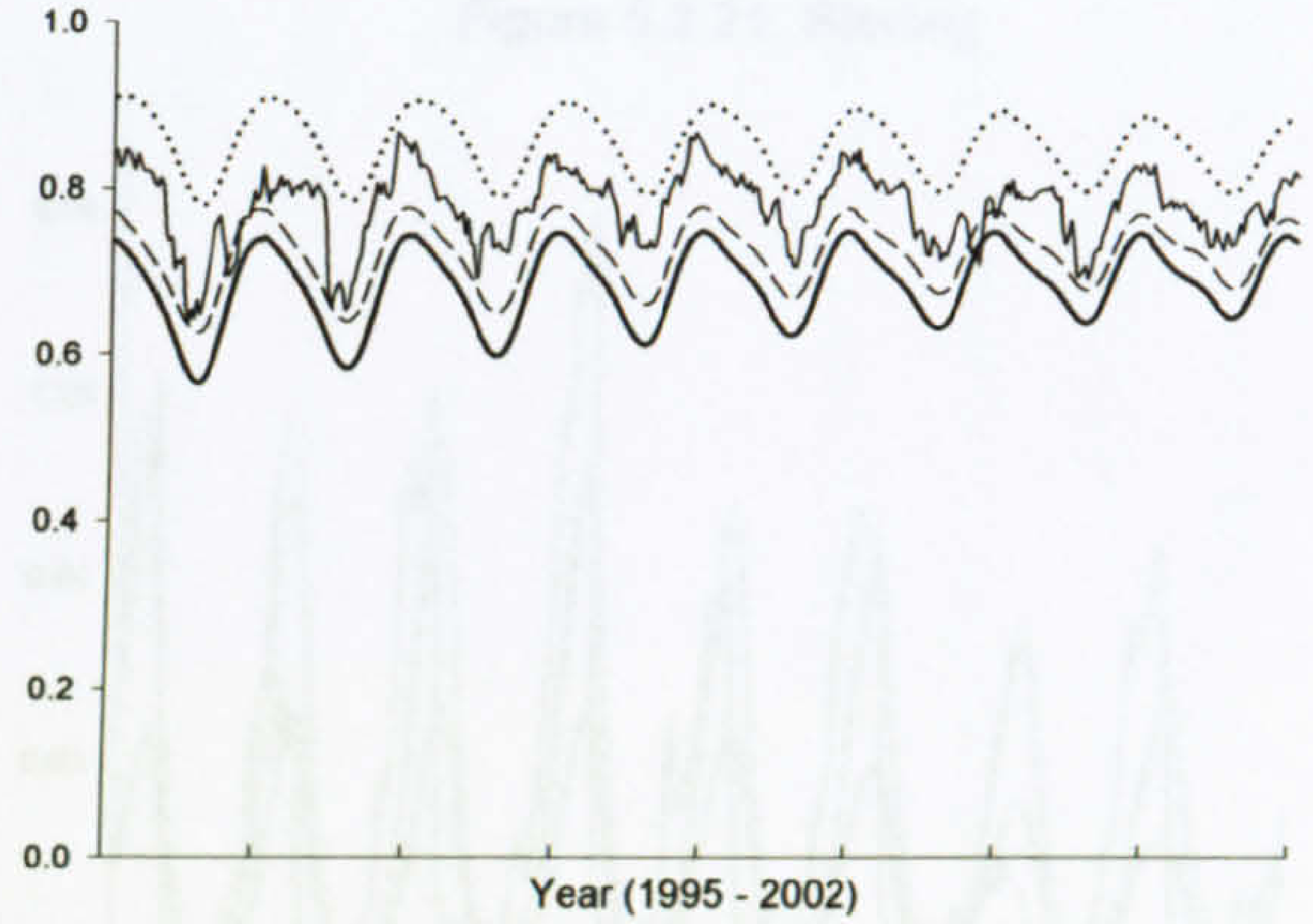

Figure 5.3.15. Great Tit

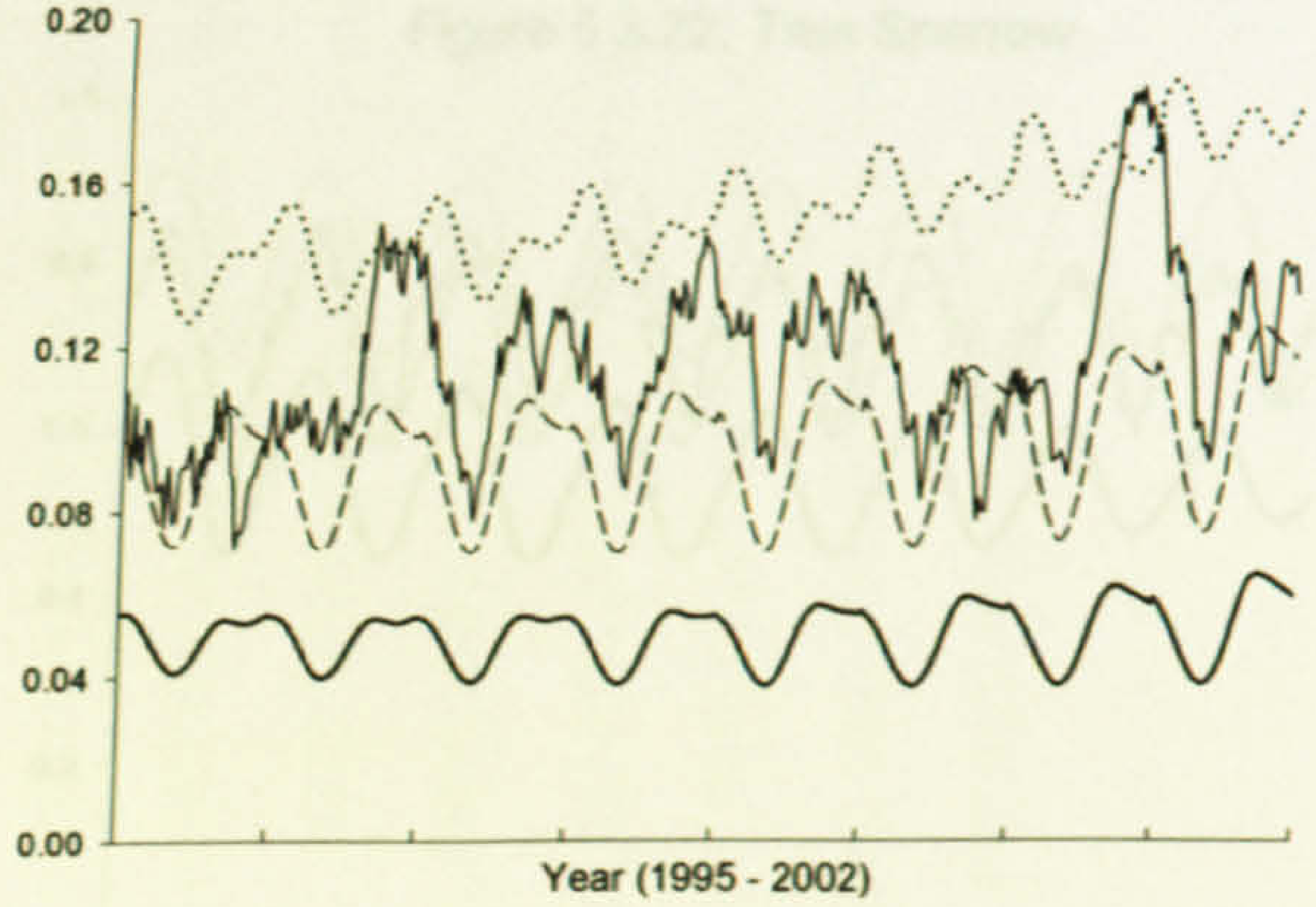

Figure 5.3.16. Nuthatch

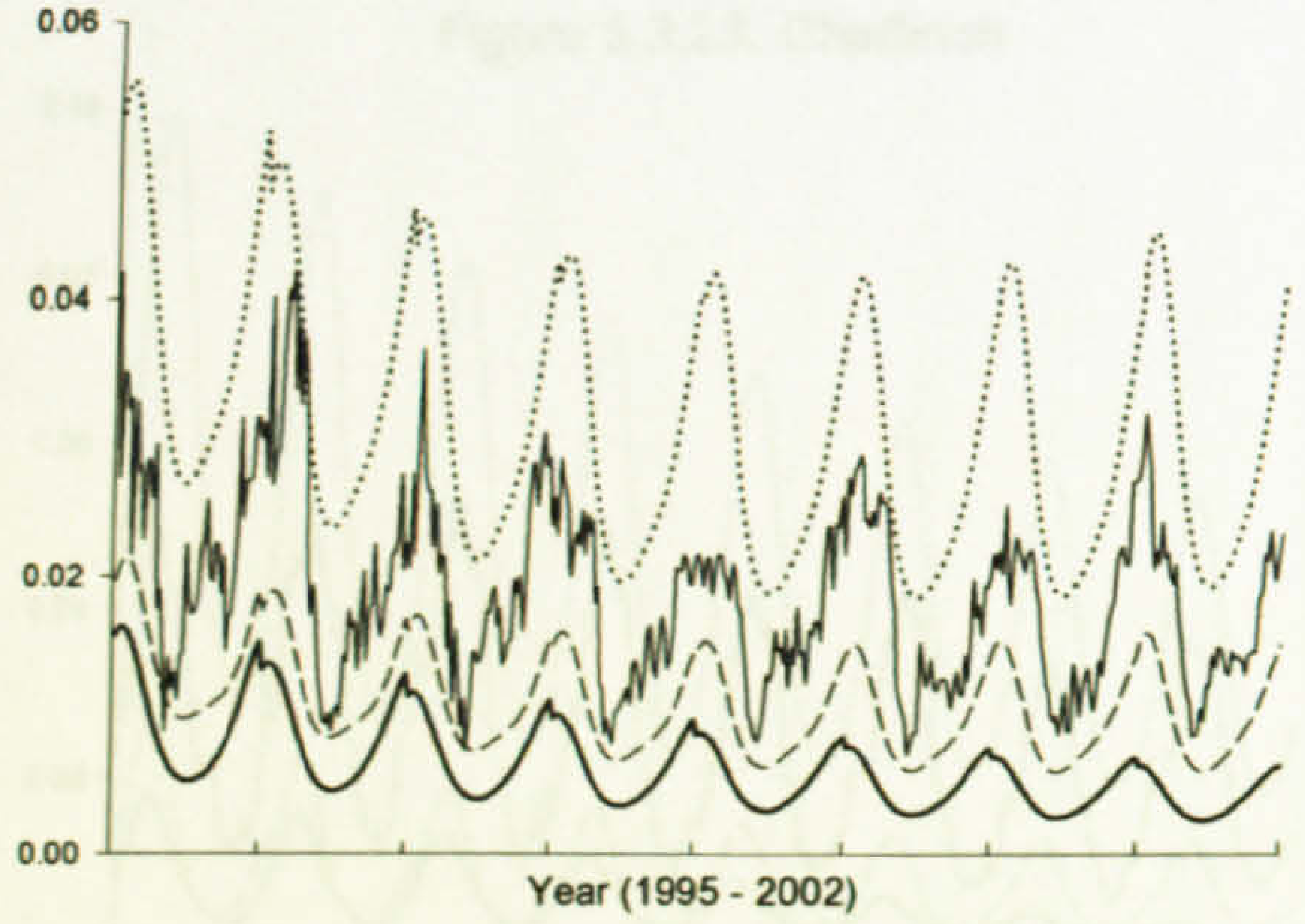

Figure 5.3.17. Treecreeper

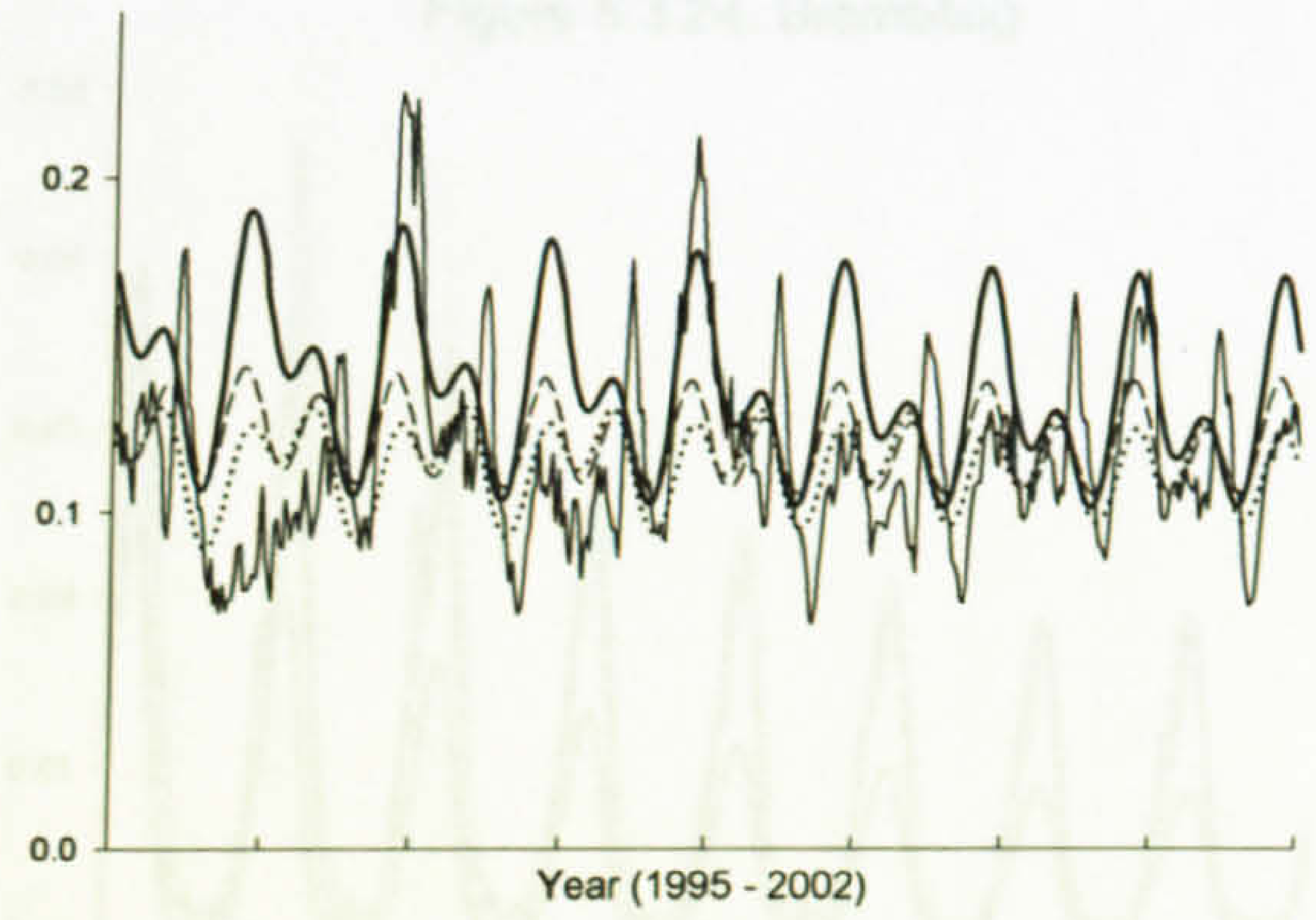

Figure 5.3.18. Jay

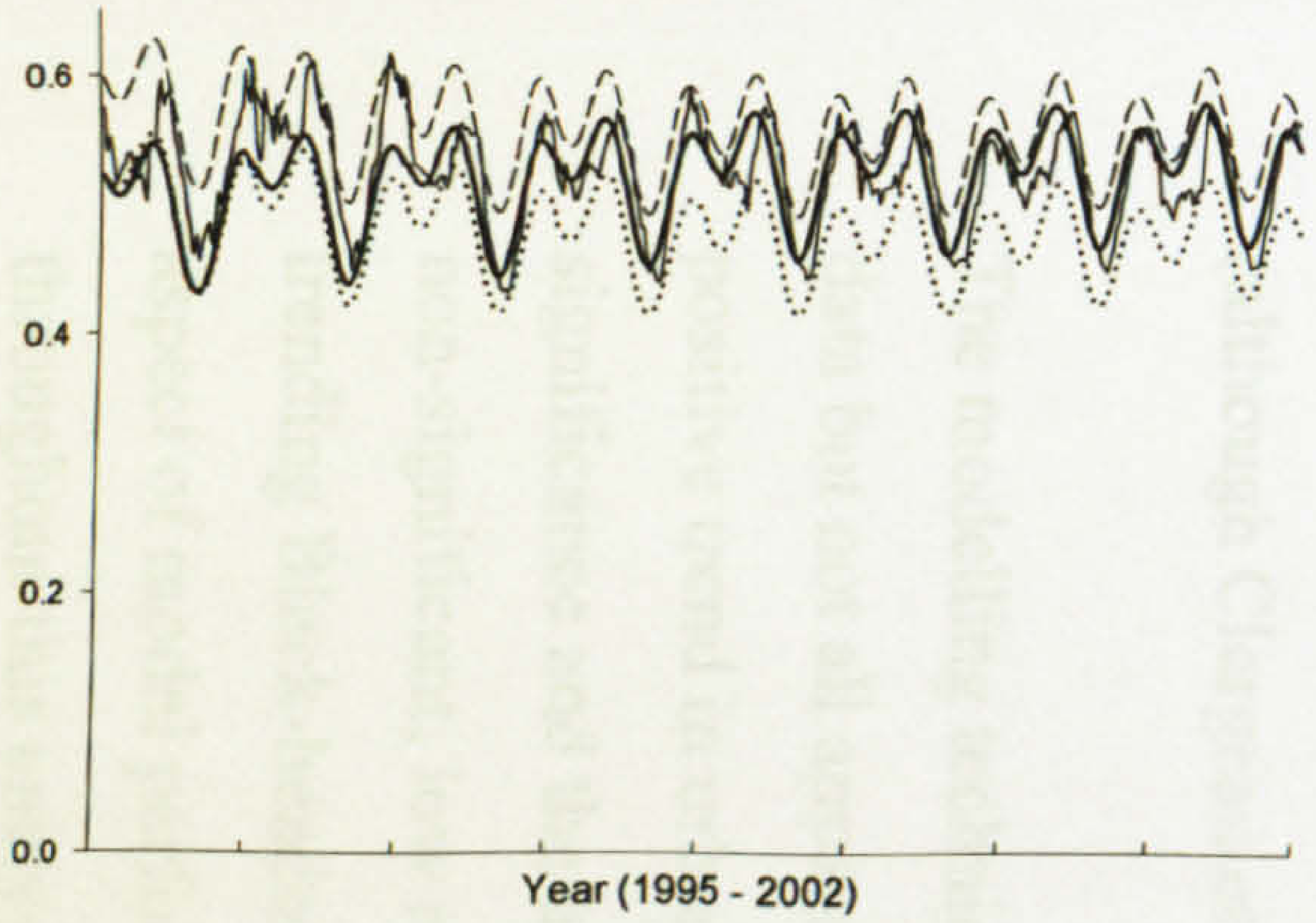

Figure 5.3.19. Magpie

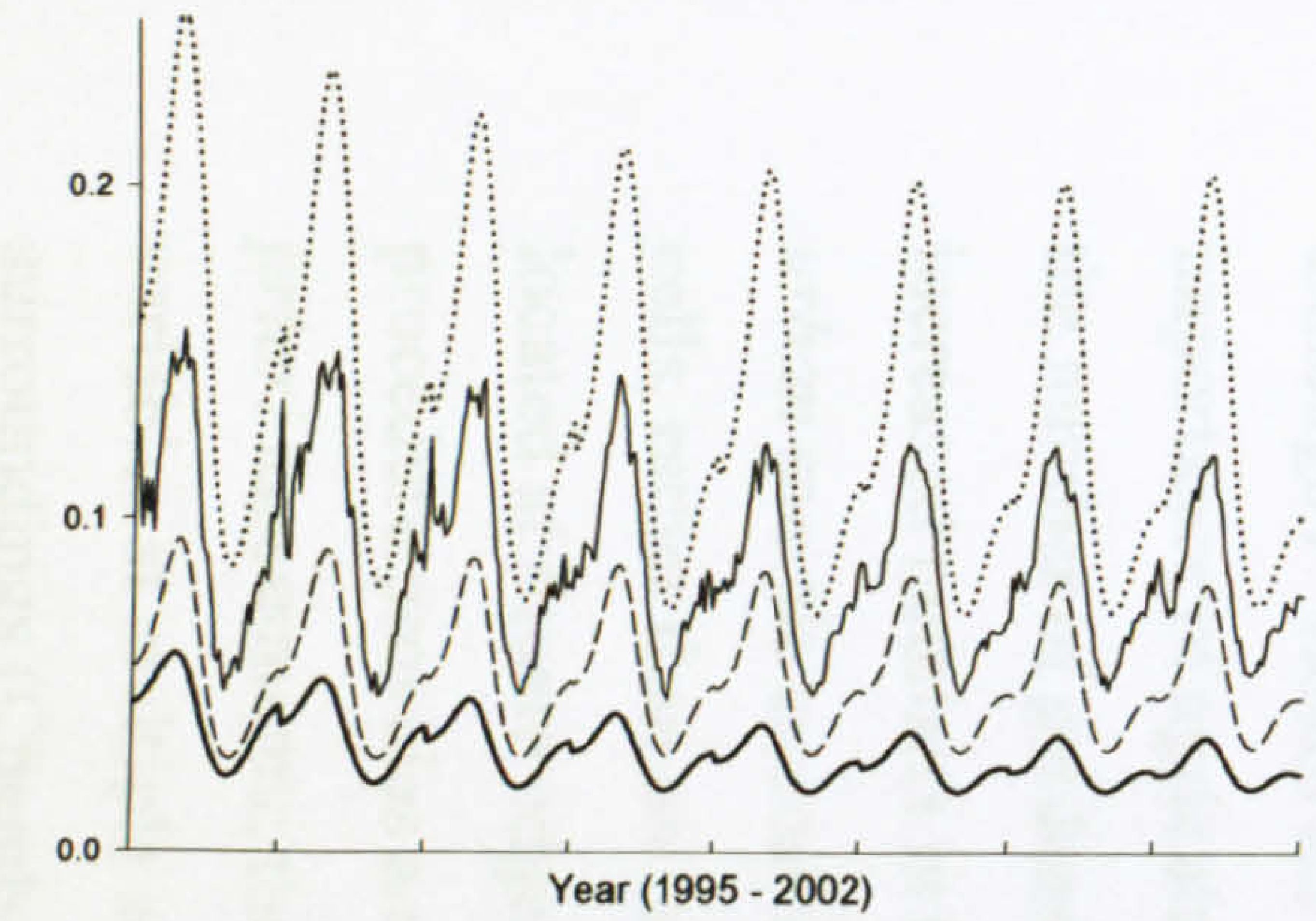

Figure 5.3.20. Rook

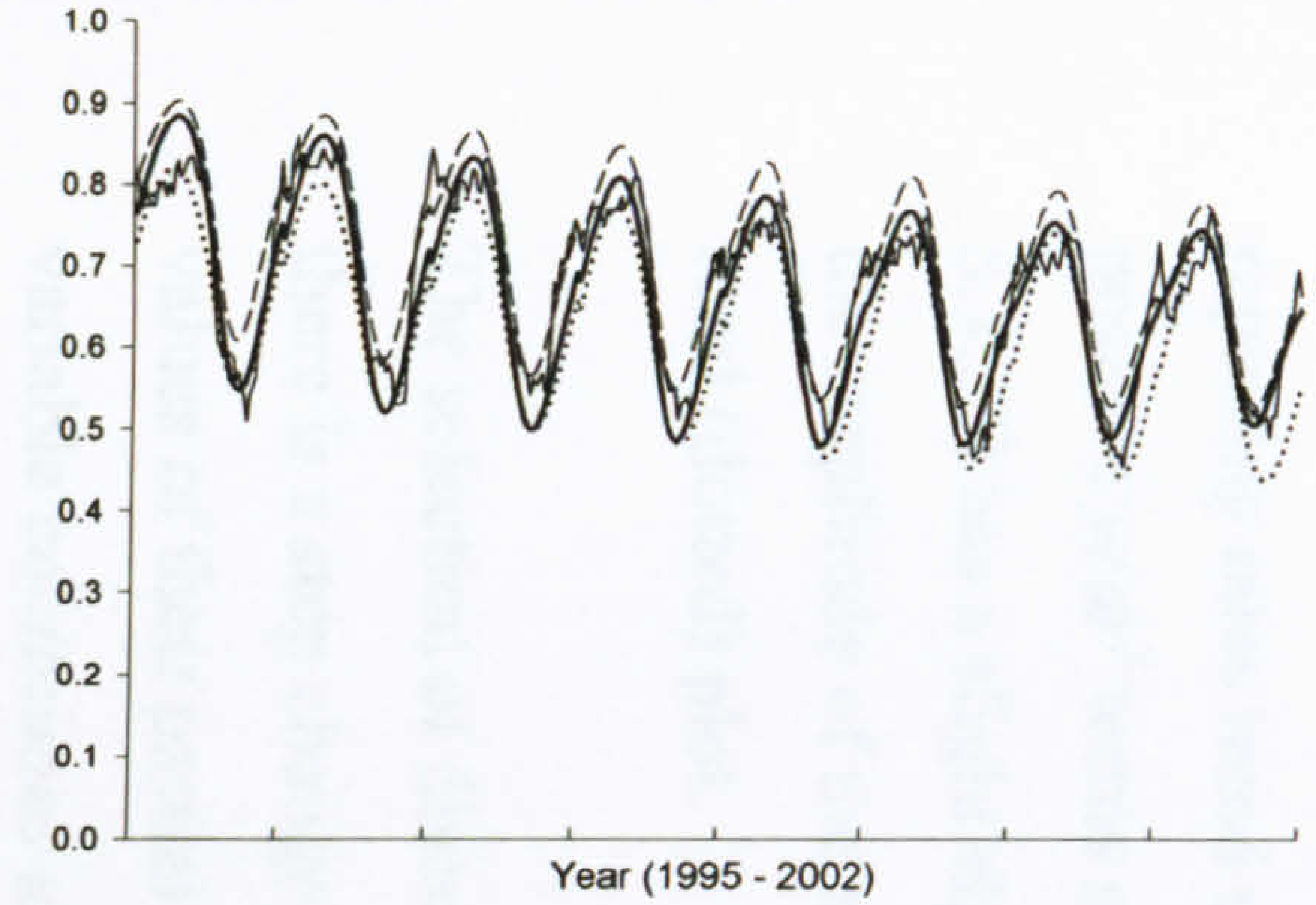

Figure 5.3.21. Starling

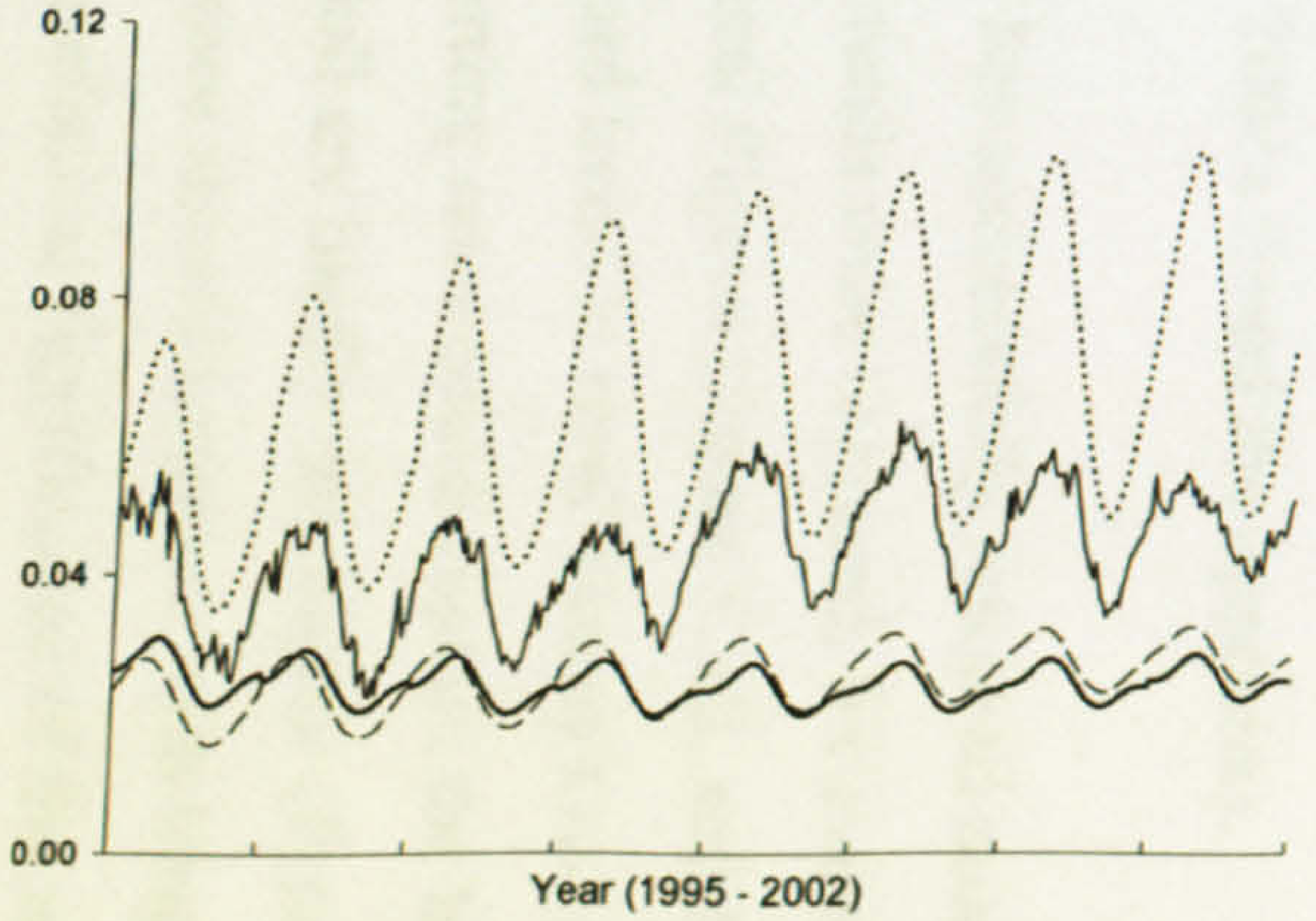

Figure 5.3.22. Tree Sparrow

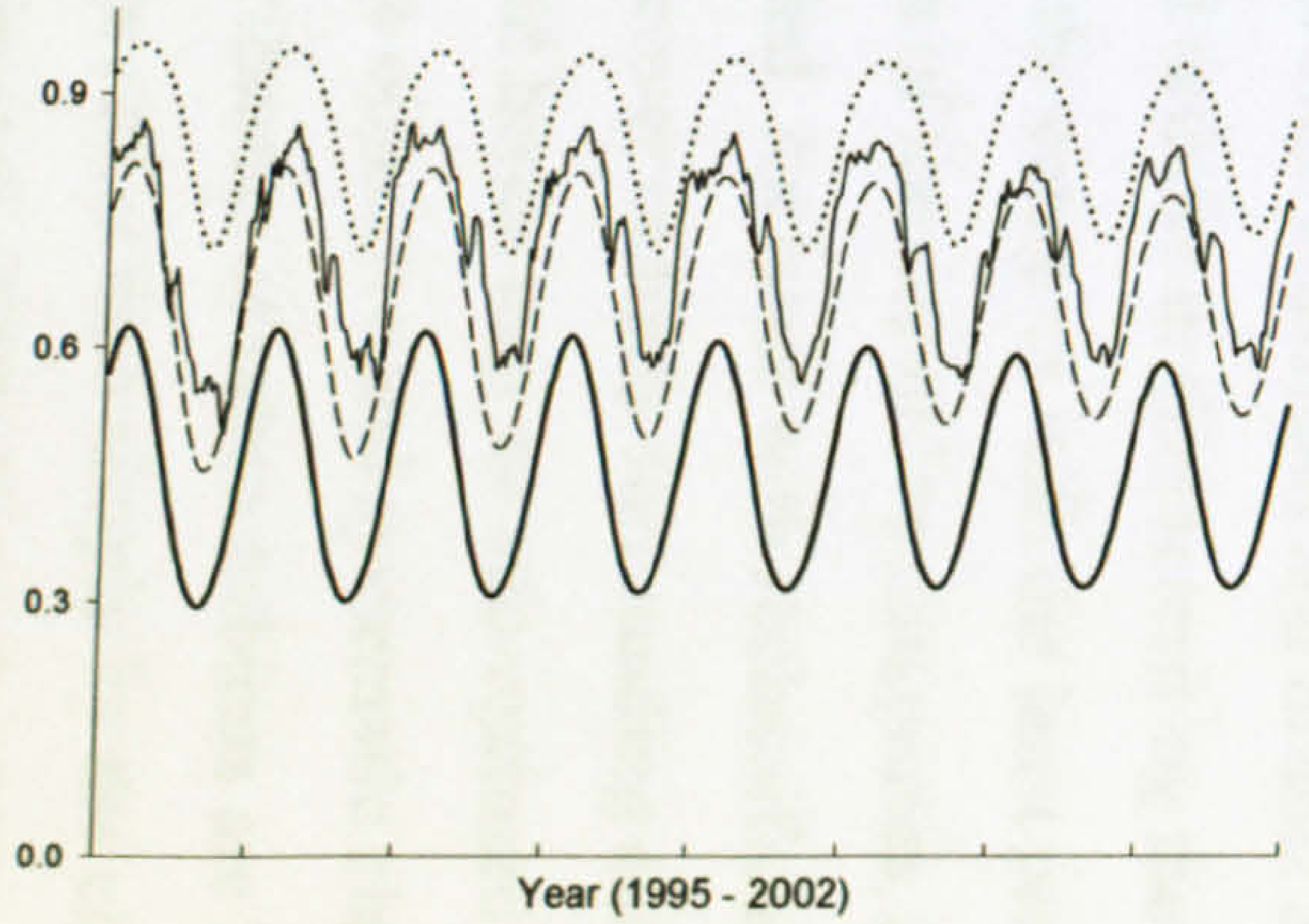

Figure 5.3.23. Chaffinch

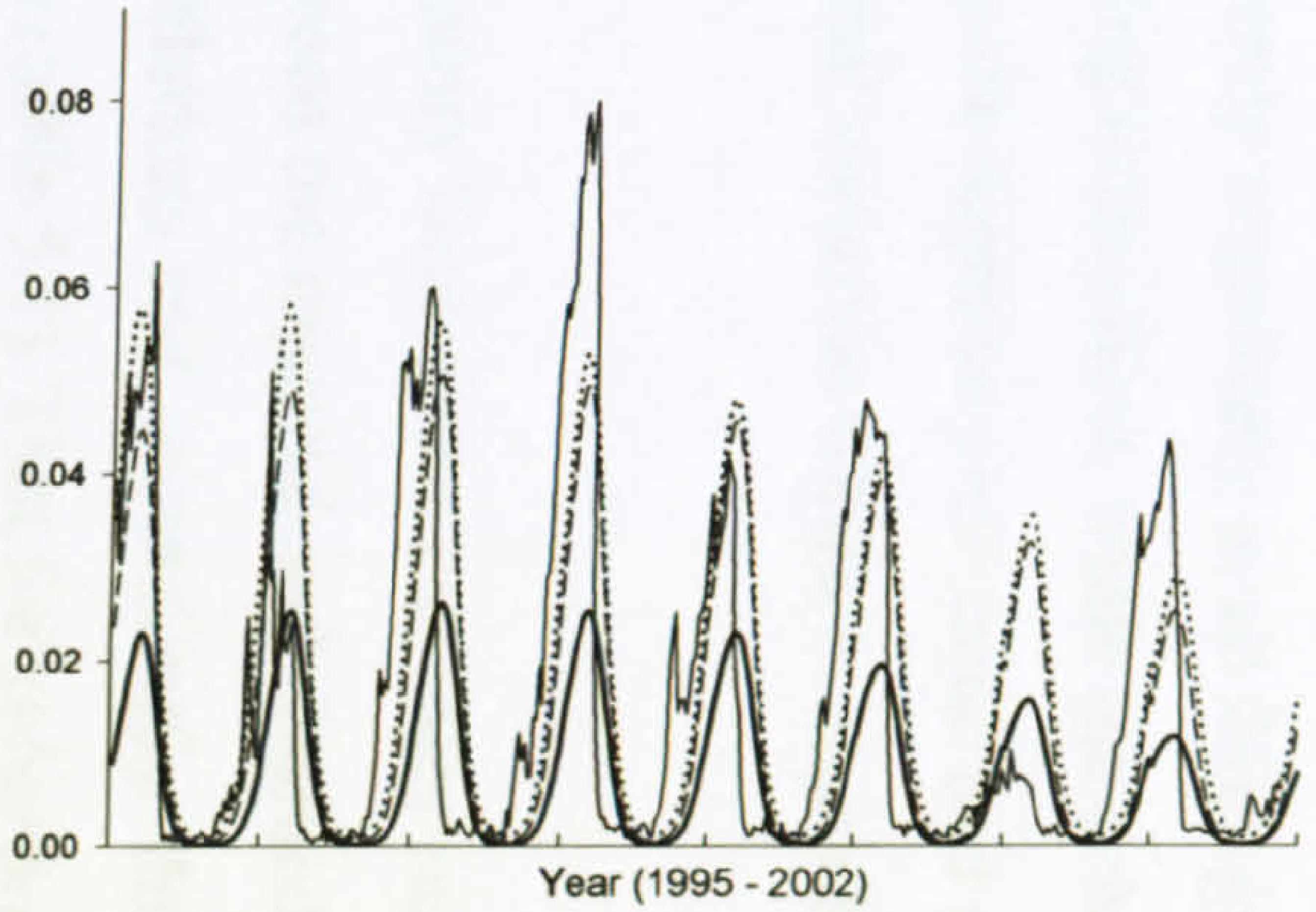

Figure 5.3.24. Brambling

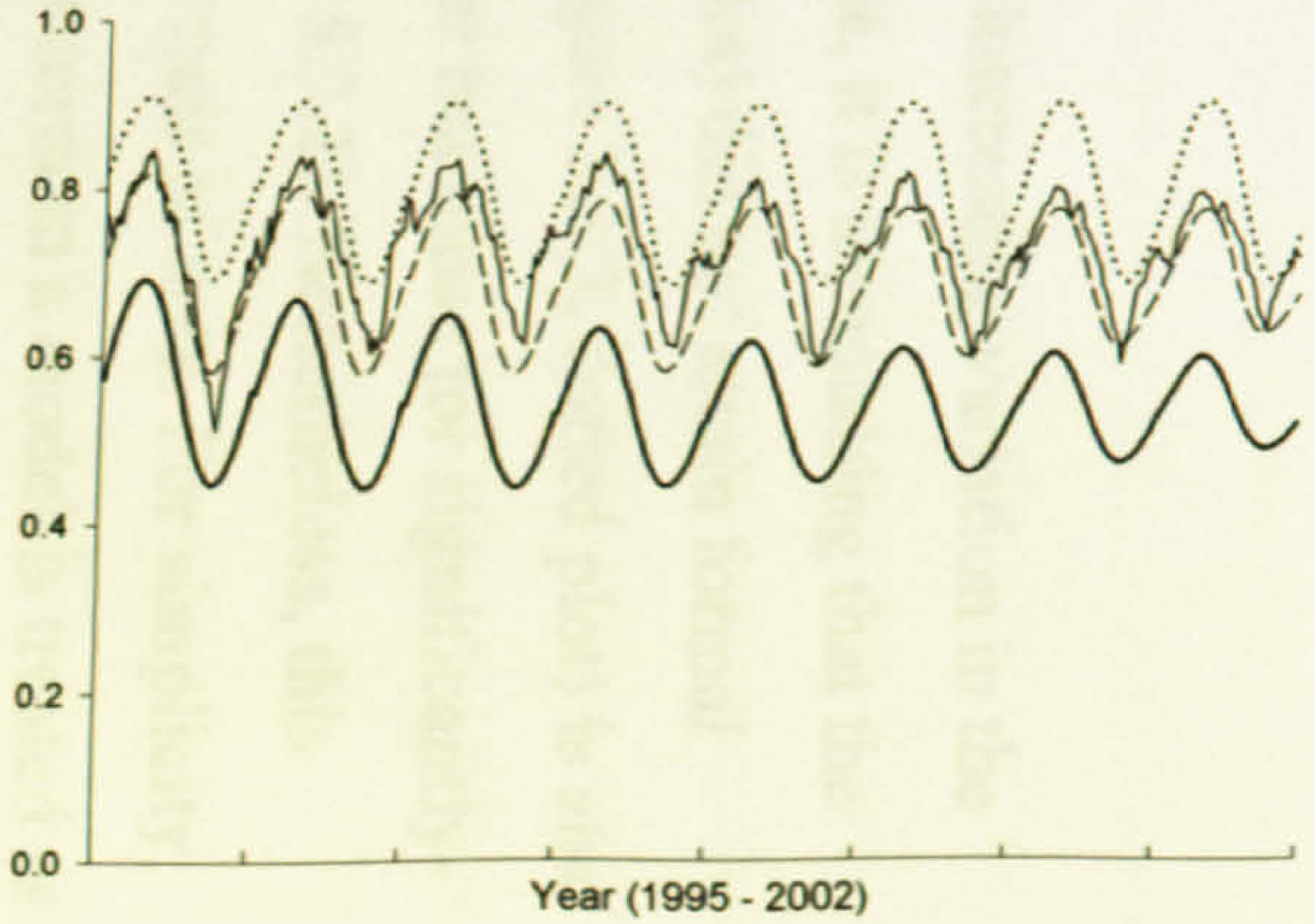

Figure 5.3.25. Greenfinch

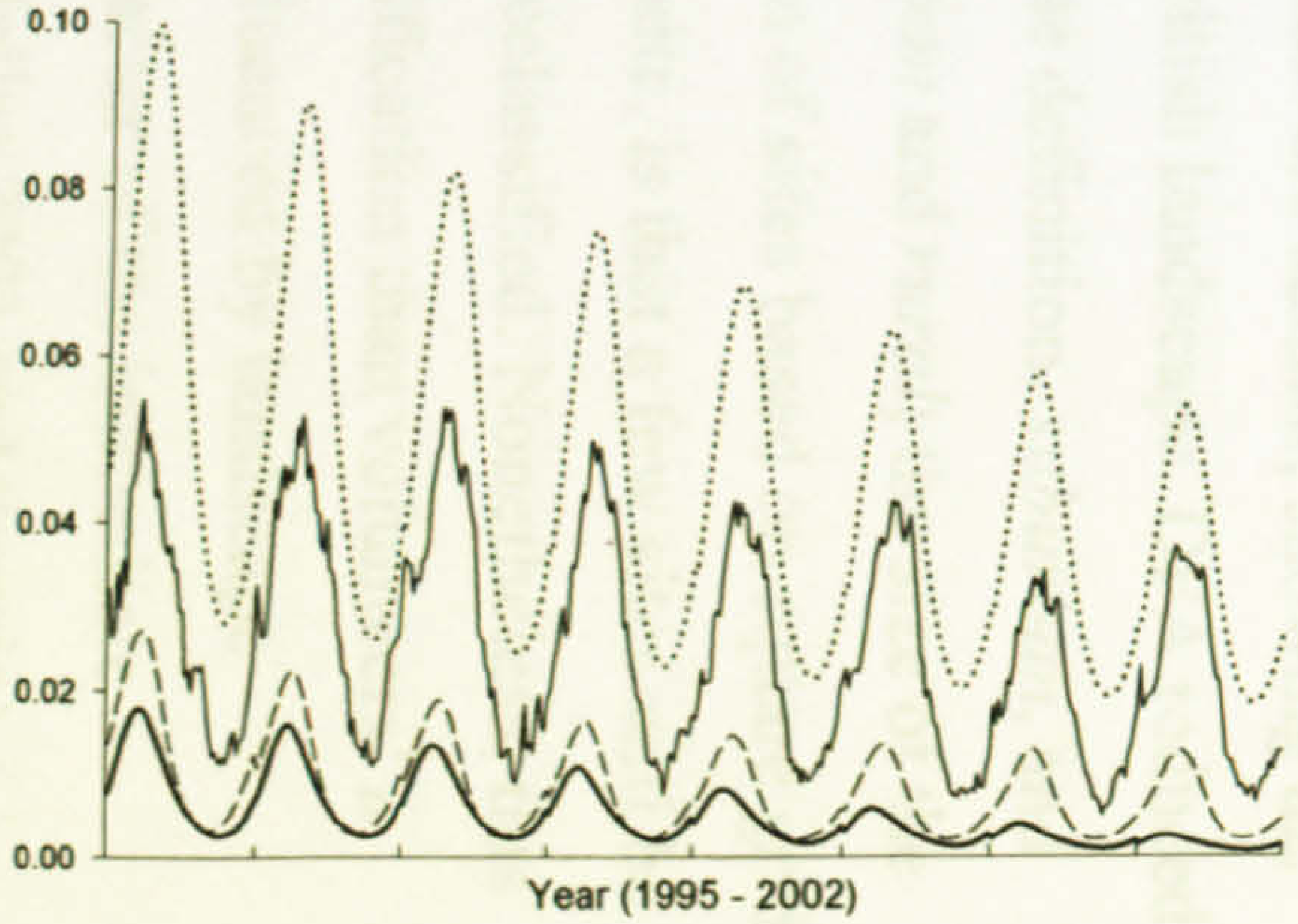

Figure 5.3.26. Yellowhammer

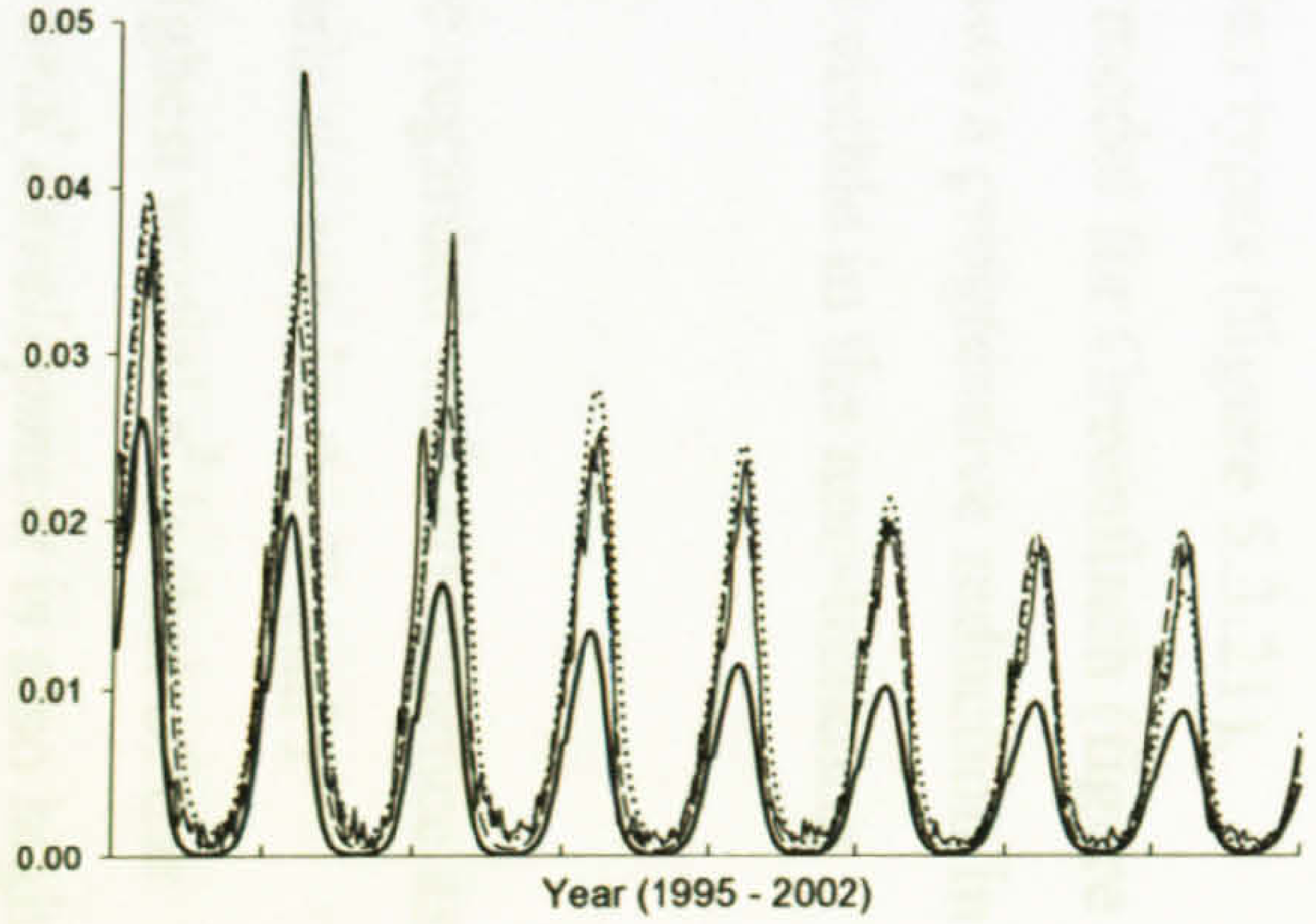

Figure 5.3.27. Reed Bunting

Wintering Fieldfare (figure 5.3.8) and Redwing (figure 5.3.9) show steadily decreasing trends in all three garden types. The positive *year*^{2} term is not significant for *urban* Blackcap (figure 5.3.11) whereas it is in the other two garden classes. Starling modelled reporting rates trend uniformly negatively in all three garden types (figure 5.3.21), positive *year*^{2} terms showing little effect, while the *urban* model for Greenfinch (figure 5.3.25) has a slight significant negative *year* trend and shows a progressive reduction in the amplitude of the seasonal variation which is much less visible in the non-trending rural (dotted) plot.

The selection of discriminatory land cover variables can be regarded with confidence as there is a step change between the rejected and retained variable sets in the F and *P* values of their partial correlations and, reassuringly, the highest partial r^2 is that of the variable *continuous urban* (table 5.1). That for *suburban/rural development* is also high, although r^2 values for *improved grassland* and *arable cereals* are similar, showing the importance of agricultural activity in characterising the British landscape. DFA reduced the number of gardens in the category with the least precise definition, *suburban*, and increased numbers in both of the definitive categories, *urban* and *rural*; the size of the *urban* sample almost tripled. An issue with reclassification of sites based on square grid cells, rather than on land cover radially surrounding each site, is that a few sites will be located at square edges and hence may be sub-optimally reclassified. Nonetheless, this procedure provides a more objective and systematic classification than volunteers' *a priori* assessments; the avifaunas of urban habitats are influenced by landscape variables at multiple scales rather than simply by the character of the immediate surroundings (Chamberlain et al. 2004; Hostetler 2001; Melles 2001 and therein) (although Clergeau et al. 2001a found the opposite).

The modelling technique has successfully resolved much interesting variation in the data but not all apparent trends were captured, for example, it is astonishing that the positive trend in urban Feral Pigeon (figure 5.3.2, solid plot) did not attain formal significance and the upward trend in rural Tawny Owl (figure 5.3.3, dotted plot) is also non-significant; low reporting rates could explain the latter but those for significantly-trending Black-headed Gull are hardly any higher (figure 5.3.1). Nonetheless, this aspect of model performance should improve with longer runs of data. For simplicity, throughout this analysis statistical significance of the *year* term in a model is treated as the primary indicator of a meaningful inter-year trend. However for some species, such as Woodpigeon and perhaps Robin, the overall trajectories of the modelled reporting rates are clearly modified or even dominated by *year*^{2} terms, showing the importance of looking beyond simple linear trends when assessing bird habitat usage time series.

Non-rural gardens clearly represent an important resource for birds, even if they are perhaps generally less hospitable to wild birds than *rural* ones. This analysis confirms the latter have generally higher reporting rates than either *suburban* or *urban* gardens for the majority of the species considered here, but also shows that for many of these species the difference is not substantial and that for a number of species, including Starling and House Sparrow (both red-listed as of high conservation concern in the UK (Gregory et al. 2002)), more surprisingly Jay which has been declining somewhat since 1970 (Eaton et al. 2005) and the winter-visiting Redwing, *urban* and *suburban* gardens have reporting rates similar to or even higher than those in *rural* gardens. This underlines the importance of these non-rural habitats for certain species. Nonetheless, there is little or no variation in the *urban* gardens independent of matching trends in non-urban sites; what is interesting, however, is that the number of species showing significant variation is substantially less in the *urban* sample, suggesting that urban gardens may be in some way buffered from changes occurring at non-urban sites. In general, agriculture is the dominant influence on the ecology of the non-urban habitats of most of the species considered here and British agriculture has undergone rapid change in recent years with considerable effects on populations of formerly abundant birds (e.g. Gibbons & Avery 2001; Siriwardena et al. 1998). In contrast, the typical configuration and management of the average British urban garden is probably relatively stable. Other plausible influences might include warmer temperatures, lower predation and supplementary food (Chapter 1) although this requires further investigation; other possible causes include lower urban sample sizes reducing statistical power of the models and generally lower urban bird diversity. The insectivorous Wren (figure 5.3.5), whose long-term general population trend is a moderate increase (Crick et al. 2004), seems to be an exception, its modelled reporting rate in *rural* gardens (non-significant *year* term) appears less influenced than those in *suburban* and *urban* (both significant *year* terms, table 5.1.b) by a general population decline after the cold winter of 1996/97.

There are some interesting differences in the height, timing and breadth of the modelled reporting rate peaks. The models predict Goldcrests (figure 5.3.12) arriving later in *suburban* (dashed) and *urban* (solid) gardens than in *rural* (dotted), but for Blackcaps (figure 5.3.11) the coincident *urban* (solid) and *suburban* (dashed) peaks are earlier than those of the *rural* (dotted) plots. The *rural* winter modelled reporting rate peak for Coal Tit (figure 5.2.10) is broader than those for *suburban* and *urban* gardens whereas that for Black-headed Gull (figure 5.3.1) is narrower. The models predict that *rural* Woodpigeons (figure 5.2.9) increase garden use later in spring and early summer than those in *suburban* and *urban* habitats; autumn departure time is the same in all three samples. The winter peak in modelled reporting rate for *rural* Sparrowhawks (figure 5.2.11) is very pronounced, in *suburban* and *urban* samples the winter peak is generally broader with a small peak in late winter.

Although very few formally significant positive trends were resolved by the models, this is not to say that all urban birds are exhibiting negative trends. By inspection of the modelled reporting rate plots, species such as Goldfinch (figure 5.2.8), Robin (figure 5.3.6) and Woodpigeon (figure 5.2.9), which have significant positive $year^2$ terms only, together with species such as Great Tit (figure 5.3.5), Long-tailed Tit (figure 5.3.13), Feral Pigeon (figure 5.3.2) and even the red-listed Bullfinch (figure 5.2.7) for which neither term is significant, have modelled reporting rate trajectories that show evidence of positive change in the *urban* garden sample. At the time of this analysis, none of these changes could be expressed mathematically as simple trends, however GBW is ongoing and longer runs of data may well improve this.

Even with only eight years' data, modelling GBW reporting rates in this way provides far more information than can be covered in one thesis chapter and potentially sheds light on many conservation issues. As one example, many observers and campaigners cite increasing levels of corvid and/or raptor predation as one possible cause of recent declines in urban bird numbers despite their not affecting populations in the wider countryside (Thomson et al. 1998). This appears still less plausible from the modelled GBW data as not only is the urban reporting rate trajectory for Sparrowhawk (figure 5.2.11) clearly negative towards the end of the period considered (despite very low reporting rates the negative $year^2$ term is only marginally non-significant at $P=0.07$) but the model for Magpie (figure 5.3.19) has no significant *year* or $year^2$ terms in the *urban* sample over this period (despite the species undoubtedly becoming more urbanised over the previous 30 years in many British cities) and has significant negative *year* terms in the non-urban models.

Of the five species with significant *year* trends in both *urban* and *rural* gardens and significant inter-year variation in linear trends between the three garden classes over the period, the two red-listed species are trending more negatively in urban than in *rural* gardens. This may surprise those who consider built habitats to be refuges for the commensal House Sparrow and the garden-loving Song Thrush. Perhaps equally surprising is the less negative *urban* trend for the amber-listed Dunnock, a classic suburban and large-garden species that is largely insectivorous. However, in Sheffield (pers. obs) they are adapting with notable success to urban habitats.

Negative *year* and non-significant $year^2$ terms and visible downward trajectories in urban modelled reporting rate plots for Crows (figure 5.2.5) and Jackdaw (figure 5.2.4) suggest that the ongoing urbanisation of corvids may not be proceeding as implacably as many observers believe; these are both designated 'pest' species, controlled in the UK under General Licences (DEFRA 2004b), so their population trends are of economic as well as conservation interest.

5.4. Conclusion

Urban garden reporting rates provide an effective monitoring tool for the wild birds of this important and perhaps increasingly significant habitat and they are amenable to formal mathematical modelling from which inter-year trends can be examined and tested for significance. The divergence of urban and non-urban modelled reporting rate trajectories for some species of conservation concern and/or economic interest suggests the urban population ecology of these species would repay further investigation and that longer time series of GBW data are well worth collecting.

6. Composite trends in urban garden bird reporting rates

Abstract

In the light of recent upturns in wild bird populations in agricultural habitats due to successful habitat conservation and restoration, a composite index of bird reporting rates in urban gardens over a comparable time period was calculated and examined for any similar recent upward trajectory. None was found and in fact the composite reporting rate index for urban gardens failed to track recent upward trends in the same index for non-urban gardens. This suggested that for this subset of species at least, urban garden birds had not so far benefited from the conservation actions that had successfully arrested the declines of non-urban populations.

6.1. Introduction

The disturbing declines of some British bird species in the past 25 years have to some extent been arrested in the wider countryside by more sympathetic management of agricultural land since the mid 1990s. Most notably, the U.K. government's index of farmland bird populations has increased by 5% between 1998 and 2002 (DEFRA 2004c). Wintering birds in particular are helped by specific agri-environment options such as Countryside Stewardship (Peach et al. 2001), game cover (Parish & Sotherton 2004) and hedgerow improvement (Norton et al. 2004). However, it is questionable whether the success of such measures is reflected in the bird populations of urban areas, which occupy the second largest proportion of Britain's land area after agriculture and also support significant numbers of birds of conservation importance (Gregory & Baillie 1998). As discussed in previous chapters, private gardens are arguably the most important component of the available bird habitat in urbanised areas (Gaston et al. in press) and greater numbers of birds than previously realised rely on them (Bland et al. 2004). In this chapter, the reporting rate trajectories of a suite of garden species are compared between urban and non-urban gardens and over a comparable timescale (1995 – 2002) to that of the 5% farmland bird index increase cited above.

6.2. Methods

Garden bird reporting rate data from the BTO/CJ Garden BirdWatch (GBW) project (Cannon 2000) were used to construct composite indices of weekly garden bird prevalence for urban and non-urban sites separately. The majority of species recorded by the GBW project are not typically urban, so for this comparison a subset of ten species was used to construct the index. The ten species chosen were those that had been previously identified by the UK government's Department for Environment, Food & Rural Affairs (DEFRA) as typical of towns and gardens and included in their provisional biodiversity index, designated T1 UK (DEFRA 2004a). These were Collared Dove, Robin, Blackbird, Song Thrush, Blue Tit, Magpie, Carrion Crow, Starling, House Sparrow and Greenfinch. As described in Chapter 5, recorders' subjective classifications of their gardens as 'urban', 'suburban' or 'rural' were used as the training set in a discriminant function analysis that objectively re-classified sites according to the land cover within their 1km grid square using NERC Centre for Ecology & Hydrology Land Cover Map 2000 data (Fuller et al. 2002). For each of the resulting three sets of re-classified gardens (Chapter 5), geometric means of the weekly reporting rates for the ten provisional index species were calculated to produce the basic weekly index values (Gregory et al. 2003; Newson et al. 2004). These means were also averaged over each of the four 13 week quarters of each of the eight years, in order to examine seasonal variation.

6.3. Results

Figure 6.1.a shows the composite reporting rate indices for rural, suburban and urban gardens from 1995 to 2002. Over the last four years of the period considered, the suburban (pink) and rural (blue) indices stabilised and even recovered somewhat from a low in 2000, while the urban (red) index continued to decrease, albeit more slowly. The difference between the urban and rural index values increased with time (figure 6.1.d). For the first quarter of the year (January – March, weeks 1-13) in particular, figure 6.1.c shows that in 2001 and 2002 this recovery was not apparent in the urban data. The average reporting rate trajectories for urban gardens in the other three quarters of the year (not shown) tracked those of rural and suburban gardens somewhat more accurately, but there was nonetheless a similar overall divergence between urban and non-urban indices in all four quarters over the survey period (figure 6.1.d, Spearman's rank-order correlation between values for weeks 1-13 and weeks 14-26, 27-39 and 40-52 respectively, $r_s = 0.76$ $P = 0.03$, $r_s = 0.76$ P = 0.03, $r_s = 0.79$ $P = 0.02$). Construction of an index for the same ten species using the reporting rates predicted by generalised linear modelling in chapter 5 showed a similar divergence (not shown).

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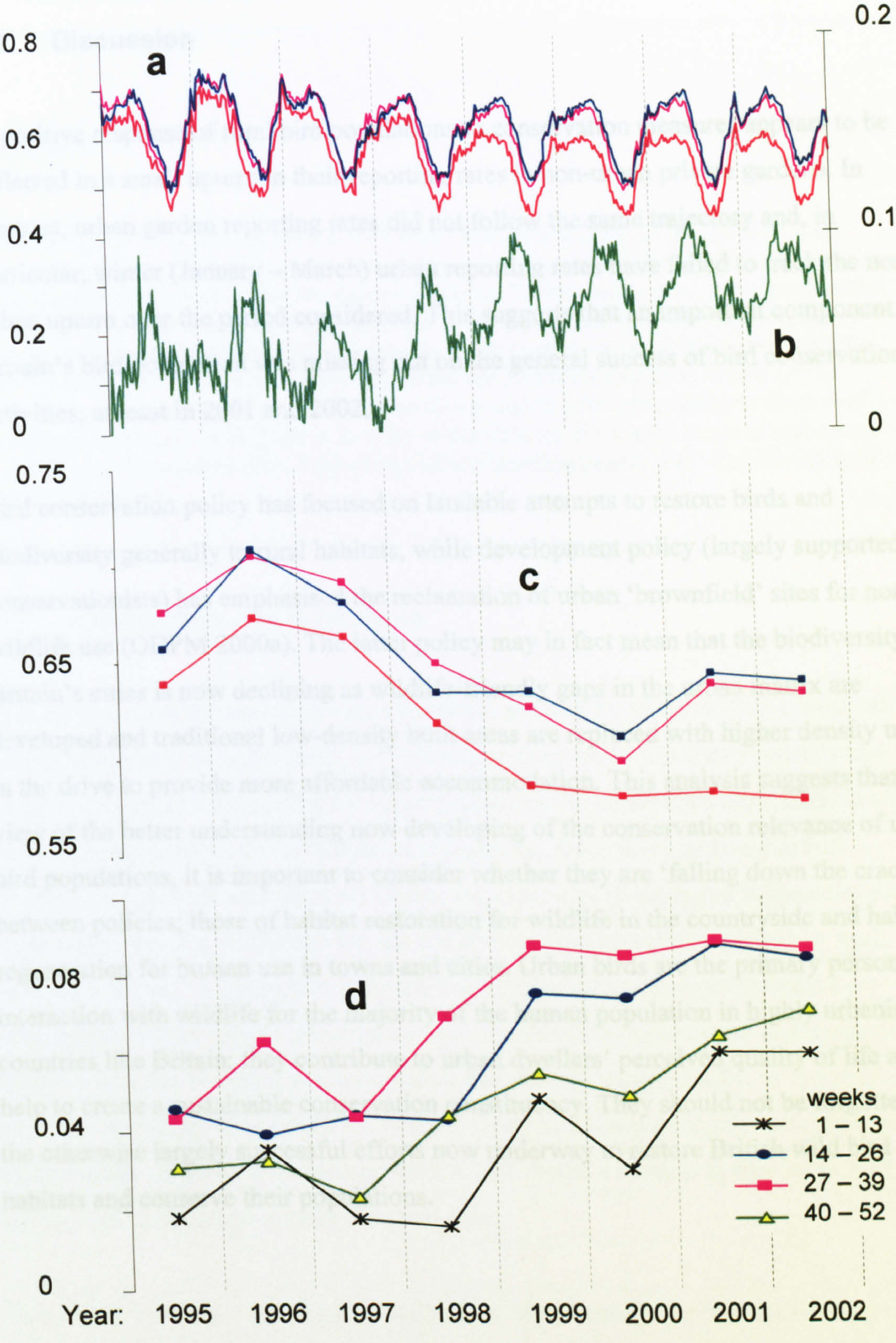


Figure 6.1.a. – d. Divergence between urban and non-urban composite garden reporting rate indices for Collared Dove, Robin, Blackbird, Song Thrush, Blue Tit, Magpie, Carrion Crow, Starling, House Sparrow and Greenfinch. **a.** composite index (geometric mean of weekly reporting rates) for the ten species in urban (red) suburban (pink) and rural (blue) gardens (left axis). **b.** difference between rural and urban index values (green, right axis). **c.** 13 week means of weekly composite index over weeks 1 – 13 (January – March) for urban (red) suburban (pink) and rural (blue) gardens. **d.** differences between 13 week mean values of rural and urban indices.

6.4. Discussion

A positive response of rural bird populations to conservation measures appears to be reflected in a small upturn in their reporting rates in non-urban private gardens. In contrast, urban garden reporting rates did not follow the same trajectory and, in particular, winter (January – March) urban reporting rates have failed to track the non-urban upturn over the period considered. This suggests that an important component of Britain's bird population was missing out on the general success of bird conservation activities, at least in 2001 and 2002.

Bird conservation policy has focused on laudable attempts to restore birds and biodiversity generally to rural habitats, while development policy (largely supported by conservationists) has emphasised the reclamation of urban 'brownfield' sites for non-wildlife use (ODPM 2000a). The latter policy may in fact mean that the biodiversity of Britain's cities is now declining as wildlife-friendly gaps in the urban matrix are developed and traditional low-density built areas are replaced with higher density units, in the drive to provide more affordable accommodation. This analysis suggests that in view of the better understanding now developing of the conservation relevance of urban bird populations, it is important to consider whether they are 'falling down the crack' between policies; those of habitat restoration for wildlife in the countryside and habitat regeneration for human use in towns and cities. Urban birds are the primary personal interaction with wildlife for the majority of the human population in highly urbanised countries like Britain; they contribute to urban dwellers' perceived quality of life and help to create a sustainable conservation constituency. They should not be forgotten in the otherwise largely successful efforts now underway to restore British wild bird habitats and conserve their populations.

7. The Breeding Birds of SK3388

Abstract

Breeding densities of birds in the SK3388 study area during 2002, 2003 and 2004 were censused by territory mapping; seven vocal species were successfully mapped and areas of breeding activity delineated for two colonial species. Seven species bred at higher densities than predicted from other urban censuses although Great Tit and Starling were scarcer, due to ongoing colonisation and decline respectively. A novel method of mapping core breeding activity zones was devised and implemented for the territorial species to enable spatial comparison of breeding activity and habitat. Compared to core urban habitats, the overall breeding bird density of SK3388 is low due to the absence of large numbers of commensal synanthropes. However it does support significant breeding populations of species typical of non-urban habitats.

7.1. Introduction and Objectives

Having examined the use of private residential gardens by wild birds on a national scale, particularly in urban areas, the remaining chapters of this thesis report some insights gained into the ecological opportunities and/or constraints applicable to wild birds in urban gardens through field investigations. Does this highly-modified environment provide sufficient ecological opportunities to support a representative, sustainable breeding avifauna? Or, are the ecological constraints imposed by such habitats reflected in a breeding avifauna that is depauperate and/or dependent on immigration? This chapter presents an investigation into the structure and dynamics of a highly urbanised breeding avifauna which had two objectives; firstly, to quantify the complete breeding bird population of a relatively large area of highly-urbanised habitat and secondly to derive a systematic measure of spatial variation in species richness, for subsequent comparison with habitat variables.

There have been very few field investigations of the breeding avifaunas of areas of homogenous, old-established residential urbanisation, because urban field ornithology to date has generally focused on either ecologically anomalous 'habitat islands' such as parks, or on whole-city atlases providing large-scale, summarised distribution and species data (Chapter 1). Even in the UK, until the advent of the BTO/JNCC/RSPB Breeding Bird Survey (BBS) in 1994 which covers all habitat types, no systematic national census covered urban habitats; volunteers for the BTO Common Birds Census, the national territory mapping survey and precursor of BBS, were asked not to include them in survey plots (J.H.Marchant pers. comm.). Hence, despite the success of isolated studies (e.g. Bland 1979) and a considerable body of work from eastern Europe, particularly Poland (e.g. Luniak 1994; Tomialojc 1998), little general interest has been taken in the birds of urban residential areas and general experience of urban bird census methods, particularly in the UK context, is lacking.

This chapter reports the results of a field study to quantify the breeding bird population of 100 ha of old-established urban residential habitat as accurately as possible and map its spatial distribution, using territory mapping. Changes in the community over three years are identified and discussed and the densities of the main species mapped are compared with those of other urban and non-urban habitats. A method of systematically delineating core zones of breeding activity based on territory maps derived from field data, is described and implemented in preparation for further analysis (chapter 8).

7.2. Methods

7.2.1. Study Site

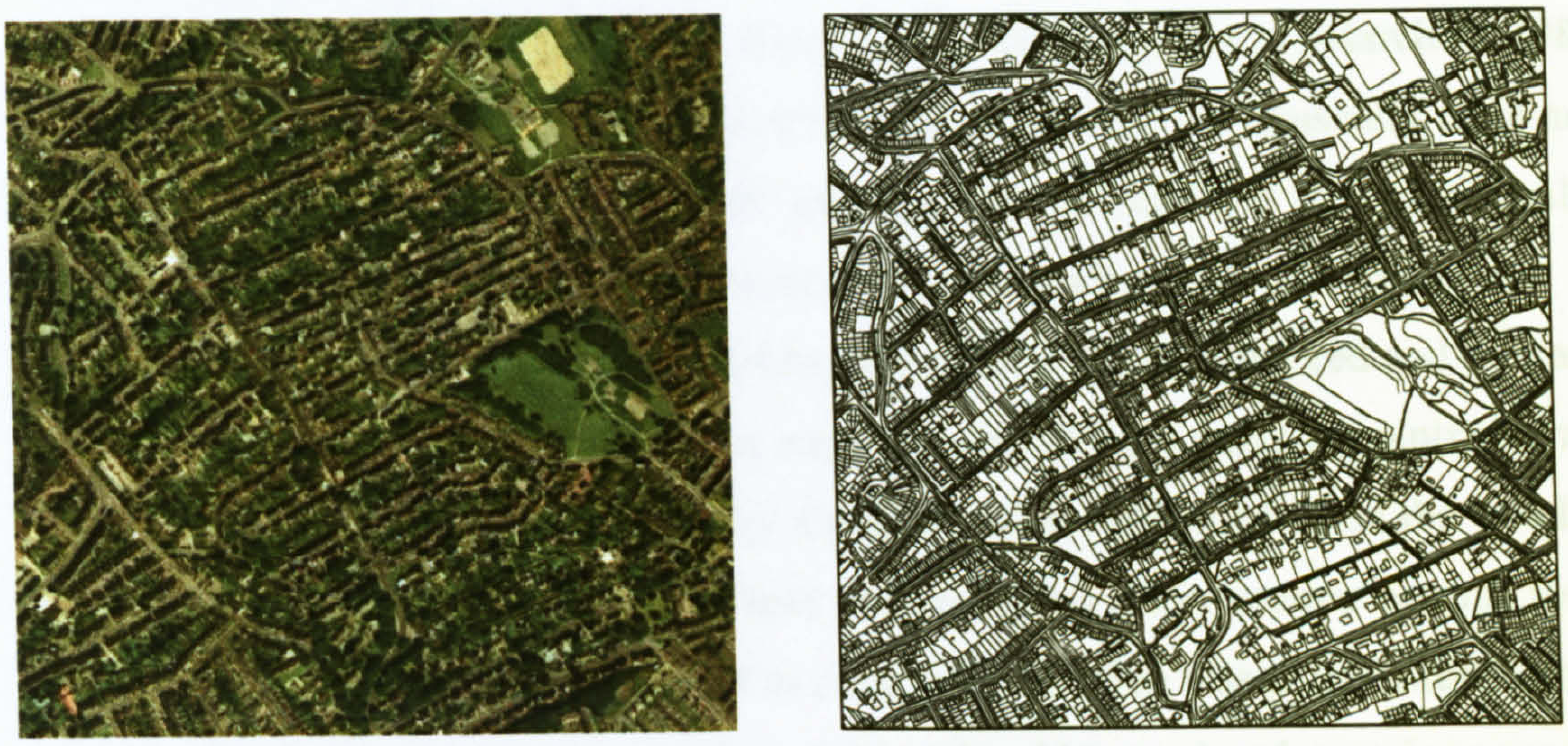
The study site for this and subsequent chapters and the primary field research site for this thesis was the 1 km × 1 km Ordnance Survey (Great Britain) National Grid square designated SK3388, located in the west of Sheffield, England and centred on N 53° 23′ 32″, S 1° 29′ 52″. Although Sheffield is to some extent polycentric in its more recent development, the area to the west of the city has been constrained from developing a typical late 20th century 'urban sprawl' by an adjacent National Park and hence has more or less retained a traditional concentric urban morphology. A non-residential core of 'primary urbanisation' forms the centre and a residential suburban outer ring characterised by relatively large private homes and gardens and abutting rural habitats can be designated 'tertiary urbanisation'. SK3388 is located within an intermediate ring of 'secondary urbanisation', primarily high-density, low-rise, relatively old-established (mostly 19th century) homes with small private yards or gardens.

Very few 1km × 1 km National Grid squares within Sheffield do not contain ecological anomalies such as industrial sites or pre-20th century parks with large mature trees but

SK3388 is relatively homogeneous and dominated by residential housing, mostly terraced (contiguous small two-storey homes with small backyards) with some larger detached homes. There are a few low-rise apartment blocks and a shopping street runs the length of the plot although even above these shops there is typically residential accommodation with small backyards used by some birds. One small park and one grassed recreation ground cover a total of 6.8 ha of the study area but both are of recent origin in ecological terms (1970s) and contain no large mature trees likely to attract woodland species, as in older parks. In effect, they are a continuation of the surrounding residential garden habitat which is therefore the dominant habitat type in determining the avifauna. Within the 100 ha study area there are approximately 3000 residential homes; allowing for parks and roads the mean land area per home is approximately 275 m^2; the distribution of areas being right-skewed with numerous small plots and a few large. Figure 7.1 shows the vegetation cover, layout of roads and buildings and numbers of homes per 100 m × 100 m grid square in the SK3388 study area, together with the location of this 1 km × 1km square within the city of Sheffield.

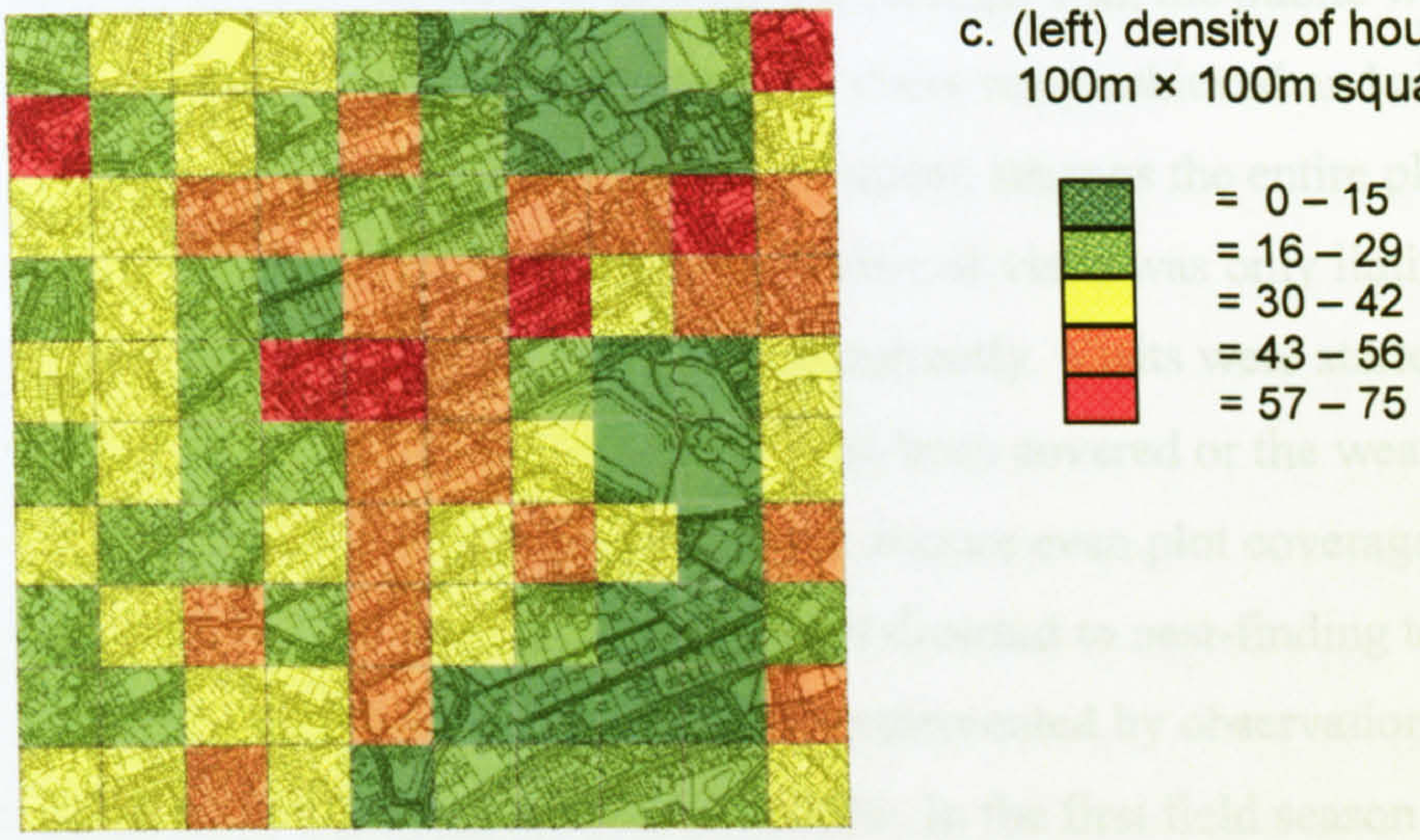
7.2.2. Bird Census

The primary fieldwork method was territory mapping (Bibby et al. 2000; Gregory et al. 2004), which although it has been applied in urban habitats (Tomialojc 1980) nonetheless normally relies on good visibility within the habitat to locate birds. This is generally not available in an environment consisting largely of continuous terraced housing and numerous small private gardens, most of which are invisible from public roads. However, with the advent of downloadable, detailed, portable maps delineating individual buildings and yards and given the friendly nature of Sheffield householders, it proved possible in this study to accurately map singing territorial passerines to within a few metres using public roads and selected vantage points. This method was complemented by gathering data on non-vocal, non-territorial species not amenable to territory mapping. All observations of all species seen or heard were mapped during the census visits and casual observations during other fieldwork were noted. Systematic mist netting in the study area during the same period failed to produce any species undetected by territory mapping or casual observations and further supporting information was obtained by searching for scarce species (such as Tawny Owl, Stock Dove and Blackcap) and acquiring garden bird lists and reports of nests from residents.

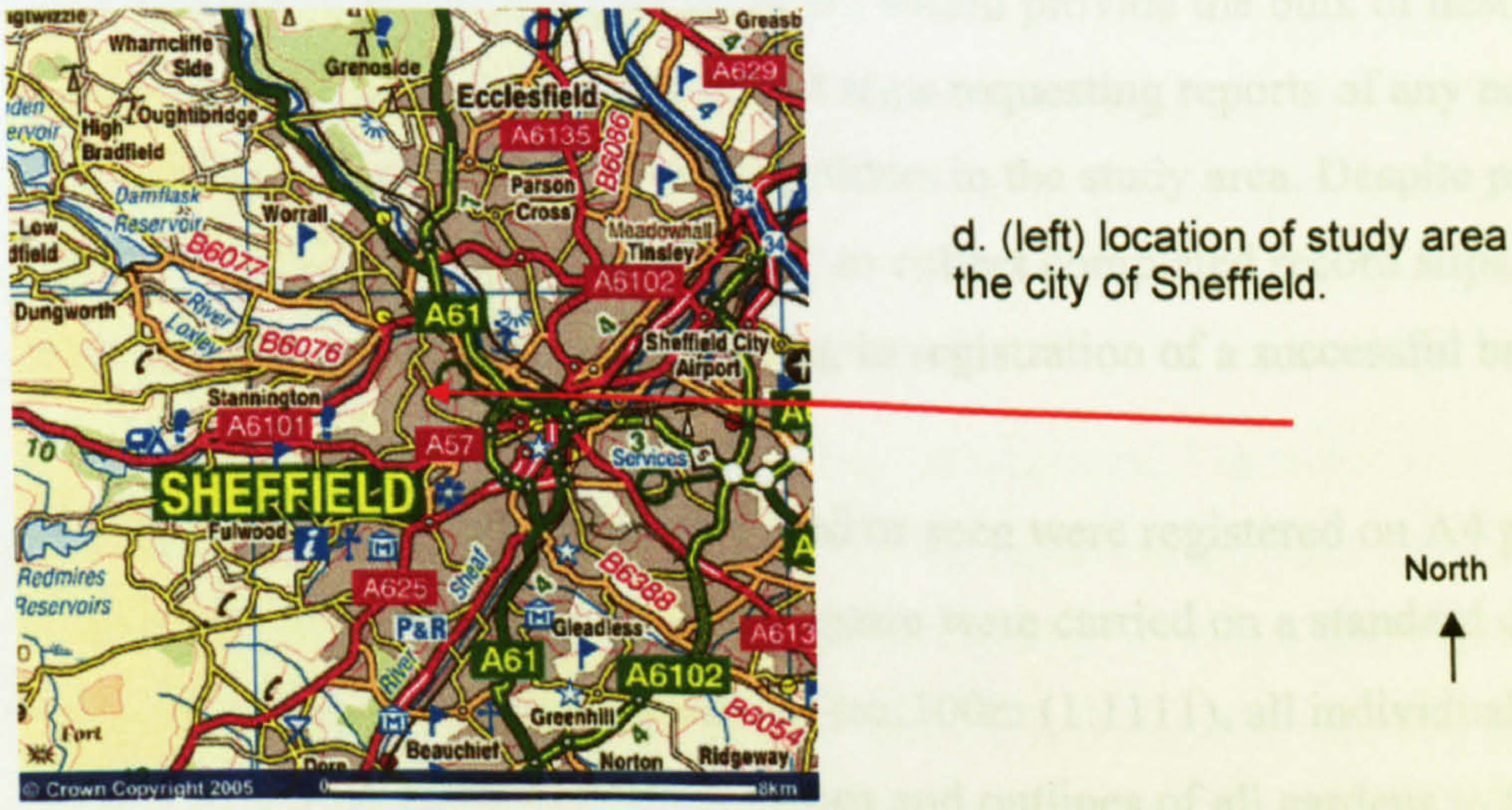


a. Aerial photograph.

b. Streets and buildings map.



c. (left) density of houses per 100m × 100m square.



d. (left) location of study area within the city of Sheffield.

Figure 7.1 a – d. The SK3388 Study Area (1 km × 1 km). Grid north to top of page
a. from Cities Revealed® aerial photography © The GeoInformation Group, 2001.
b. and d. from Ordnance Survey map data © Crown copyright.

Territory mapping was undertaken during three breeding seasons, 2002, 2003 and 2004, generally following the BTO Common Birds Census (CBC) protocol (Marchant 1983; Marchant et al. 1990 pp. 7-11), although the urban habitat and the unusually large area covered (100 ha, compared to 20 ha CBC average for woodland and 70 ha for farmland) imposed slight modifications. It was impractical to enter all private gardens as this would have been extremely time-consuming due to both distance walked and interaction with the public; some groups of gardens could be viewed from vantage points but most registrations were based on calls or song. Censuses were performed when the weather was suitably dry and reasonably still, visits were curtailed if the weather became too cold or wet such that most birds ceased to sing. Visit duration was partly a function of observer fitness (the study area rises from 95 m asl to 210 m asl and contains over 17 km of roads, all of which had to be walked for a complete census), confidence and familiarity to the public. Numerous interactions with the public were time-consuming in the first season. During 2002 only five visits were achieved and all required two days to cover the 100 ha plot, whereas in subsequent seasons the entire plot was covered in approximately eight hours and the number of visits was only limited to seven by the need to undertake other fieldwork concurrently. Visits were started shortly after dawn, continued until either the entire plot had been covered or the weather deteriorated and were started from different positions to ensure even plot coverage over the season. In line with CBC guidelines, time was not diverted to nest-finding to the detriment of mapping; the mapping of nests was supplemented by observations during other fieldwork and/or reports from the public. In the first field season (2002) it was envisaged that reports from householders would provide the bulk of nest registrations, hence 2000 publicity flyers with record slips requesting reports of any nests in gardens were printed and distributed to householders in the study area. Despite providing phone, e-mail and postal contacts and offering to collect completed record slips, fewer than 10 responses were received, none resulting in registration of a successful breeding attempt.

During each census visit, all birds heard or seen were registered on A4 paper maps; 25 maps each covering a 200m × 200m square were carried on a standard clipboard. The scale of the maps was approximately 9cm:100m (1:1111), all individual buildings were clearly shown together with street names and outlines of all gardens to facilitate accurate registration, these maps were downloaded as postscript files from the JISC/EDINA *Digimap* service. Subsequently all registrations for each of the vocal territorial species were transferred onto individual A1 paper maps of the whole 100ha plot and territories delineated using the standard BTO CBC protocol with advice and validation from an experienced professional CBC analyst (D.E. Balmer pers. comm.).

Table 7.1. Dates of territory mapping visits.

Year:	**2002**	**2003**	**2004**
Visit	**Date**	**Date**	**Date**
A	29.3.02 and 30.3.02	5.3.03	15.3.03
B	9.4.02	27.3.03	3.4.03
C	24.4.02 and 25.4.02	15.4.03	13.4.03
D	16.5.02 and 17.5.02	23.4.03	25.4.03
E	11.6.02 and 12.6.02	12.5.03	11.5.03
F		21.5.03	26.5.03
G		11.6.03	13.6.03

Two semi-colonially breeding species, House Sparrow and Starling, occurred in sufficient numbers for mapping of breeding presence and absence to be worthwhile in terms of assessing relationships with habitat variables. A third such species, Feral Pigeon, occurred only as small flocks at fixed locations. House Sparrows were impossible to census accurately in the time available, as they occurred in small, active groups that tended to remain in cover or within their roof nest sites during the survey period and the exact size of groups could rarely be observed due to visibility constraints. All groups seen and heard were mapped and nesting sites observed and counted as far as possible. To compensate for under-estimation of group size and to allow for birds nesting at the rear of buildings (in almost all cases only the fronts of buildings could be seen), a correction factor was estimated based on the relative proportions of fronts and rears of buildings visible where these species were seen; as in previous urban House Sparrow censuses (J.Tully pers. comm.). This correction was so close to two (1.98) that the numbers of visible pairs was simply doubled to give an indicative density figure. This may be a significant under-estimate and must be treated with extreme caution.

Positioning of sightings on the map was more successful in terms of reliable information generation; although these do not delineate individual territories in these two colonial species, they clearly indicated zones of presence and absence, accordingly, these were mapped as for the territorial species although core activity zones around centroids (see below) were not generated. Although Starlings are also semi-colonial, individual pairs could be mapped with more confidence as the breeding density of this species was much lower than for House Sparrow. Although a few pairs nesting behind buildings may have gone unseen and hence the density figures could be underestimates, they can be treated with much less caution than those for House Sparrow as most singing males were successfully registered during early census visits.

For the seven vocal territorial species plus House Sparrow and Starling, the breeding densities estimated from the cumulative mapped registrations were compared with breeding density and survey plot area data from a large number of previous published studies (data compiled and generously made available by Marco Pautasso, University of Sheffield). In order to correctly compare the densities found in SK3388 with densities from other surveys, the negative relationship within species between observed breeding density and survey plot area (Gaston & Blackburn 2000; Pautasso & Gaston 2005) must be taken into account. To control for this effect of plot area in the derivation of predicted breeding densities from previous survey data, log (density) / log (plot area) scatterplots were constructed and their OLS regression lines used to calculate the predicted density values for 100 ha shown in the species account density comparison tables. Density estimates from the BTO/JNCC/RSPB Breeding Bird Survey (Noble et al. in press) were also obtained (S.Newson pers. comm.) for human habitats, defined as 'land relating to human habitation in a city or town, on the outskirts of a city or town or in the countryside, e.g. village or hamlet'. These were also compared with the mapped densities and are designated UK BBS in the species account tables.

7.2.3. Analysing the mapped territories

All territories were digitised as polygons in a Geographic Information System (GIS) (ESRI® ArcMap™ 8.3, ArcInfo), to facilitate interspecific and interseasonal comparison and enable the data to be subsequently spatially analysed with respect to environmental variables (chapter 8). Using estimated territories produced by the CBC method for spatial analysis of environmental covariates of breeding species richness is problematic. The cumulative registrations of bird activity accurately enumerate territories (all that is required of the method in its usual census function) and give clues as to their sizes and shapes, for example where males are observed in territorial conflict. However, in most cases the sizes and shapes of the territories drawn by the analyst are, at best, indicative, for example where closely-grouped registrations indicate a territory but to draw a circle tightly round them would delineate an area smaller than would actually support a breeding pair. Intensive fieldwork is required to accurately delineate territories even in a small area (let alone 100 hectares), furthermore, species and individuals differ in the extents to which birds forage outside the core defended area, to which territories are defended or porous to conspecifics and to which territories are contiguous or have neutral zones between them. The problem is exacerbated by the dependence of estimated territory sizes on numbers of registrations which in turn depends on number of census visits. In 2002, only 5 census visits were achieved which is adequate for territory enumeration but the estimated territories for that year are consequently smaller than those for 2003 and 2004 (seven visits), for Blue Tit (t test, $t = -3.65$, $P < 0.001$, DF = 88), Blackbird (t test, $t = -4.07$, $P < 0.001$, DF = 194), Dunnock (t test, $t = -3.06$, $P = 0.004$, DF = 32) and Robin (t test, $t = -8.19$, $P < 0.001$, DF = 64), although they were not significantly different in Wren (t test, $t = -1.2$, $P = 0.283$, DF = 31) and Great Tit (t test, $t = -1.43$, $P = 0.19$, DF = 8) and the difference was marginally non-significant in Magpie (t test, $t = -1.91$, $P = 0.063$, DF = 44).

Consequently, a more objective method of delineating zones of bird breeding activity was required for spatial analysis of breeding species richness and its environmental covariates. A systematic approach to defining the core activity zone of each territorial pair that was fieldwork-based yet standardised was developed. It was assumed that 'core activity zones' of breeding pairs, analogous to the home range 'core areas' studied by Hatchwell et al. (2001), take the form of 'rubber discs'(terminology attributed to Julian Huxley (Perrins & Birkhead 1983)) and are essentially circular around a central point, which might often be the nest although not always. It was also assumed that in saturated habitat patches they abut contiguously rather than being separated by any neutral zone. Due to the problems of access to the numerous small private gardens in the study area, nests could not be located for most of the territories mapped but instead the further assumption was made that the hand-drawn territories, although possibly inaccurate in size and shape, were at least accurately positioned on the map and hence could be used to define and locate the centre point of each pair's core activity zone (see figure 7.2.).

The centroid positions of each mapped territory were calculated using ArcMap and buffer circles then created around each centroid using the built-in 'buffer' function of the GIS, as shown in figure 7.3. The buffer circle radius was calculated in two stages. Firstly, the mean area of the hand-drawn territories for each species for the years 2003 and 2004 combined was calculated. The radius of the first-stage buffer circles was then specified such that isolated circles drawn with this radius would have area equal to the

2003-04 mean territory area. Intersecting core activity zones generated in this way are clipped by each other and hence represent a smaller area than the mean estimated per territory area. Therefore the buffer circle radius was increased by a correction factor to bring the total area of the core activity zones for 2003 and 2004 combined to within 1% of the total area of estimated hand-drawn territories. The two years 2003 and 2004 were used in the calculation because the numbers of census visits were the same, however the resulting calculated radius was applied to the territory maps of all three years, 2002-04. The areas of the hand-drawn territories for 2003 and 2004 were compared before the procedure to check for systematic differences in the way the territories had been drawn. Circular core activity zones were only generated for the seven vocal territorial species mapped, they are unlikely to be meaningful for semi-colonial, non-territorial species.

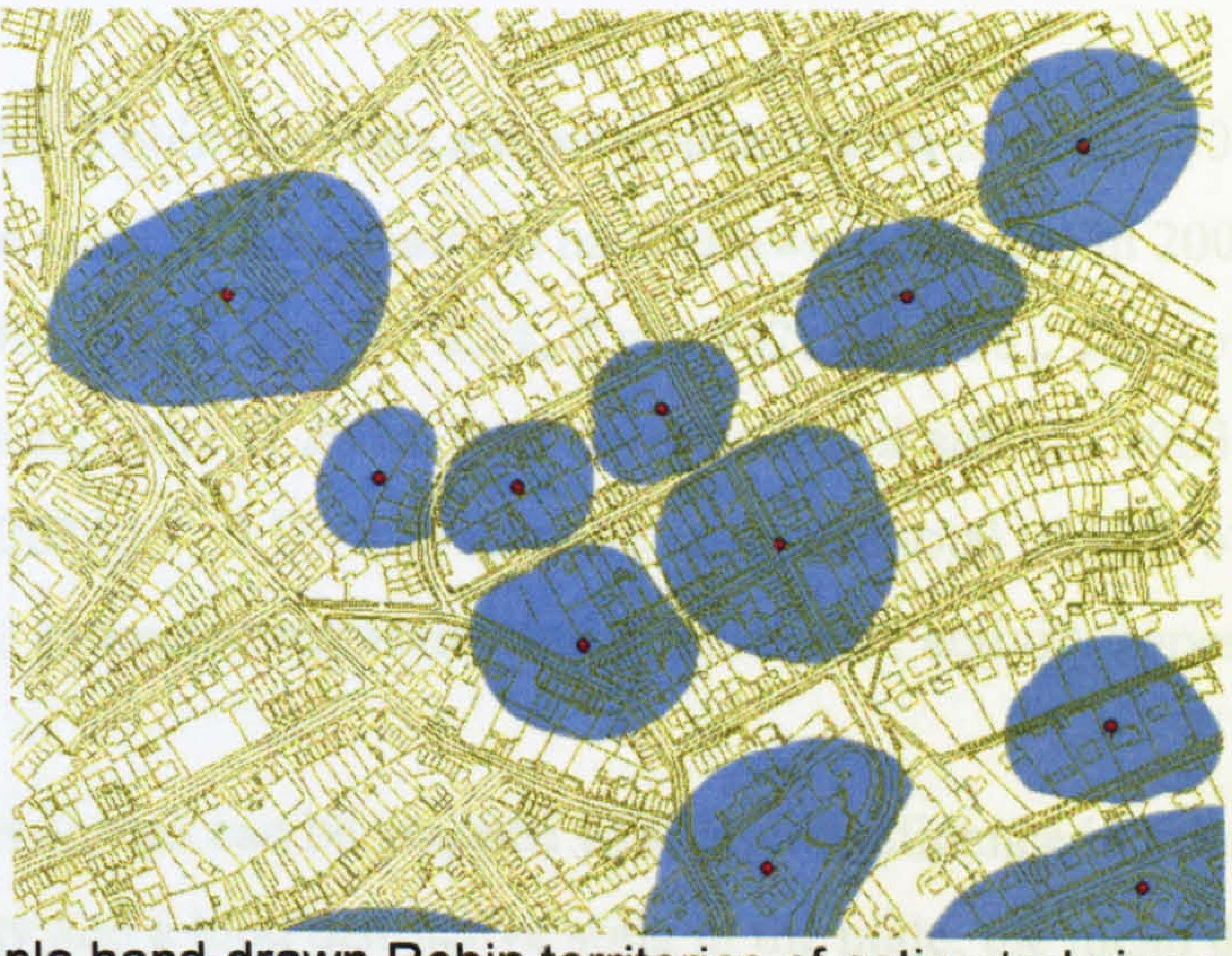


Figure 7.2. Example hand-drawn Robin territories of estimated size and shape (blue) for 2004, derived using BTO CBC protocol from field registrations of breeding activity and demonstrating typical problems of unknown true extent, shape and degree of contiguity. Red dots are positions of calculated territory centroids.

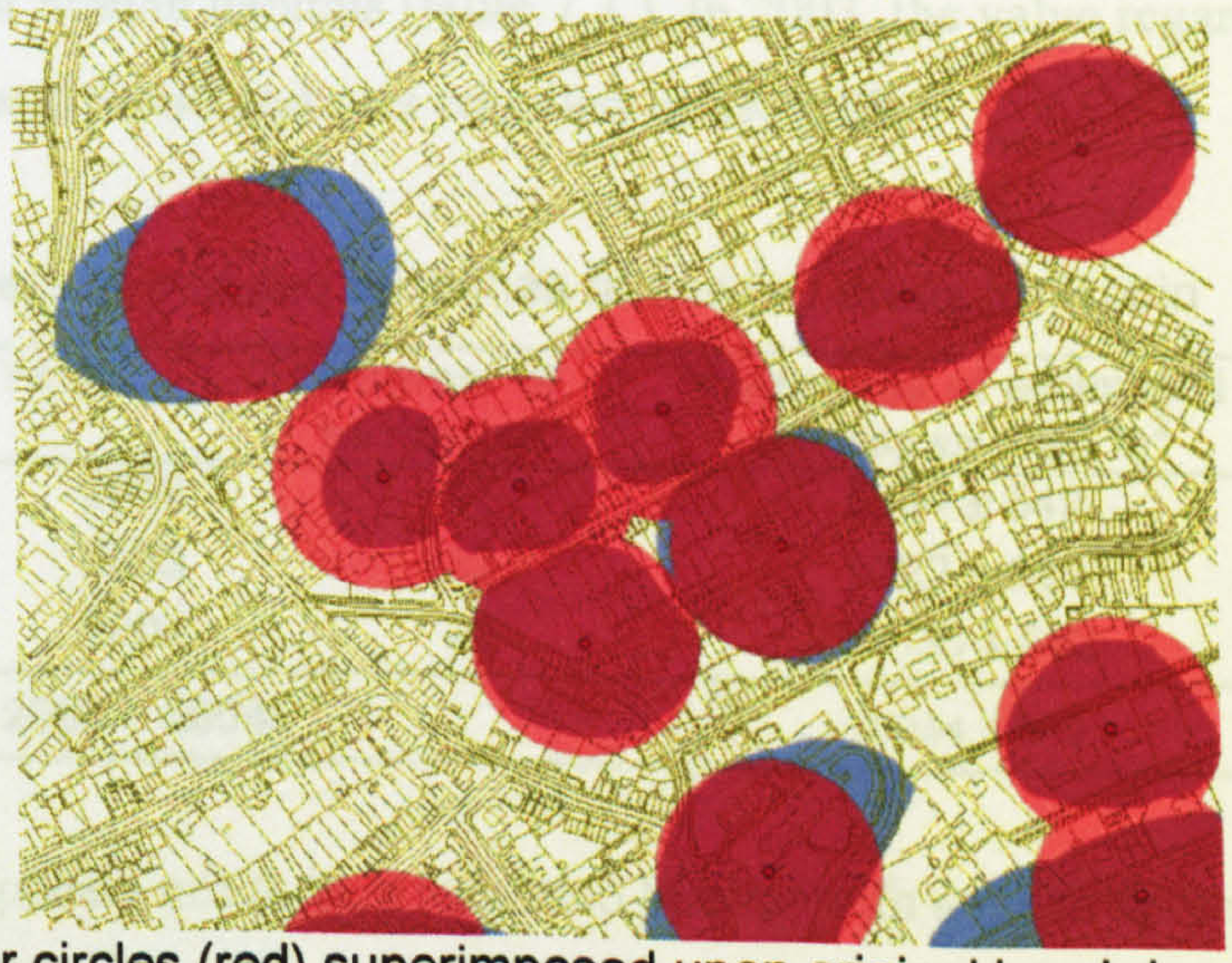


Figure 7.3. Buffer circles (red) superimposed upon original hand-drawn Robin territories (blue) to represent 'core activity zones' in 2004. Radii calculated to set areas of isolated circles equal to the mean area of the hand-drawn territories for 2003 and 2004, then corrected to compensate for the total area lost due to intersecting circles.

7.3. Results and discussion: species accounts

In this section, results of territory mapping and comparative data from literature are first presented for the seven vocal, territorial species (Robin, Dunnock, Magpie, Wren, Blackbird, Great Tit and Blue Tit) that were mapped with high confidence. Secondly, results of mapping the areas of breeding activity are presented for two semi-colonial species (House Sparrow and Starling) that were mapped with reasonable confidence, again with comparative data from literature.

7.3.1. Robin

Table 7.2 shows that Robin numbers almost doubled from 2002 to 2003 but fell back again in 2004. The areas of the estimated hand-drawn territories in 2003 and 2004 were not significantly different (*t* test, $t = 0.74$, $P = 0.462$, DF = 38). The corrected radius of the core activity zones was 57.26 m, their corrected total area for 2003 and 2004 combined was 532086 m^2, 0.1% less than the estimated total of 532668 m^2. Figure 7.5 shows the mapped estimated territories and circular core activity zones for Robin.

Robin breeding territories can be mapped with high confidence in urban habitat due to strong territoriality and a loud distinctive song in the male, the mean density observed over the three years was almost three times the value predicted by the regression line (figure 7.4), however it was very similar to the BTO CBC density for farmland and the UK BBS value for human habitats (table 7.3.). In 2003, the value regarded as typical for British farmland and woodland was equalled in SK3388.

Table 7.2. Numbers of mapped territories and mean areas for Robin

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	17	5284 ± 549
2003	32	9722 ± 634
2004	20	10536 ± 892
2003 + 2004:		10044 ± 519

For Robin, this appears not to be a saturated habitat with a mean annual mapped occupancy for 2003 and 2004 of only 27% of the study area. Robins are territorial in winter as well as in the breeding season, which may influence urban densities. Resident breeders must compete with influxes of wintering individuals to the relatively warm urban habitat with its abundant artificial food; this winter competition may depress the all-year carrying capacity of the habitat. In Robins, breeding territory area tends to be about twice that of winter territories defended by individuals on the same site (Cramp et al. 1977 - 1994). It has also been reported that at low densities, Robin territories are often more aggregated than might be expected from the habitat and rarely exceed 20000 m^2 even if surplus habitat is available (D.G.C.Harper in Cramp et al. 1977 - 1994).

Table 7.3. Comparison of territory densities for Robin

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
degenerate forest in Morocco	1.5
ash and alder forest in Poland	7
Garden-poor area in Bristol 1978 (Bland 1979)	7.2
BTO CBC other habitats (Gates et al. 1993)	8.05
Predicted from compiled urban data (figure 7.4.)	*8.7*
UK BBS	20.7
BTO CBC farmland (Gates et al. 1993)	21.7
THIS STUDY mean ± SE	**23.3 ± 4.48 N =3**
forest in Morocco	25.8
'average for farmland and woodland' (Mead 1984)	30
mixed ancient forest in Poland	48
Garden-rich area in Bristol 1978 (Bland 1979)	91
BTO CBC woodland (Gates et al. 1993)	104.4
'maximum in Britain'	250 - 300

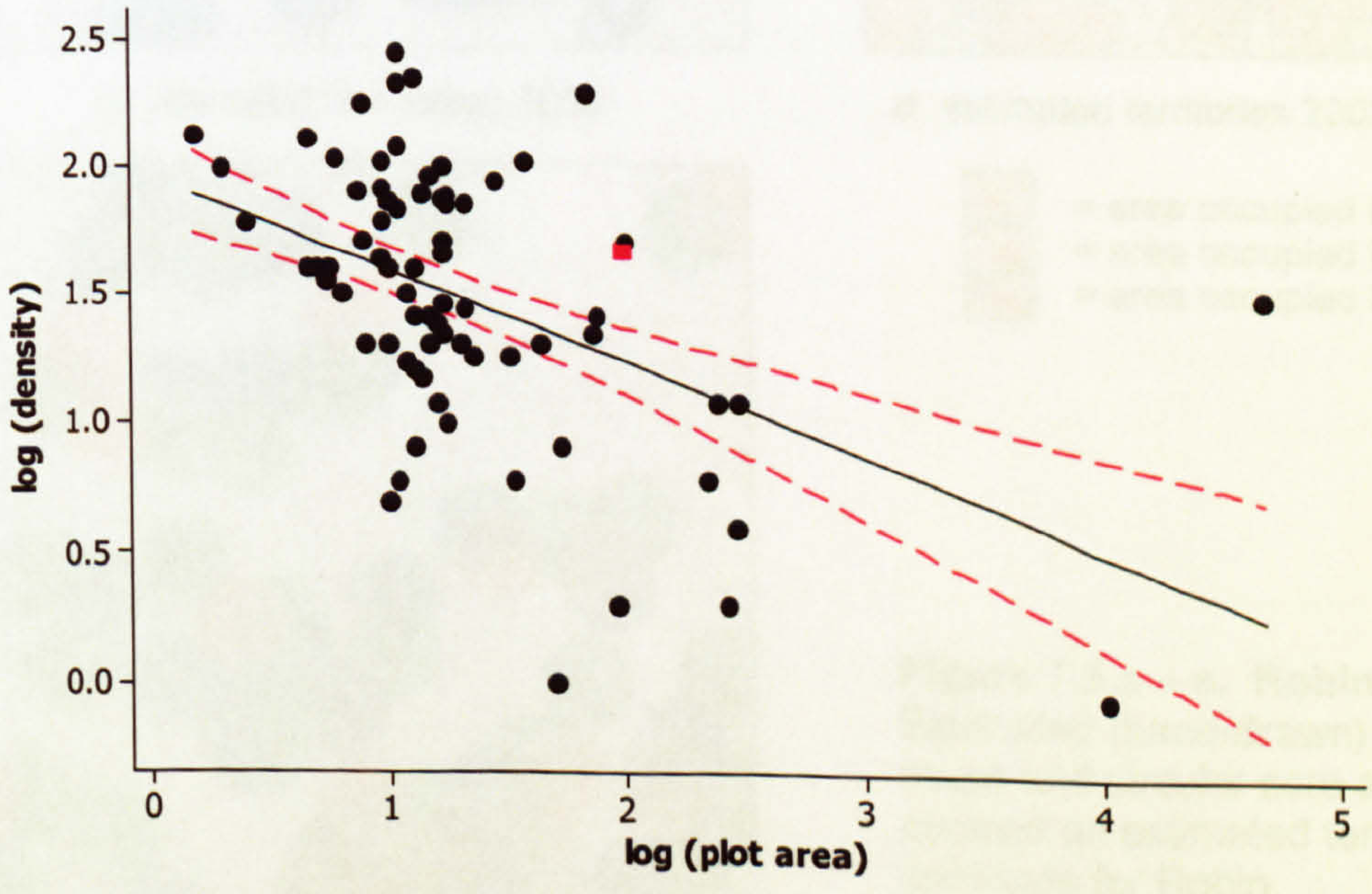
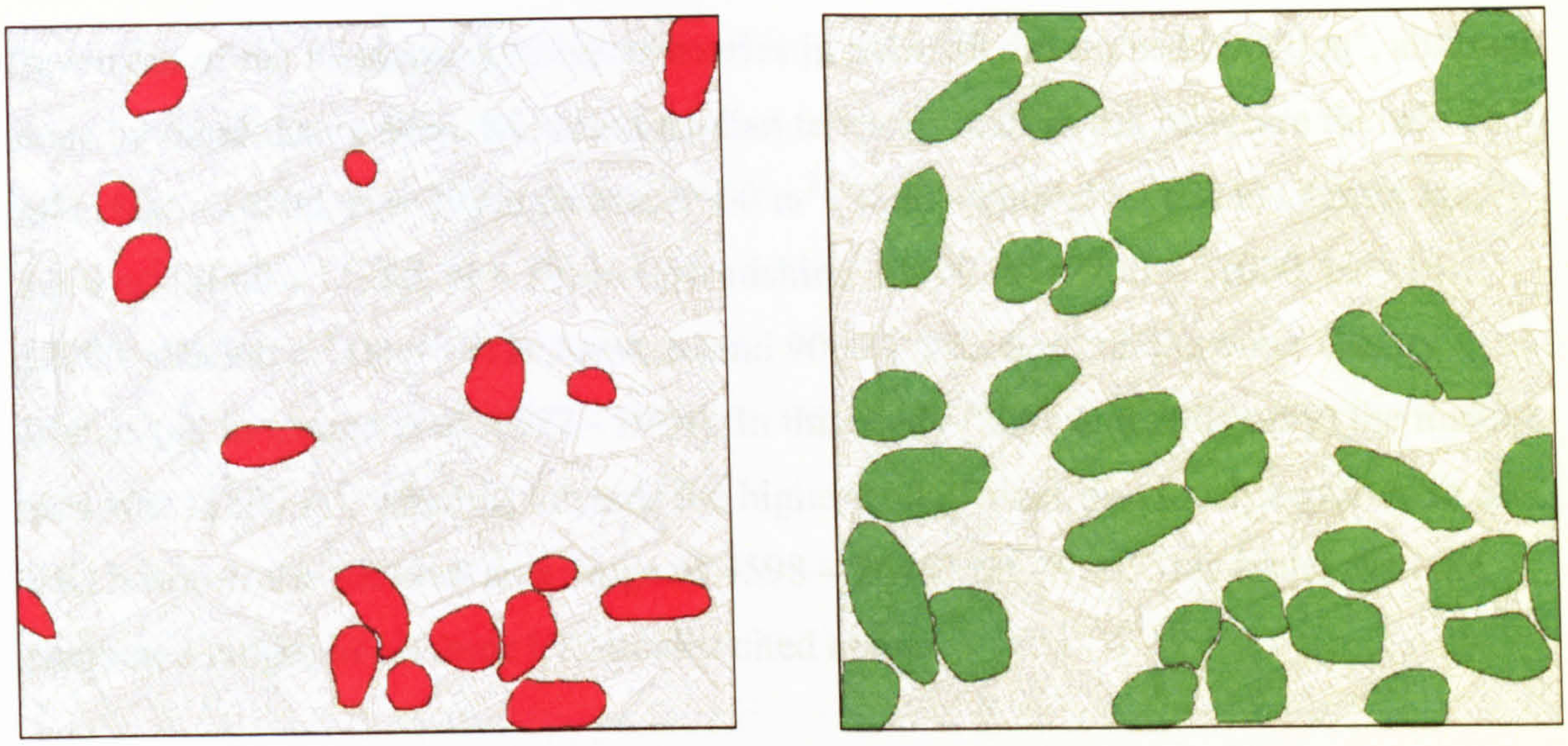
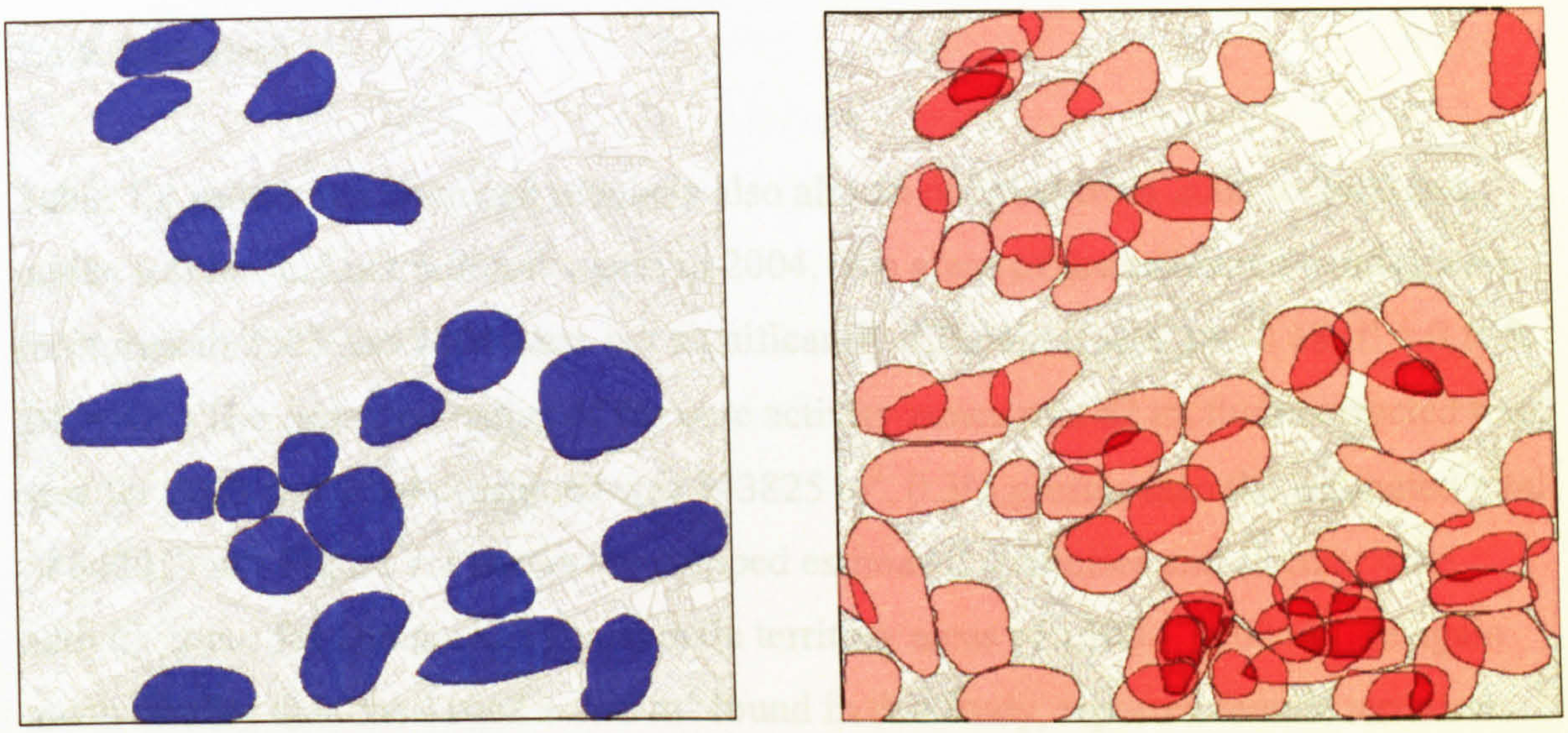


Figure 7.4. Plot of log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Robin. Regression: log(density) = 1.96 – 0.361 log(plot area). $F_{1,94}$= 31.2, r^2 = 24.9%, P < 0.001. Dashed red plots = 95% confidence limits. Data from literature (N = 95): black. Data from this study: red.



a. estimated territories: 2002

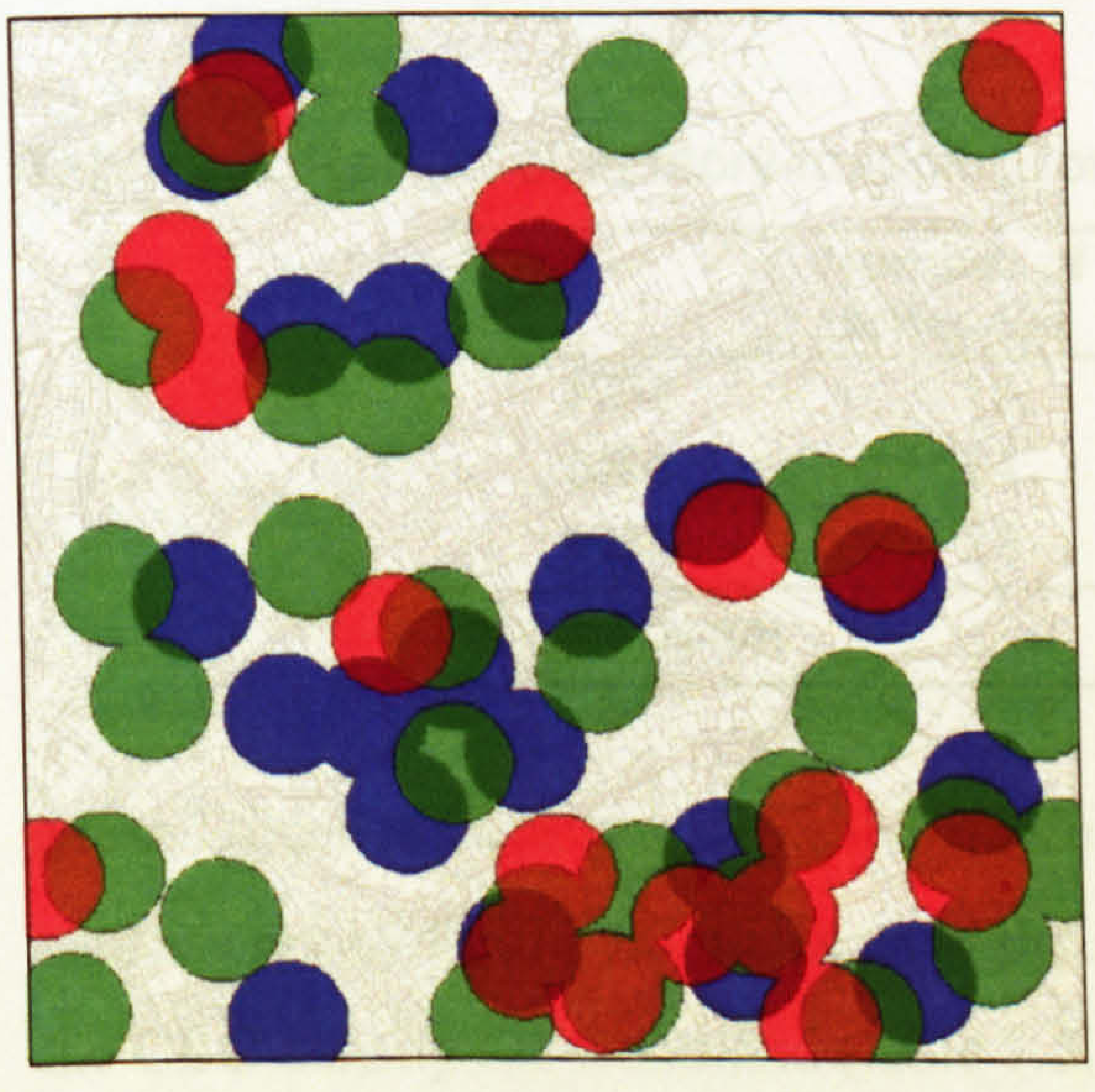
b. estimated territories: 2003



c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

🟥 = area occupied in 1 season
🟥 = area occupied in 2 seasons
🟥 = area occupied in 3 seasons



e. circular core activity areas 2002 -04

🟥 2002 🟩 2003 🟦 2004

Figure 7.5.a – e. Robin
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Robin.
1 km × 1 km, SK3388 study area.

Seven out of the 52 mapped Robin territories in SK3388 did exceed 20000 m^2, although none by more than a third. Recorded median territory sizes in the literature include 5500 m^2 (1800 – 14700, N = 29) in Devon, 5600 m^2 (2500 – 8300, N = 63) in Cambridge, 8000 m^2 (3000 – 11200, N = 53) in Oxfordshire, 14400 m^2 (7200 – 21000, N = 18), 12000 – 23000 m^2 (N = 14) at Antwerp and 9000 – 15000 m^2 on the outer Canary Islands (all in Cramp et al. 1977 - 1994). In this study (2003 and 2004 only) the median area was 11509 m^2, which is towards the higher end of sizes previously reported in the UK, however the SK3388 area range of 4598 – 26451 m^2 (N = 53) is larger than the combined ranges of all three UK studies cited above.

7.3.2. Dunnock

Table 7.4 shows that Dunnock numbers also almost doubled from 2002 to 2003 but, unlike Robins, did not fall back again in 2004. The areas of the estimated hand-drawn territories in 2003 and 2004 were not significantly different (*t* test, $t = -0.18$, $P = 0.858$, DF = 46). The corrected radius of the core activity zones was 62 m, their corrected total area for 2003 and 2004 combined was 543825 m^2, 0.3% greater than the estimated total of 542013 m^2. Figure 7.7 shows the mapped estimated territories and circular core activity zones for Dunnock. Typical male territory areas of 1500 – 3000 m^2 are again much smaller than the 11062 ± 746 m^2 found in this study, reported female territories elsewhere are even smaller, as little as 800 m^2 (Cramp et al. 1977 - 1994).

Table 7.4. Results of territory mapping for Dunnock

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	13	7588 ± 854
2003	24	10923 ± 1056
2004	25	11194 ± 1075
2003 + 2004:		11062 ± 746

Mean Dunnock density in SK3388 is almost three times the value predicted for a 100ha census area by figure 7.6, twice as high as the UK BBS density and only slightly below the CBC density for woodland (table 7.5.). Dunnock is a successful urban species in Sheffield (pers. obs), nesting in unpromising patches of core urban habitat so it is not surprising to find relatively high densities in the relatively benign gardens of SK3388.

Singing males can be mapped with high confidence, even in urban habitat, but estimation and comparison of breeding densities is complicated by this species' polyandrous breeding system. Commonly, females frequent the territories of more than one male which then coalesce, the α – and β – males using the same perches for singing (Cramp et al. 1977 - 1994). Polygamous territories are larger than monogamous, perhaps reflected in the distribution of territory areas for 2003 and 2004 combined being not normal (KS test, $P = 0.014$) in this study but right-skewed. The degree of polyandry is negatively correlated with habitat quality, one study in farmland hedgerows found 11 monogamous and 14 polyandrous territories (Bishton 2001). The proportion of birds in polyandrous systems might be expected to be higher in urban habitats if their resource density is lower, but even if the mean territory density in this study (20.7 ± 3.8 territories km^{-2}) is multiplied by three to give a high-end estimate of breeding individuals km^{-2} the result (62 ± 11.5) is very low compared to figures for Cambridge Botanic Garden (640 birds km^{-2}) and woodland and scrub in southern England (230 birds km^{-2}) although "much lower breeding densities are recorded in woodland and other areas with sparse or localised undergrowth", as suggested by the BTO CBC (all comparative and behavioural data from Cramp et al. 1977 - 1994 unless stated, original references therein). There is probably room for more Dunnocks in SK3388 as the mean annual mapped occupancy rate for 2003 and 2004 is only 27% of the study area.

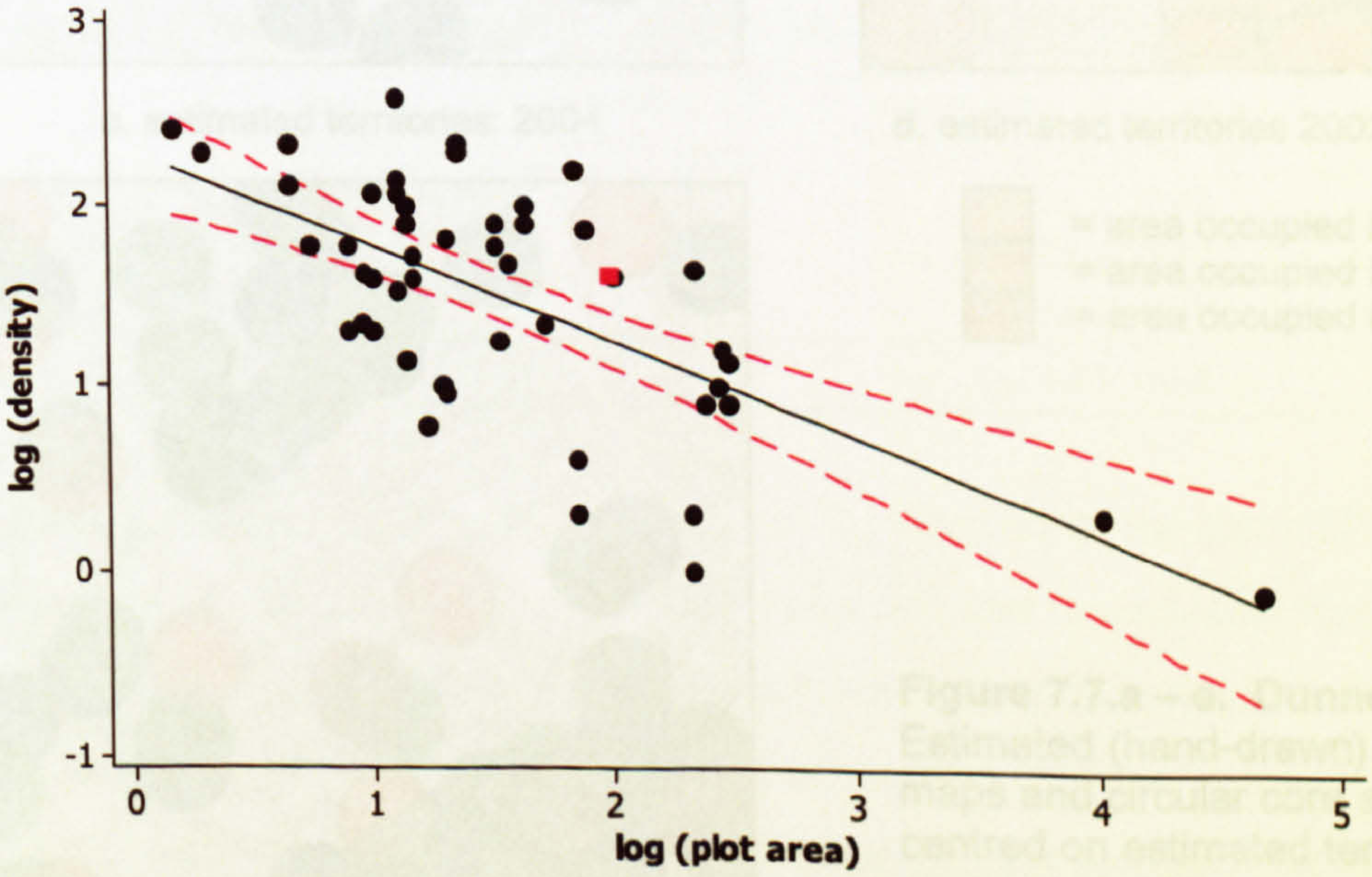
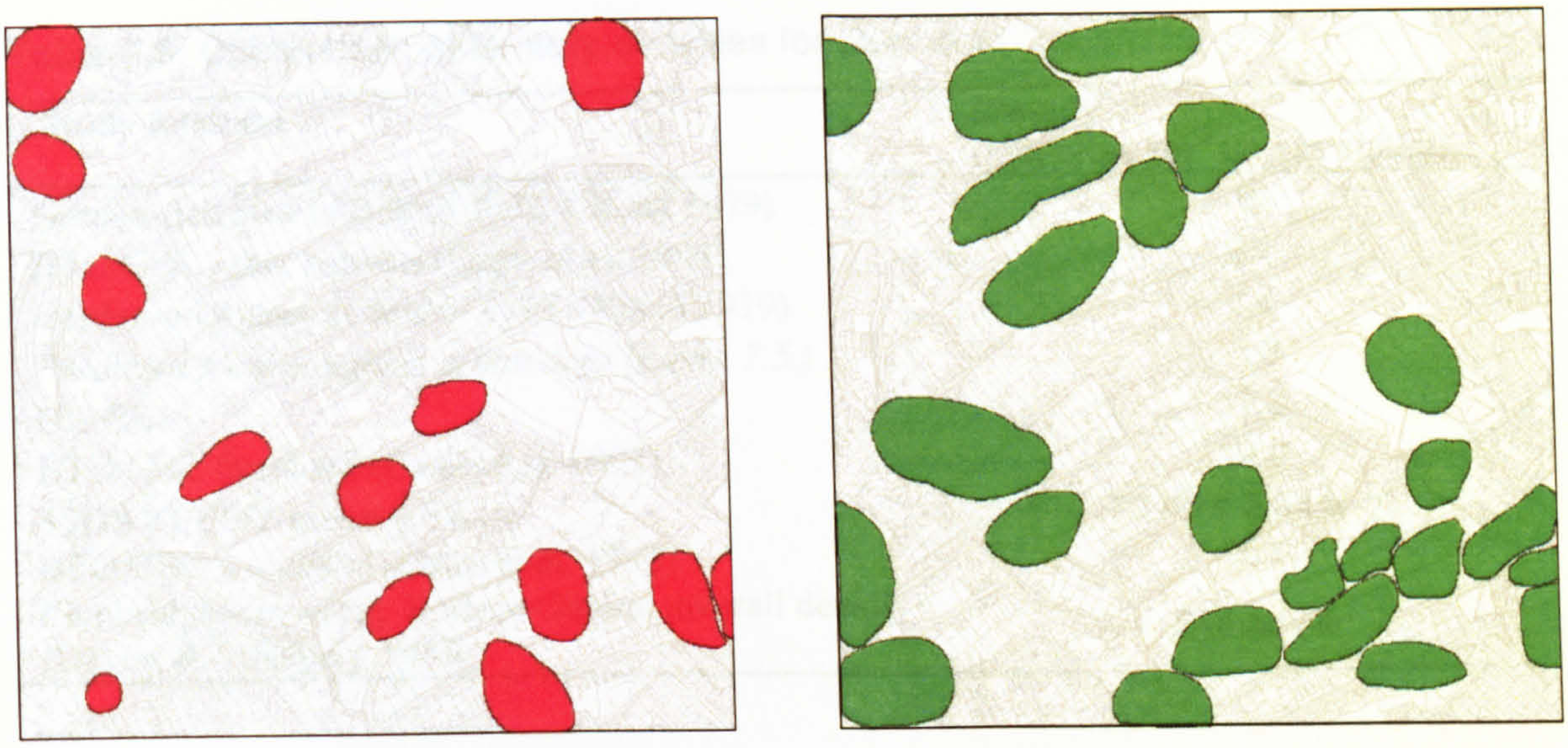
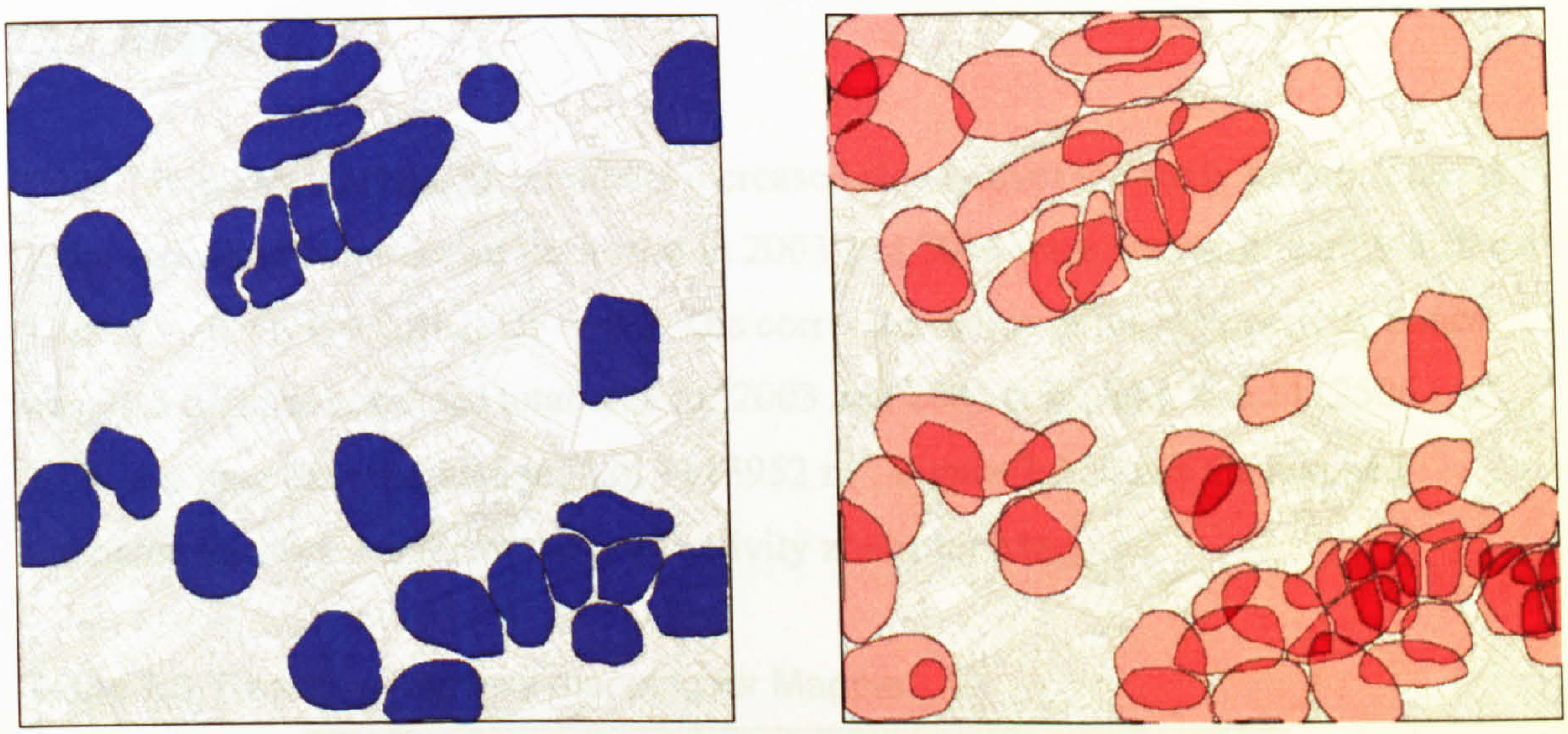


Figure 7.6. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Dunnock. Regression: log(density) = 2.31 – 0.532 log(plot area). $F_{1,53} = 41.57$, $r^2 = 44.0\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 54): black. Data from this study: red.



a. estimated territories: 2002

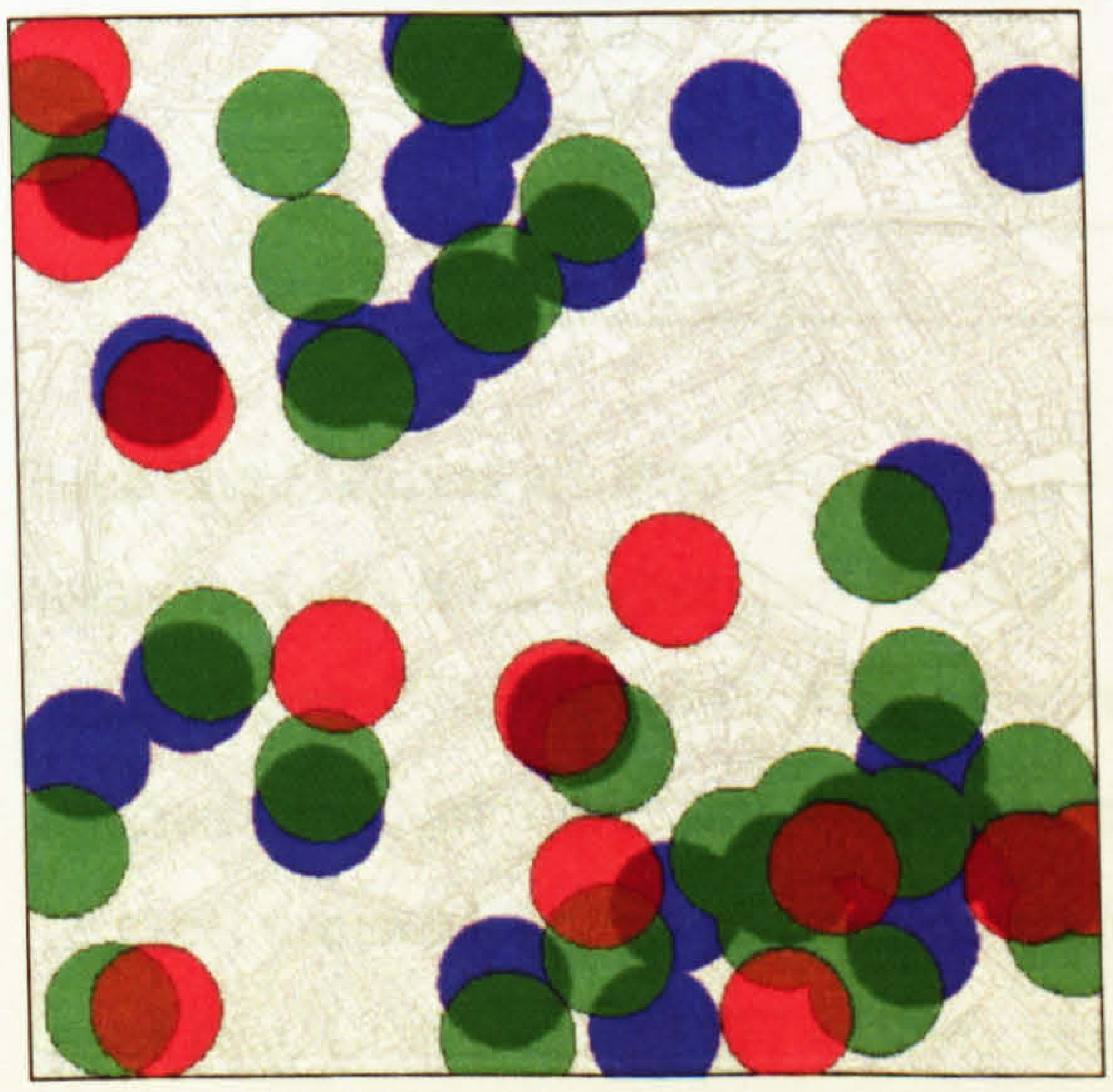
b. estimated territories: 2003



c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

🟥 = area occupied in 1 season
🟥 = area occupied in 2 seasons
🟥 = area occupied in 3 seasons



e. circular core activity areas 2002 -04

🟥 2002 🟩 2003 🟦 2004

Figure 7.7.a – e. Dunnock
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Dunnock.
1 km × 1 km, SK3388 study area

Table 7.5. Comparison of territory densities for Dunnock

Study location	Density (territories km^{-2} unless stated)
Garden-rich area in Bristol 1978 (Bland 1979)	0
BTO CBC other habitats (Gates et al. 1993)	3.1
Garden-poor area in Bristol 1978 (Bland 1979)	7.2
Predicted from compiled urban data (figure 7.5.)	*8.8*
UK BBS	12.8
THIS STUDY mean ± SE	**20.67 ± 3.84 N =3**
BTO CBC woodland (Gates et al. 1993)	26.6
Cambridge University Botanic Garden, overall density (Davies & Lundberg 1984)	640 adults

7.3.3. Magpie

Table 7.6 shows that Magpie numbers increased slowly over the study period. The areas of the estimated hand-drawn territories in 2003 and 2004 were not significantly different (t test, t = -0.74, P = 0.462, DF = 40). The corrected radius of the core activity zones was 91.5 m, their corrected total area for 2003 and 2004 combined was 1112506 m^2, 0.1% less than the estimated total of 1113952 m^2. Figure 7.9 shows the mapped estimated territories and circular core activity zones for Magpie.

Table 7.6. Results of territory mapping for Magpie

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	18	19904 ± 1896
2003	22	26053 ± 2677
2004	23	23512 ± 2127
2003 + 2004:		24754 ± 1693

Breeding Magpies are easy to census due to the visibility of the nests; SK3388 density was about one third higher than the BBS value and four times higher than the predicted value (figure 7.8), but would have to increase by half again to reach the maximum for northern England (table 7.7). Comparison of reported densities is complicated by the fact that urban Magpie densities throughout Europe have increased rapidly in recent years (e.g. Cramp et al. 1977 - 1994). Hence, year of survey may be a confounding predictor of density in the regression, although a reasonable amount of variation in log (density) is explained by log (plot area) (r^2 =32%) and Sheffield supports higher Magpie densities than cities in the south and east of England (pers. obs.). It would be unwise to assess habitat saturation from mapped territory area as breeding density is probably limited more by the availability of nesting trees than any other factor; although a few pairs in SK3388 nest as little as 3m from the ground in garden bushes. Also, inter-territorial spaces may be occupied by non-breeding adults, competing for food (Birkhead 1991).

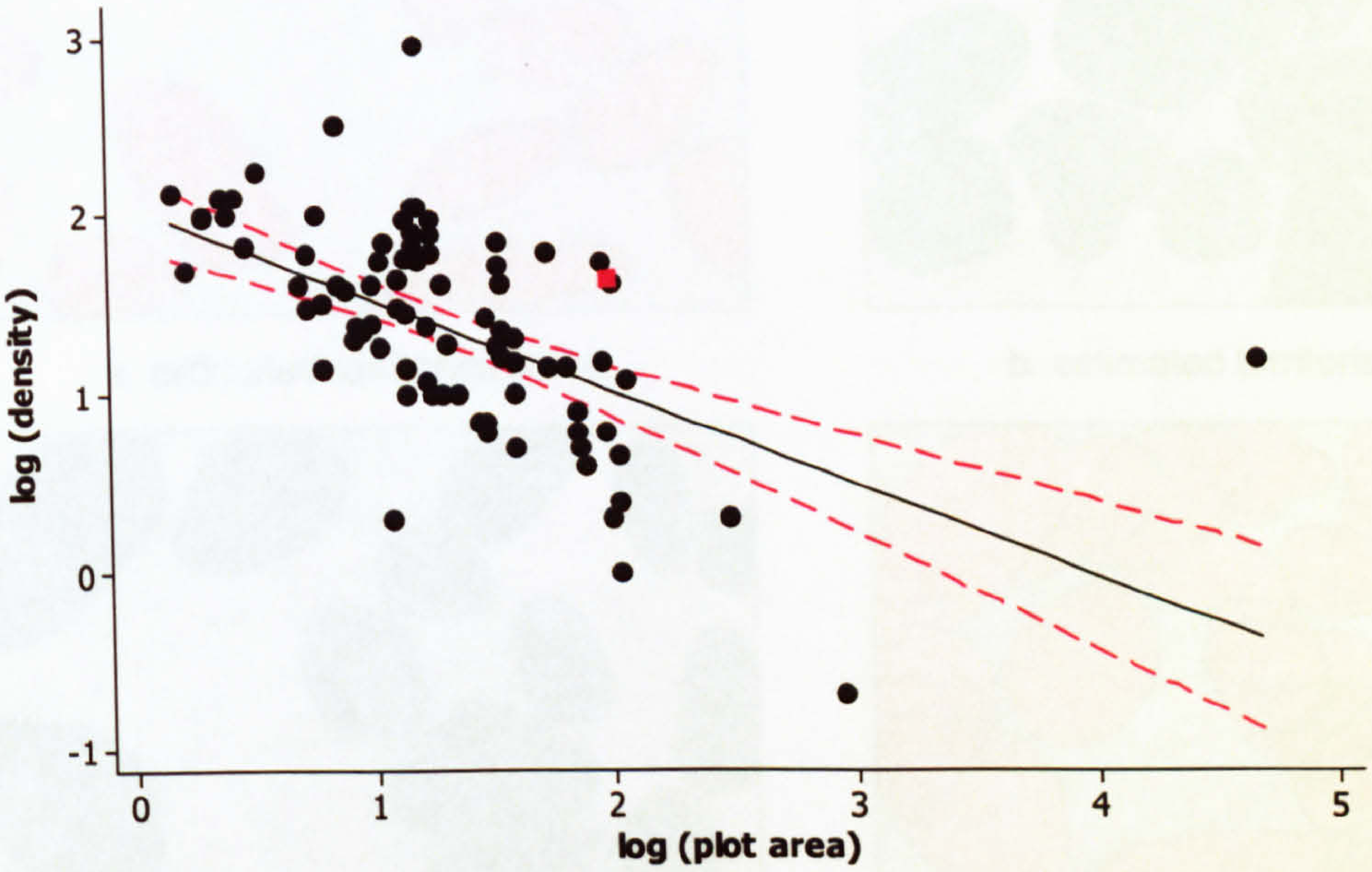
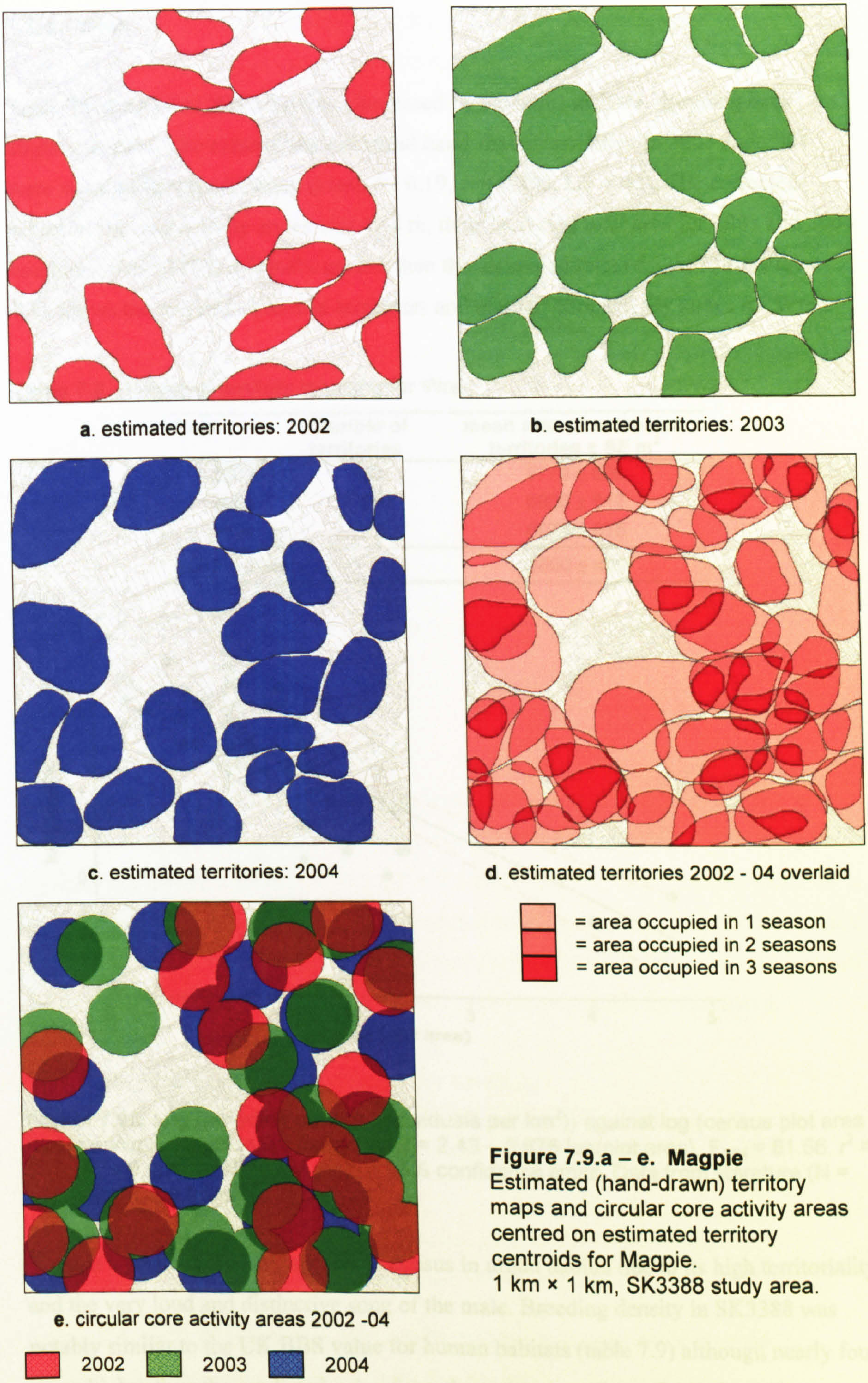


Figure 7.8. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Magpie. Regression: log(density) = 2.04 – 0.517 log(plot area). $F_{1,100} = 46.7$, $r^2 = 31.8\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 54): black. Data from this study: red.

Table 7.7. Comparison of territory densities for Magpie

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
BTO CBC other habitats (Gates et al. 1993)	1.2
suburban northwest Poland (Gorski & Kotlarz 1997)	1.2 (from 0.9 in 1978)
Five towns in Slovenia 1998 (Vogrin 2003)	5.0 ± 0.58
Predicted from compiled urban data (figure 7.8.)	*5.05*
BTO CBC farmland (Gates et al. 1993)	5.3
Netherlands	7.3
Sheffield 1986	8.1 (from 1.3 in 1946)
urban northwest Poland 1992 (Gorski & Kotlarz 1997)	8.2 (from 3.6 in 1978)
BTO CBC woodland (Gates et al. 1993)	9.3
Turku (Vuorisalo et al. (1992) in Gorski & Kotlarz 1997)	14
Tierpark, Berlin 1969	14 (from 1.2 in 1955)
Dublin (Kavanagh 1987b)	16.4
UK BBS	16.5
THIS STUDY mean ± SE	**21.0 ± 1.53 N =3**
Polish rural villages 1992 (Gorski & Kotlarz 1997)	21.3 (from 12.4 in 1978)
Poznan (Poland) (Mizera (1988) in Gorski & Kotlarz 1997)	21 - 25
'maximum density in northern England'	32
Manchester urban parks (Groom 1993)	35.2
Sofia (Antonov & Atanasova 2003)	56.8



a. estimated territories: 2002

b. estimated territories: 2003

c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

e. circular core activity areas 2002 -04

Figure 7.9.a – e. Magpie
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Magpie.
1 km × 1 km, SK3388 study area.

7.3.4. Wren

Table 7.8 shows that Wren numbers increased by a quarter in 2003, dropping back slightly in 2004. The areas of the estimated hand-drawn territories in 2003 and 2004 were not significantly different (*t* test, $t = 0.19$, $P = 0.852$, DF = 43). The corrected radius of the core activity zones was 47.8 m, their corrected total area for 2003 and 2004 combined was 324700 m^2, 0.4% greater than the estimated total of 323382m^2. Figure 7.11 shows the mapped estimated territories and circular core activity zones for Wren.

Table 7.8. Results of territory mapping for Wren

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	20	5770 ± 806
2003	25	6800 ± 612
2004	22	6971 ± 676
2003 + 2004:		6880 ± 449

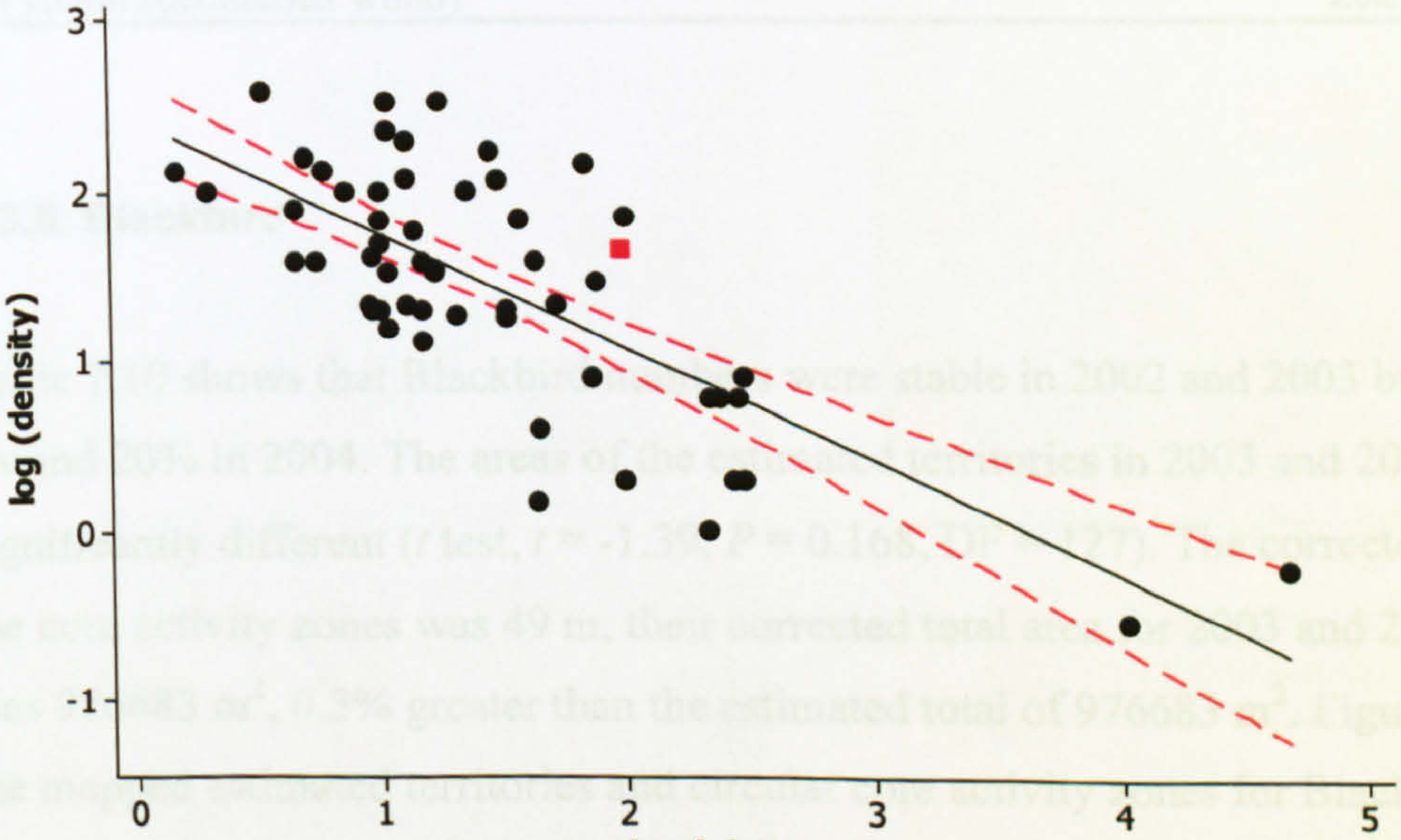


Figure 7.10. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Wren. Regression: log(density) = 2.43 – 0.675 log(plot area). $F_{1,64} = 81.56$, $r^2 = 56\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 65): black. Data from this study: red.

Wren is a particularly easy species to census in urban habitat due to its high territoriality and the very loud and distinctive song of the male. Breeding density in SK3388 was notably similar to the UK BBS value for human habitats (table 7.9) although nearly four times higher than the predicted value from the regression (figure 7.10). Insectivorous Wrens attain high densities in urban parks but are scarce across core urban areas; hence the regression line slope is notably negative and may under-predict density for a large but relatively hospitable area such as SK3388, where densities are one third lower than in farmland and an order of magnitude lower than in some rural woodlands, Saturation is low with a mean plot coverage for 2003 and 2004 of only 16.2% of total area.

Table 7.9. Comparison of territory densities for Wren

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
Orkney Moorland	2.4
Predicted from compiled urban data (figure 7.10.)	6.0
New Forest	16.2
BTO CBC other habitats (Gates et al. 1993)	17.5
UK BBS	20.4
Suffolk farmland	20.7
THIS STUDY mean ± SE	**22.3 ± 1.45 N =3**
BTO CBC Farmland (Gates et al. 1993)	33
ancient forest in Poland	20 - 50
Anglesey young conifers	63 – 99
Gwynedd sessile oak	107
BTO CBC Woodland (Gates et al. 1993)	134
man-modified habitats of western Europe	>150
Wytham (deciduous wood)	232

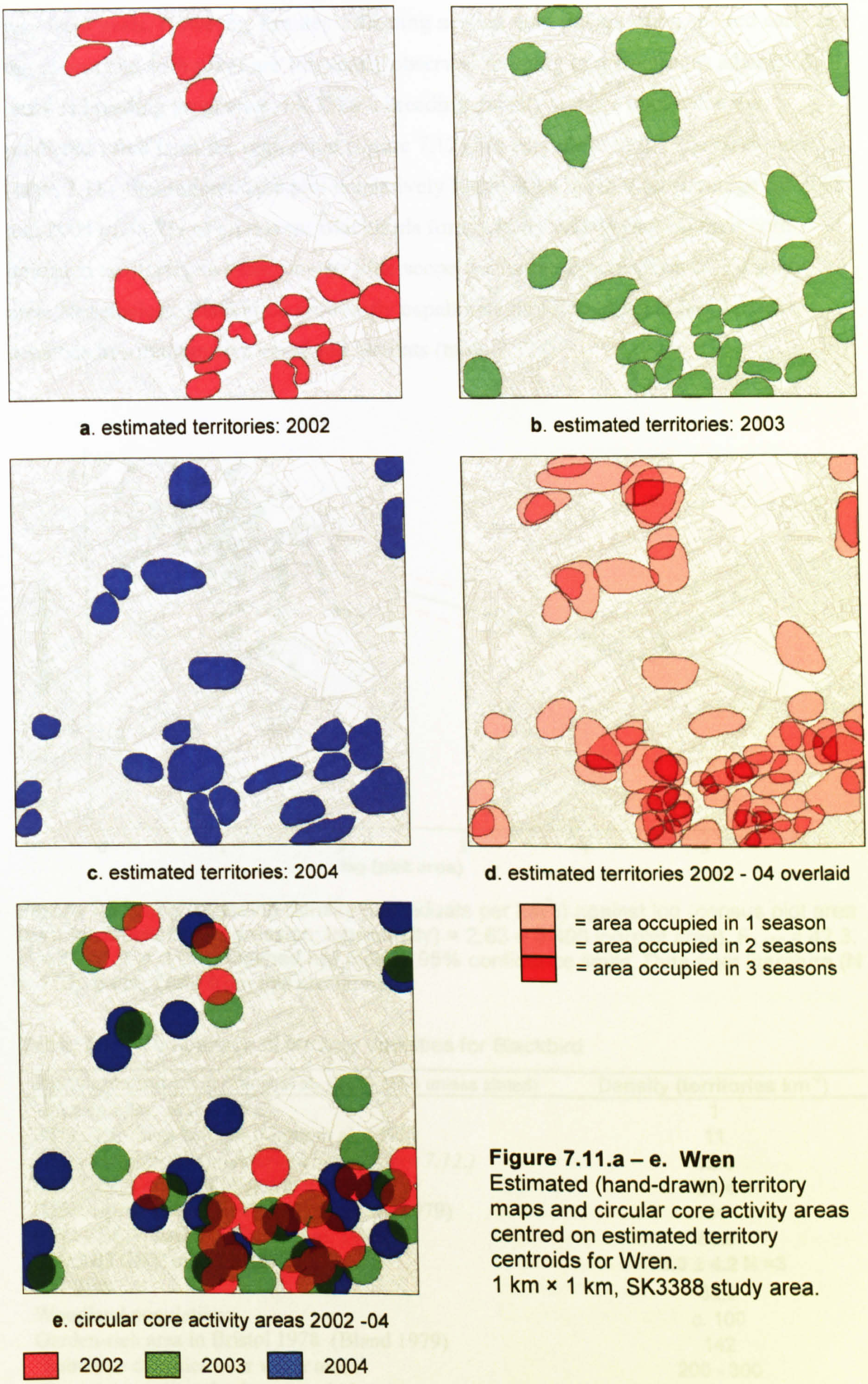
7.3.5. Blackbird

Table 7.10 shows that Blackbird numbers were stable in 2002 and 2003 but fell by around 20% in 2004. The areas of the estimated territories in 2003 and 2004 were not significantly different (*t* test, $t = -1.39$, $P = 0.168$, DF = 127). The corrected radius of the core activity zones was 49 m, their corrected total area for 2003 and 2004 combined was 976683 m^2, 0.3% greater than the estimated total of 976683 m^2. Figure 7.13 shows the mapped estimated territories and circular core activity zones for Blackbird.

Table 7.10. Results of territory mapping for Blackbird

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	81	4740 ± 334
2003	80	6182 ± 365
2004	68	7040 ± 499
2003 + 2004:		6577 ± 304

Urban Blackbird breeding territories can be mapped with reasonable confidence. Although singing males are easy to map, the amount and timing of song varies greatly between seasons, some are non-breeders and songposts are often high chimneys, some



a. estimated territories: 2002

b. estimated territories: 2003

c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

e. circular core activity areas 2002 -04

Figure 7.11.a – e. Wren
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Wren.
1 km × 1 km, SK3388 study area.

way from nests. However, females collecting nesting material are often spotted early in the season and both sexes are frequently observed foraging in greenspaces adjacent to nests as breeding progresses. SK3388's breeding density is more than twice the predicted value from the regression (figure 7.12) but very close to the UK BBS value (table 7.11). Saturation of the plot is relatively high with a mean total coverage for 2003 and 2004 of 48.7% of total area; Blackbirds forage fairly widely outside their core defended territories so there may be little scope for further colonisation of the study area. Nonetheless, Blackbirds are clearly capable of attaining much higher breeding densities in suburban and woodland habitats (table 7.11).

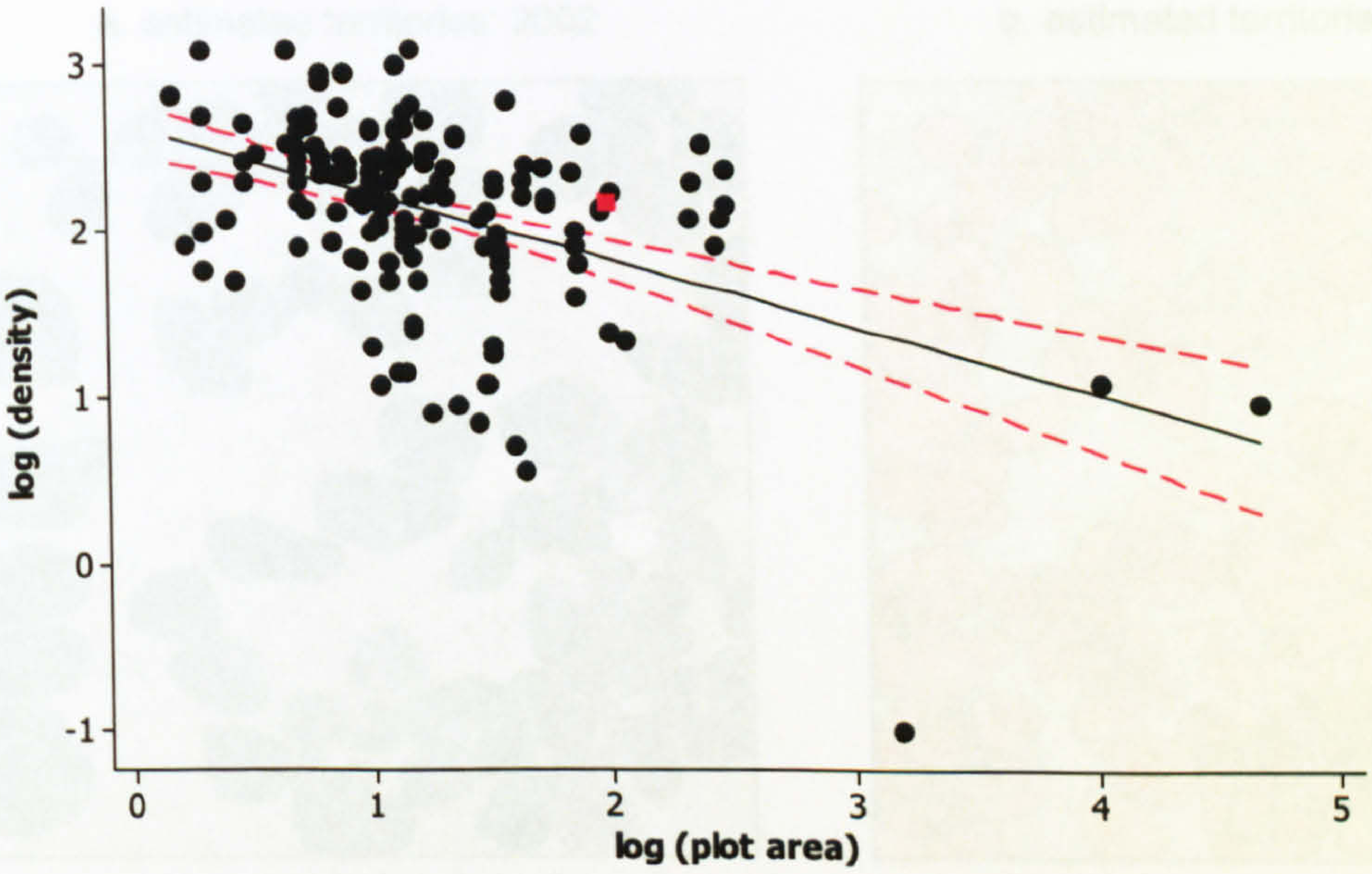
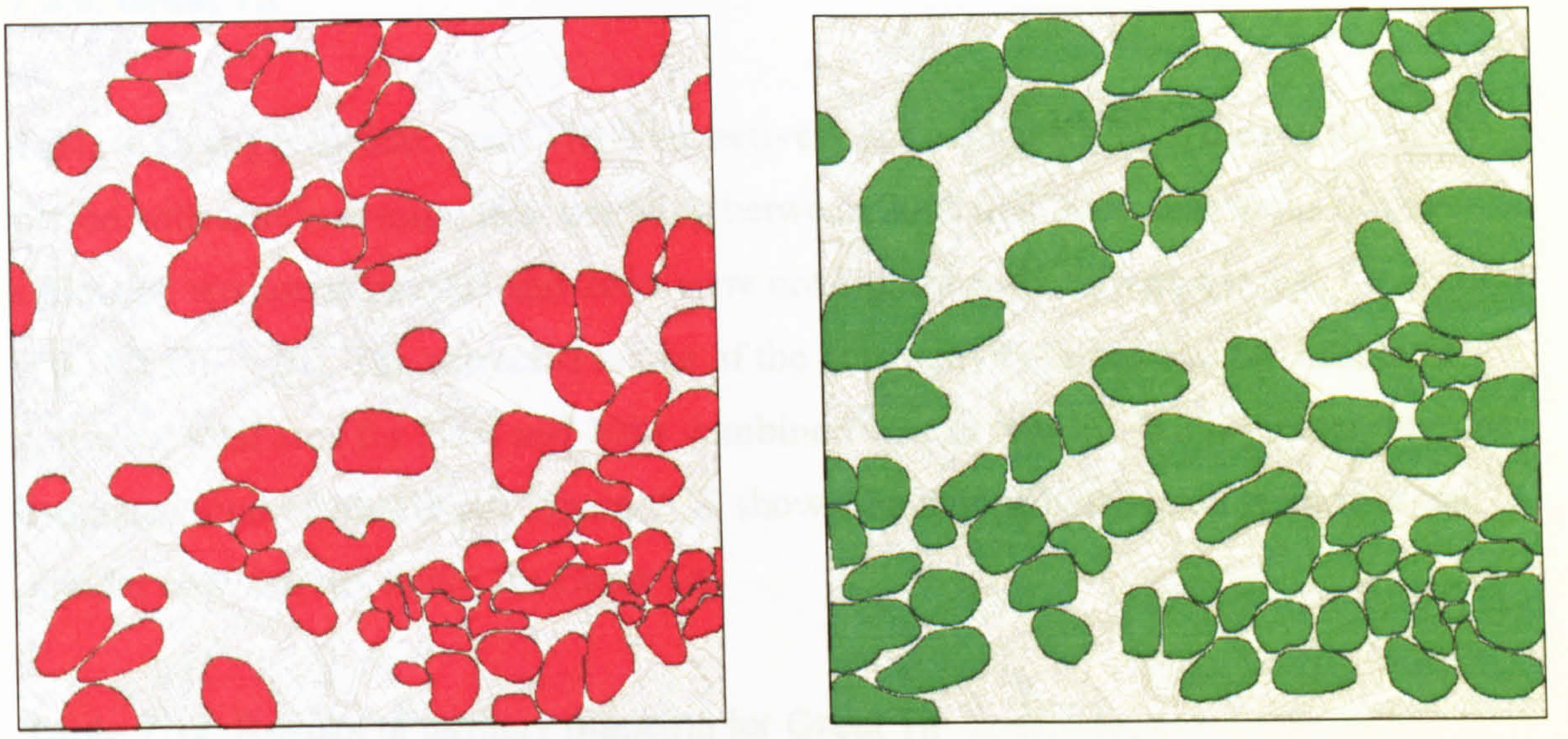


Figure 7.12. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Blackbird. Regression: log(density) = 2.63 – 0.406 log(plot area). $F_{1,169} = 42.3$, $r^2 = 20\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 170): black. Data from this study: red.

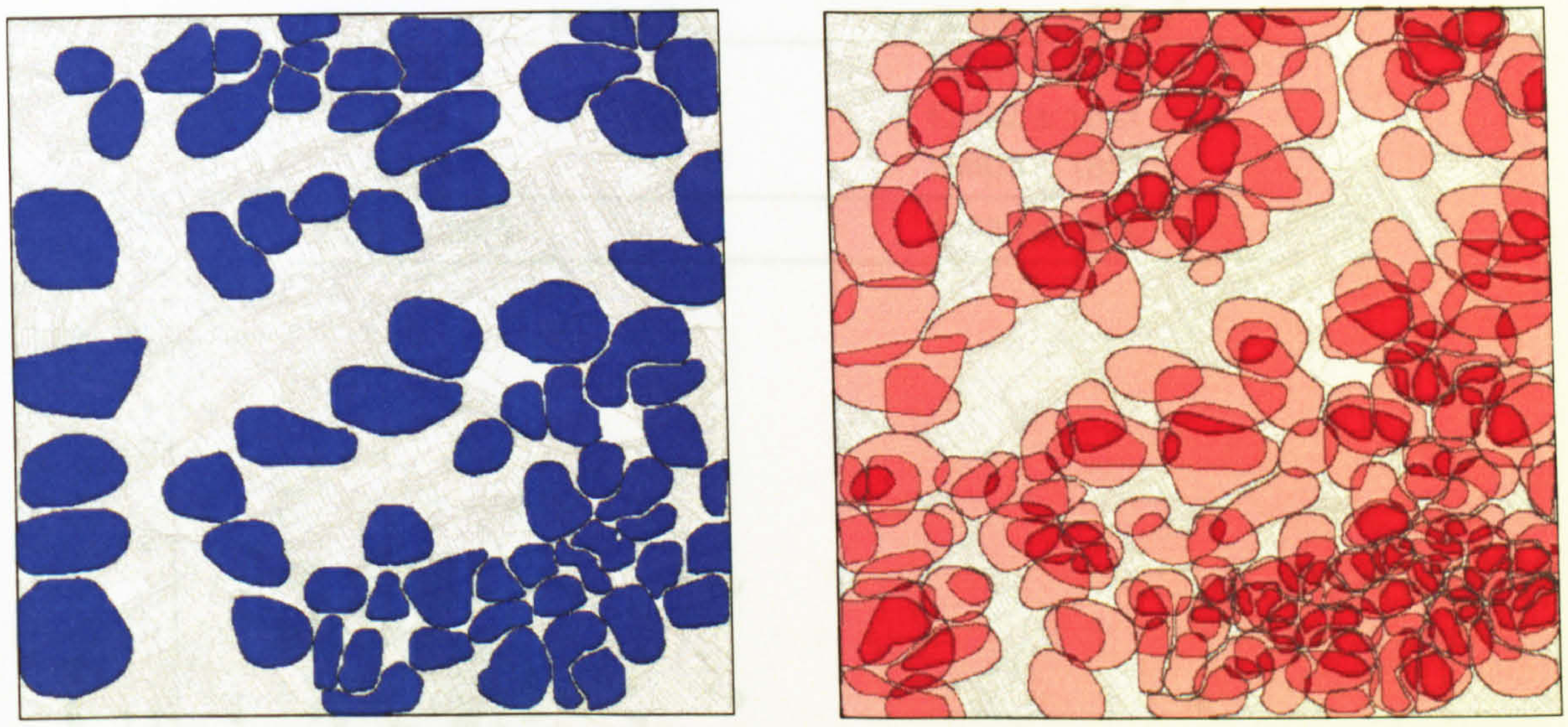
Table 7.11. Comparison of territory densities for Blackbird

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
'open country, as low as…'	1
BTO CBC other habitats (Gates et al. 1993)	11
Predicted from compiled urban data (figure 7.12.)	32.9
BTO CBC Farmland (Gates et al. 1993)	26.4
Garden-poor area in Bristol 1978 (Bland 1979)	51
BTO CBC Woodland (Gates et al. 1993)	66.9
THIS STUDY mean ± SE	**76.3 ± 4.2 N =3**
UK BBS	82.5
Woodland populations	*c.* 100
Garden-rich area in Bristol 1978 (Bland 1979)	142
'Suburban densities over wider areas'	200 - 300
'Densest, usually suburban, populations'	700



a. estimated territories: 2002

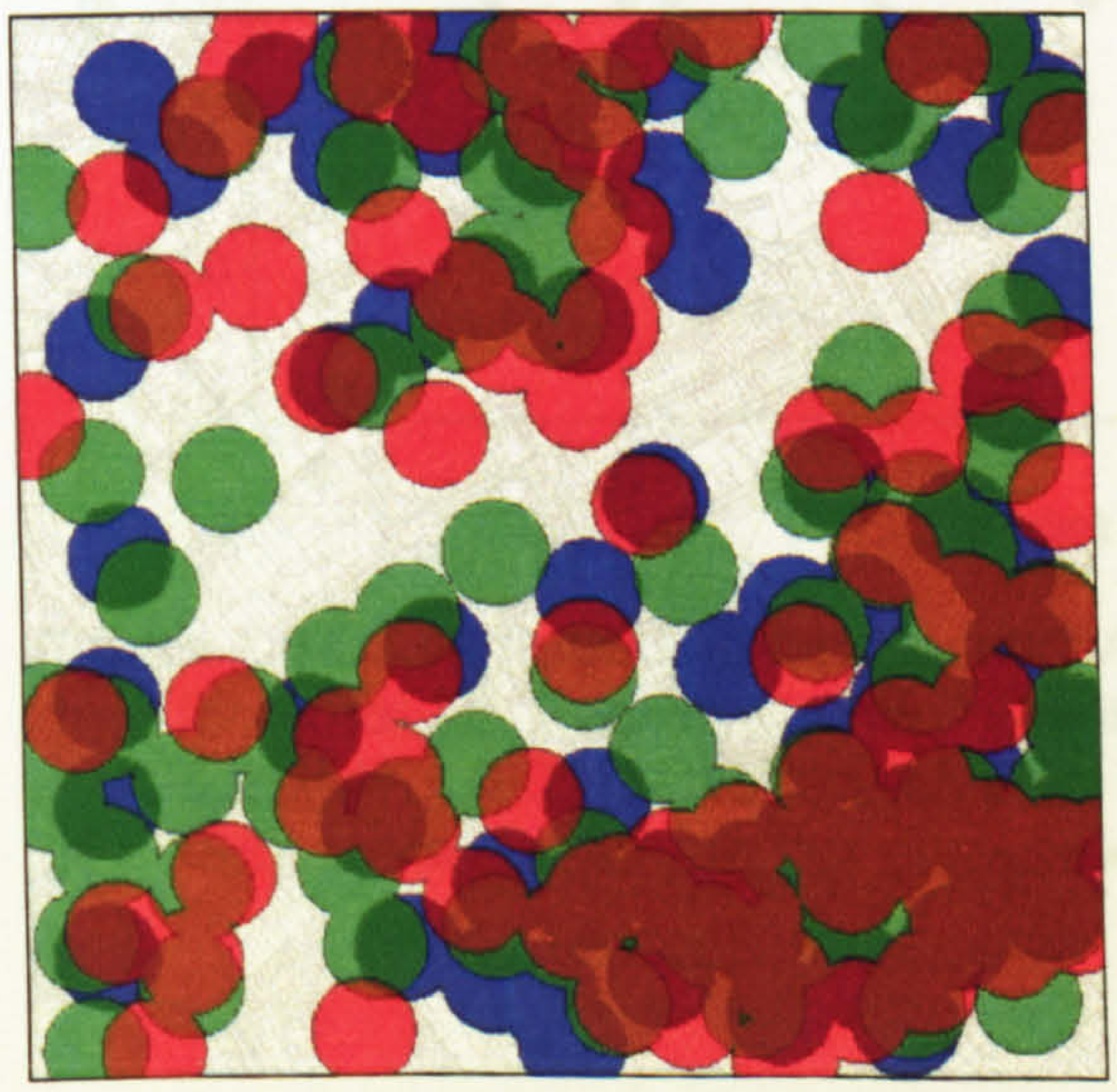
b. estimated territories: 2003



c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

🟥 = area occupied in 1 season
🟥 = area occupied in 2 seasons
🟥 = area occupied in 3 seasons



e. circular core activity areas 2002 -04

🟥 2002 🟩 2003 🟦 2004

Figure 7.13.a – e. Blackbird
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Blackbird. 1 km × 1 km, SK3388 study area.

7.3.6. Great Tit

Table 7.12 suggests that Great Tits were actively colonising SK3388 during the study period with numbers more than doubling between 2002 and 2004. The areas of the estimated territories in 2003 and 2004 were not significantly different (*t* test, $t = -1.39$, $P = 0.180$, DF = 20). The corrected radius of the core activity zones was 68.3 m, their corrected total area for 2003 and 2004 combined was 361194 m^2, 0.2% greater than the estimated total of 360316 m^2. Figure 7.15 shows the mapped estimated territories and circular core activity zones for Great Tit.

Table 7.12. Results of territory mapping for Great Tit

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	6	10768 ± 2239
2003	10	12632 ± 1044
2004	15	15600 ± 1861
2003 + 2004:		14413 ± 1210

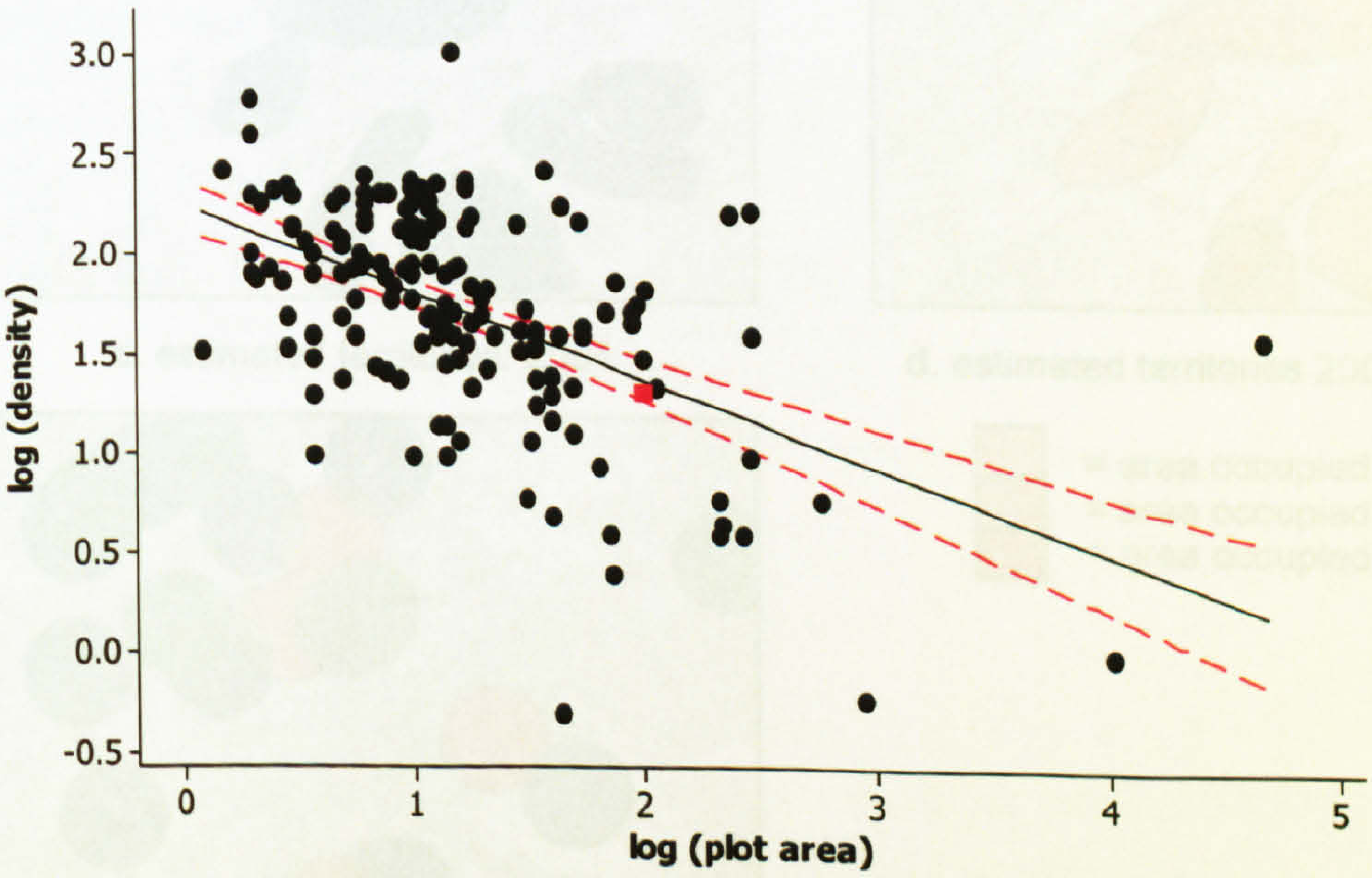


Figure 7.14. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Great Tit. Regression: log(density) = 2.24 – 0.430 log(plot area). $F_{1,195} = 71.58$, $r^2 = 26.9\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 196): black. Data from this study: red.

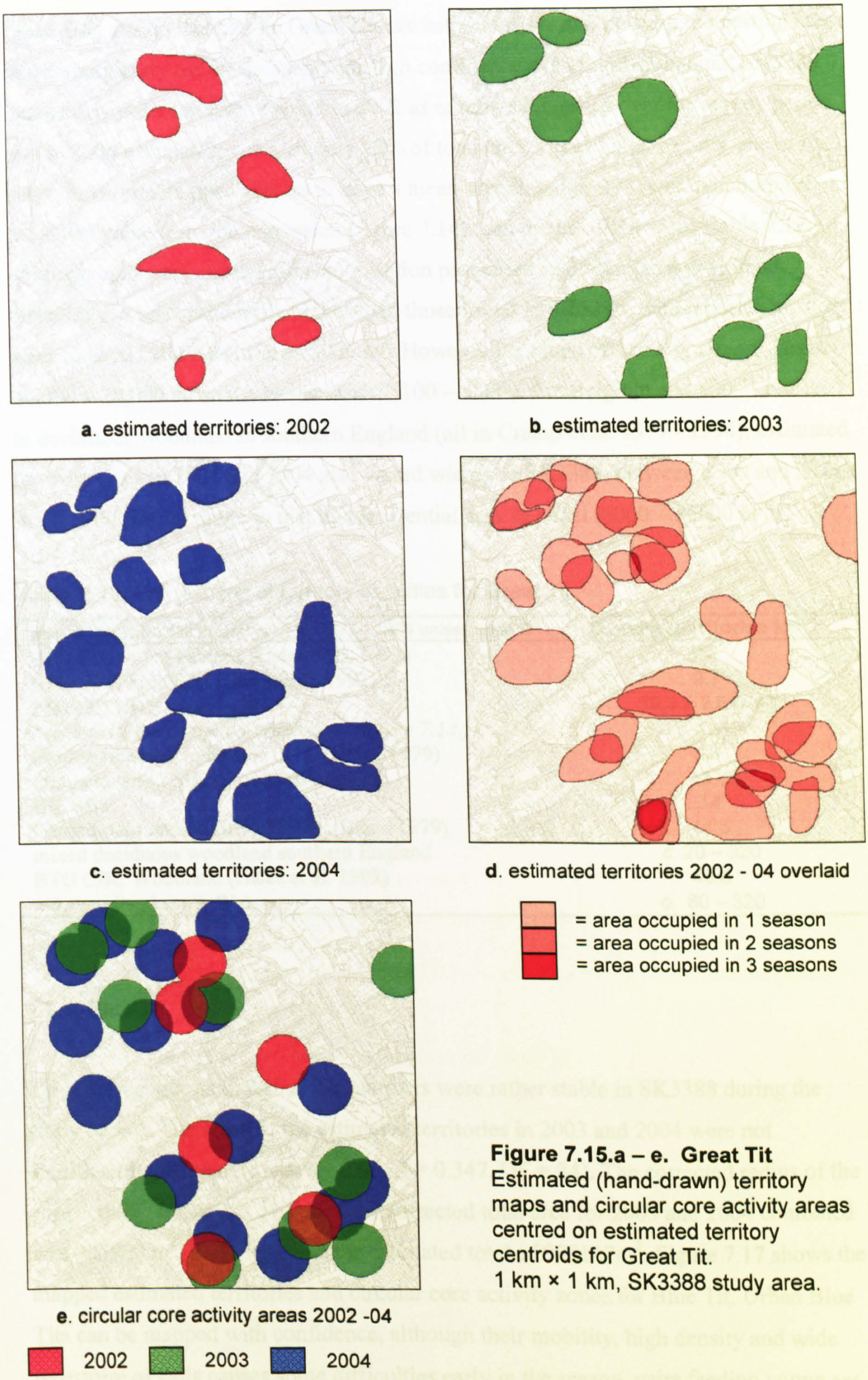


Figure 7.15.a – e. Great Tit
Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Great Tit.
1 km × 1 km, SK3388 study area.

Other than during incubation, Great Tits are active, visible and noisy in the nesting area and consequently can be mapped with high confidence even in urban habitat. SK3388 was clearly not a saturated habitat in 2002 as numbers increased over the survey period and in 2004 occupancy was still only 23% of total area. Great Tit is the only one of the seven territorial mapped species to have a mean breeding density lower than both the predicted value from the regression (figure 7.14), and the UK BBS value (table 7.13.), although both were exceeded as colonisation proceeded in 2004. Rural woodland densities can be considerably higher than those found in SK3388, with reported territory sizes in ideal habitat as little as 5000 m^2. However the range of territory sizes is large, 20,000 – 30,000 m^2 in the Netherlands, 5100 – 8500 m^2 in Belgium and 400 -17000 m^2 in deciduous woodland in southern England (all in Cramp et al. 1977 - 1994); estimated territory sizes in 2003 and 2004 also varied widely in SK3388, between 6540 and 28119 m^2, a quite similar range to that in a residential area in Israel (6000 – 36000 m^2).

Table 7.13. Comparison of territory densities for Great Tit

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
BTO CBC other habitats (Gates et al. 1993)	2.2
BTO CBC Farmland (Gates et al. 1993)	9.7
THIS STUDY mean ± SE	**10.3 ± 2.6 N =3**
Predicted from compiled urban data (figure 7.14.)	12
Garden-rich area in Bristol 1978 (Bland 1979)	13
farmland with hedges, southern England	13.8
UK BBS	14
Garden-poor area in Bristol 1978 (Bland 1979)	14.5
mixed deciduous woodland southern England	*c.* 20 – 320
BTO CBC Woodland (Gates et al. 1993)	48.6
oak woodland south Wales	*c.* 80 – 320

7.3.7. Blue Tit

Table 7.14 suggests that Blue Tit numbers were rather stable in SK3388 during the study period. The areas of the estimated territories in 2003 and 2004 were not significantly different (*t* test, $t = 0.95$, $P = 0.347$, DF = 84). The corrected radius of the core activity zones was 59.7 m, their corrected total area for 2003 and 2004 combined was 905960 m^2, 0.2% less than the estimated total of 907147m^2. Figure 7.17 shows the mapped estimated territories and circular core activity zones for Blue Tit. Urban Blue Tits can be mapped with confidence, although their mobility, high density and wide repertoire of calls causes some difficulties early in the season, pairs feeding young are easy to spot and most use nestboxes, hence mapping nest sites is easy.

Table 7.14. Results of territory mapping for Blue Tit

Year	Number of territories	mean area of estimated territories ± SE m^2
2002	42	7595 ± 616
2003	41	10897 ± 635
2004	46	10008 ± 691
2003 + 2004:		10427 ± 472

This species is associated with artificial food in Britain; breeding density in SK3388 is higher than predicted from an international dataset (figure 7.16) but lower than the UK BBS figure (table 7.15). The habitat may not be saturated, mean occupancy (2003 and 2004) is only 45% and density lower than those attained in woodland habitats.

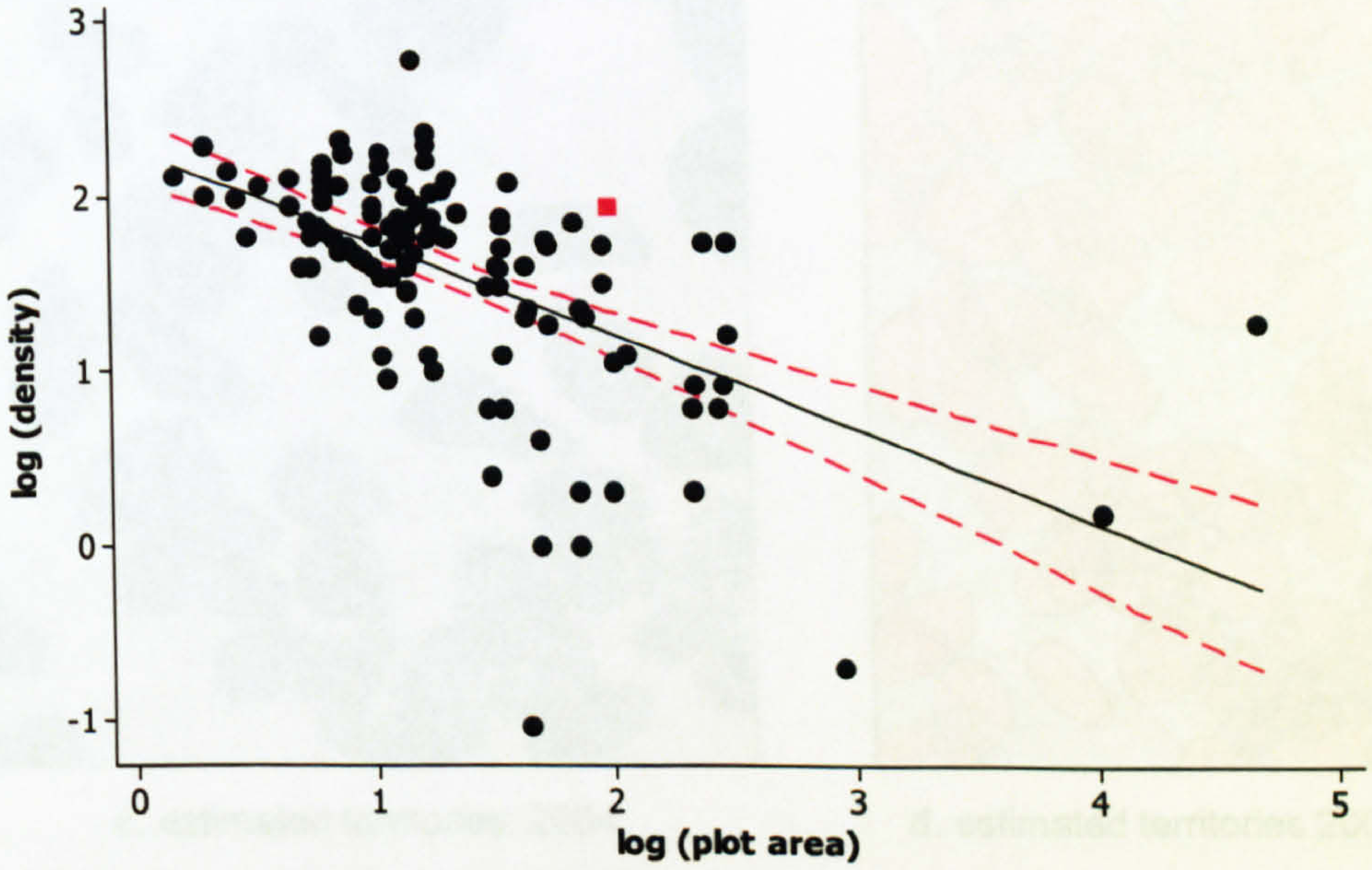
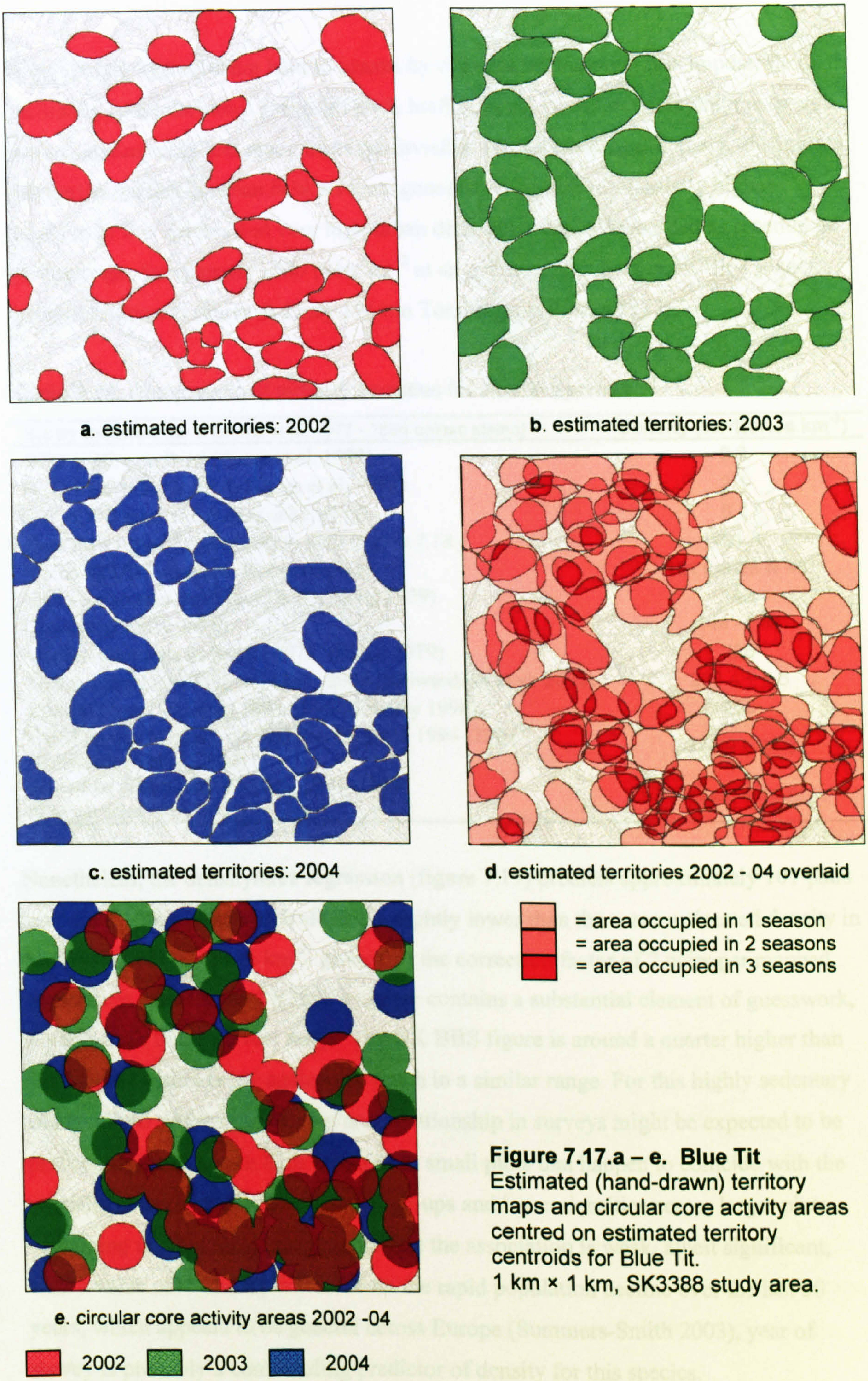


Figure 7.16. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Blue Tit. Regression: log(density) = 2.28 – 0.54 log(plot area). $F_{1,135} = 59.27$, $r^2 = 30.5\%$, $P < 0.001$. Dashed red plots = 95% confidence limits. Data from literature (N = 136): black. Data from this study: red.

Table 7.15. Comparison of territory densities for Blue Tit

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
BTO CBC other habitats (Gates et al. 1993)	6.7
Predicted from compiled urban data (figure 7.16.)	7.9
BTO CBC Farmland (Gates et al. 1993)	18.3
THIS STUDY mean ± SE	**43.0 ± 1.53 N =3**
Garden-poor area in Bristol 1978 (Bland 1979)	50
UK BBS	51.4
BTO CBC Woodland (Gates et al. 1993)	82.4
Garden-rich area in Bristol 1978 (Bland 1979)	91
Dense oak woodland, Surrey	40 - 99
Mixed woodland, Berkshire	51 – 133
Mature oak wood, Gloucestershire	136 - 372
Mature oak wood, Middlesex	190 – 590



a. estimated territories: 2002

b. estimated territories: 2003

c. estimated territories: 2004

d. estimated territories 2002 - 04 overlaid

e. circular core activity areas 2002 -04

Figure 7.17.a – e. Blue Tit Estimated (hand-drawn) territory maps and circular core activity areas centred on estimated territory centroids for Blue Tit. 1 km × 1 km, SK3388 study area.

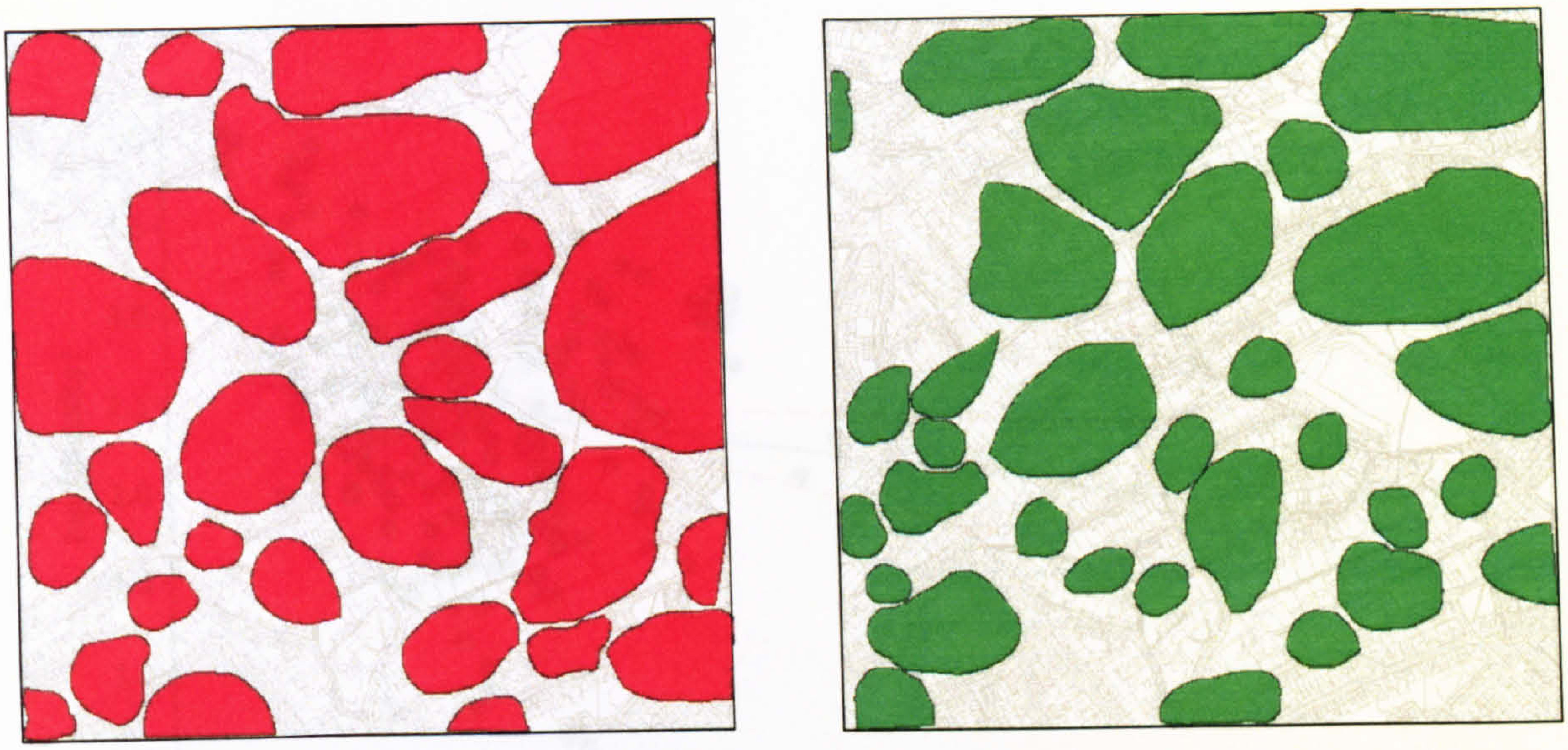
7.3.8. House Sparrow

Urban House Sparrows are hard to census by cumulative mapping; it is impossible to accurately count the small groups of birds loafing in cover without delaying the overall census unacceptably and many nests are invisible behind buildings. Table 7.16 suggests that earlier studies in urban habitats have generally recorded substantially higher densities of this species and very high urban densities were still recorded as recently as 40 years ago, for example 1000 pairs km^{-2} in an urban park in France, in 1964 (exact location unknown) (Ferry & Ferry 1964 in Tomialojc & Profus 1977).

Table 7.16. Comparison of territory densities for House Sparrow

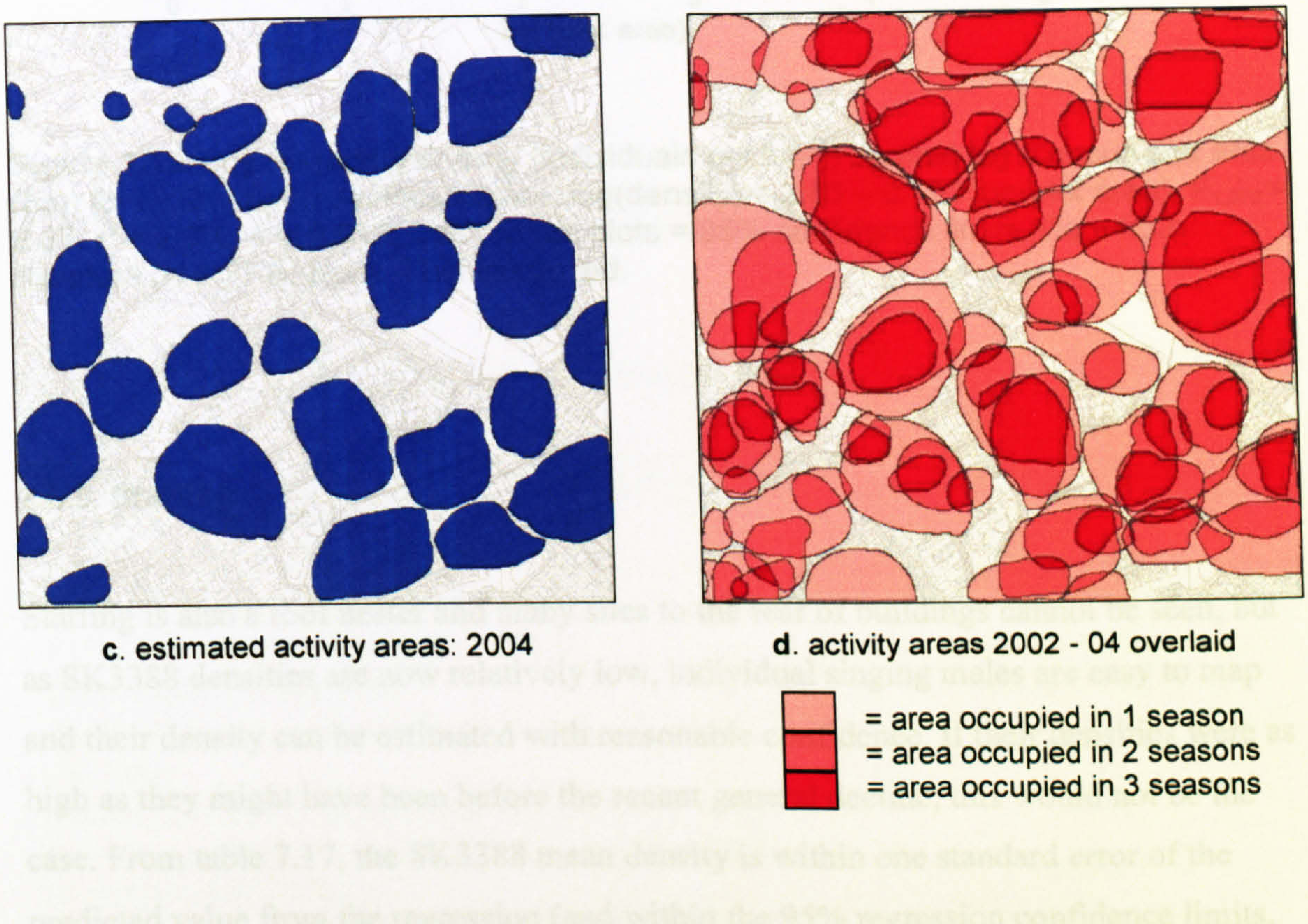
Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
BTO CBC woodland (Gates et al. 1993)	0.6
BTO CBC other habitats (Gates et al. 1993)	2.1
BTO CBC farmland (Gates et al. 1993)	6.1
Predicted from compiled urban data (figure 7.18.)	101.6
THIS STUDY mean ± SE (estimated)	**121 ± 9.26 N =3**
Garden-rich area in Bristol 1978 (Bland 1979)	142
Warsaw (Luniak 1996)	144 - 309
Garden-poor area in Bristol 1978 (Bland 1979)	225
Urban central east England 1994 -2000 (Siriwardena et al. 2002)	238.4 ± 4.6
Central Lvov (Ukraine) 1993-1995 (Bokotey 1996).	256
Rural human habitats, central east England 1994 -2000 (Siriwardena et al. 2002)	348.9 ± 38.8
Suburban central east England 1994 -2000 (Siriwardena et al. 2002)	444.0 ± 19.8

Nonetheless, the density/area regression (figure 7.19) predicts approximately 101 pairs km^{-2} for a 100ha plot, which although slightly lower than the mean estimated density in SK3388 of 121 ± 9 pairs km^{-2}, given that the correction factor of 2 pairs per mapped registration used for the SK3388 estimate contains a substantial element of guesswork, is very much in the correct range. The UK BBS figure is around a quarter higher than the SK3388 estimate but again very much in a similar range. For this highly sedentary and localised species the density/area relationship in surveys might be expected to be particularly strong, with high densities in small plots that happen to coincide with the typically small home ranges of social groups and lower densities across larger plots containing much unoccupied area. In fact the association is weak, albeit significant, with a value of r^2 of only 2.3%. Given the rapid population decline over the last 50 years, which appears to be general across Europe (Summers-Smith 2003), year of survey is probably a confounding predictor of density for this species.



a. estimated activity areas: 2002

b. estimated activity areas: 2003



c. estimated activity areas: 2004

d. activity areas 2002 - 04 overlaid

🟥 = area occupied in 1 season
🟥 = area occupied in 2 seasons
🟥 = area occupied in 3 seasons

Figure 7.18. a – d. House Sparrow
Estimated areas of semi-colonial breeding activity for House Sparrow.
Estimated numbers of pairs; 2002: 138, 2003: 120, 2004: 106.
Area mapped: 1 km × 1 km, SK3388 study area.

Figure 7.18 shows the mapped estimated breeding activity zones for House Sparrow, which is a commensal species and so the concept of habitat saturation is to some extent not ecologically meaningful, however, its ongoing decline both in the study area and elsewhere suggests the population is at its limit.

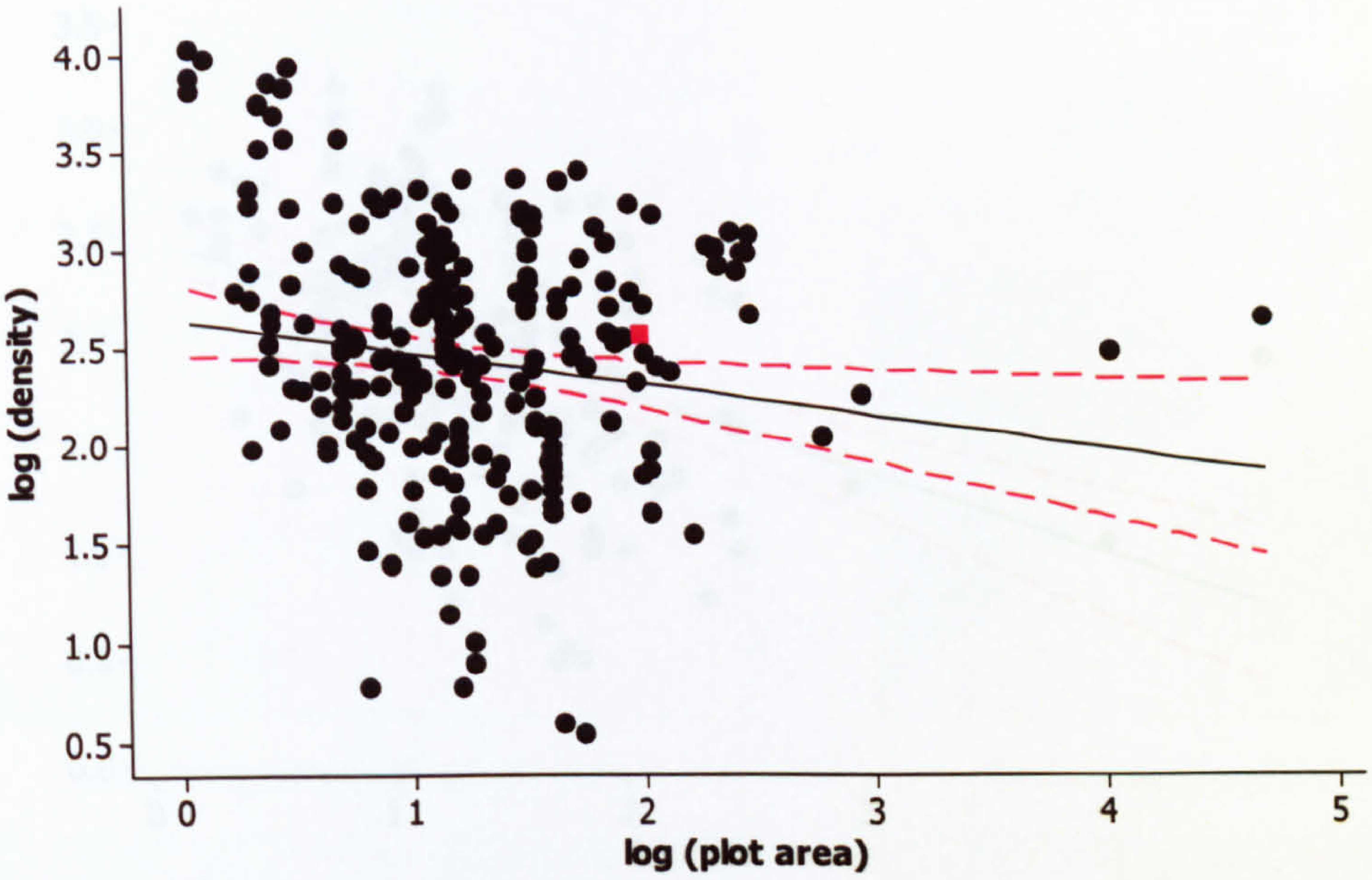


Figure 7.19. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for House Sparrow. Regression: log(density) = 2.63 – 0.161 log(plot area). $F_{1,270}$ = 6.37, r^2 = 2.3%, P = 0.012. Dashed red plots = 95% confidence limits. Data from literature (N = 271): black. This study: red.

7.3.9. Starling

Starling is also a roof nester and many sites to the rear of buildings cannot be seen, but as SK3388 densities are now relatively low, individual singing males are easy to map and their density can be estimated with reasonable confidence. If their densities were as high as they might have been before the recent general decline, this would not be the case. From table 7.17, the SK3388 mean density is within one standard error of the predicted value from the regression (and within the 95% regression confidence limits, figure 7.20) but still less than one third of the UK BBS figure and only one tenth of the value for urban central east England estimated in a recent detailed study (Siriwardena et al. 2002). Figure 7.21 shows the mapped estimated breeding activity zones for this species. There are many more buildings in SK3388 that would be suitable as nest sites and appropriate anthropogenic food is superabundant, nonetheless the population of this species appears to be at its ecological limit in SK3388 and probably declining further.

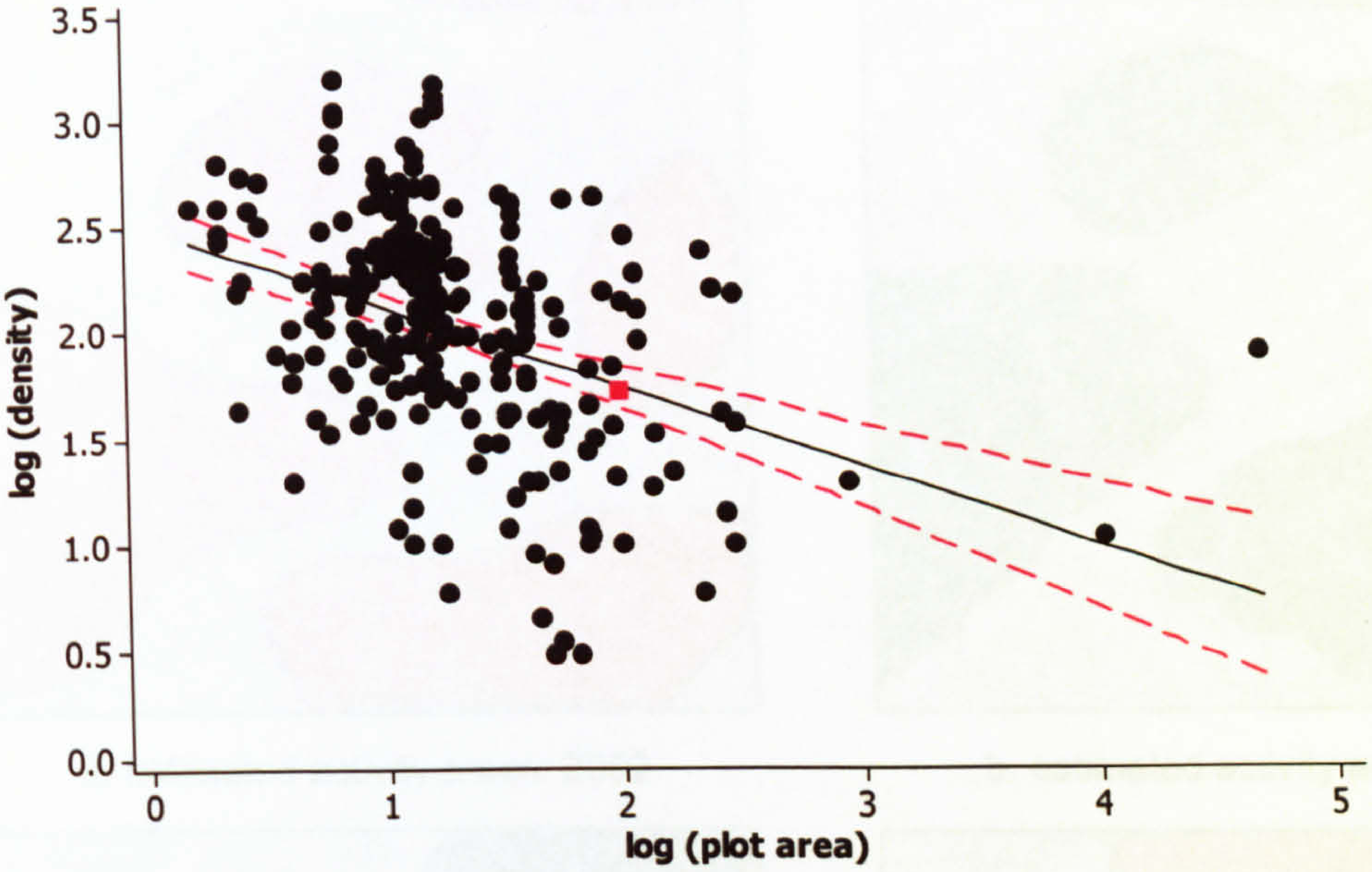
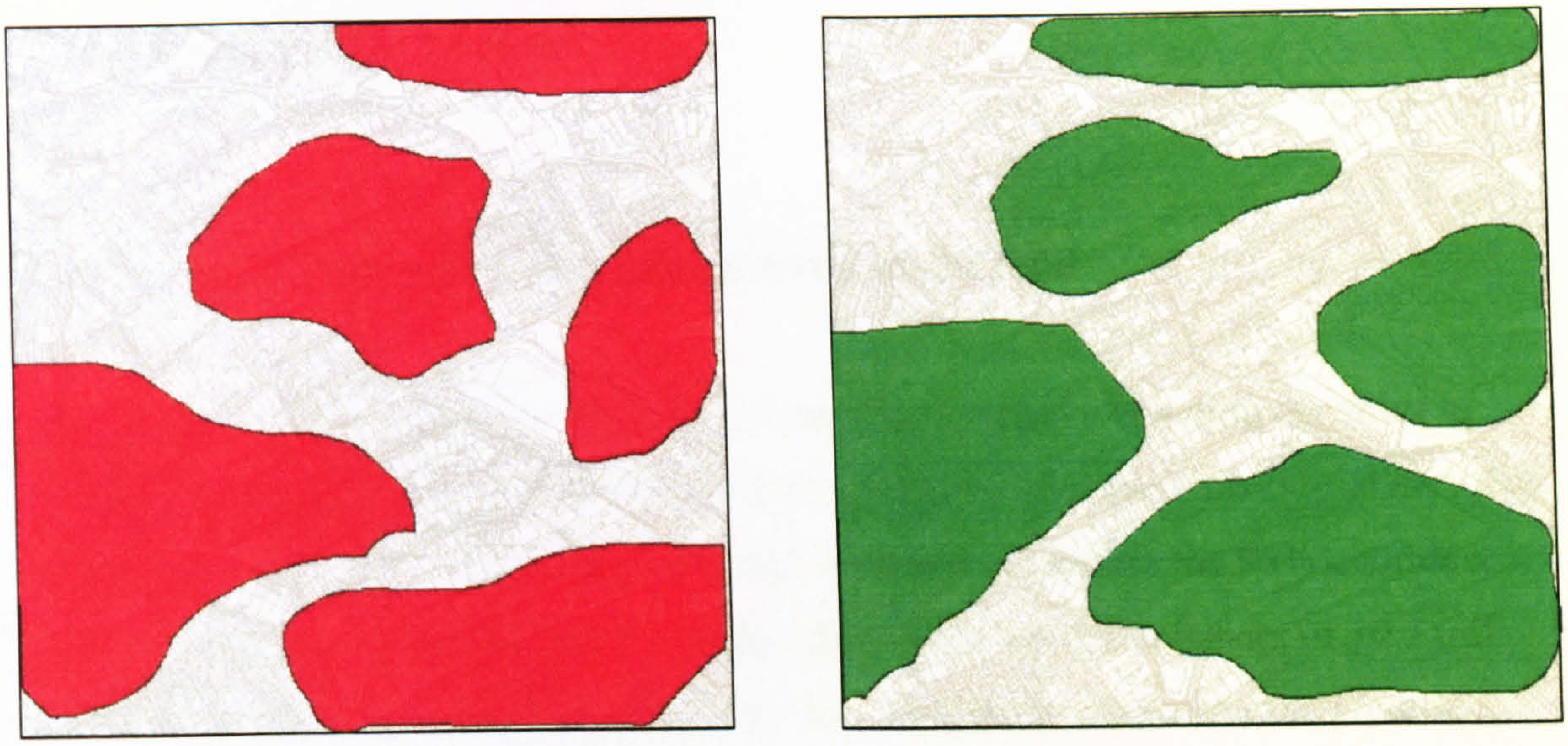


Figure 7.20. Log (breeding density (individuals per km^2)) against log (census plot area (ha)) for Starling. Regression: log(density) = 2.50 – 0.375 log(plot area). $F_{1,266}$ = 45.78, r^2 = 14.7%, P < 0.001. Dashed red plots = 95% confidence limits. Data from literature (N = 267): black. Data from this study: red.

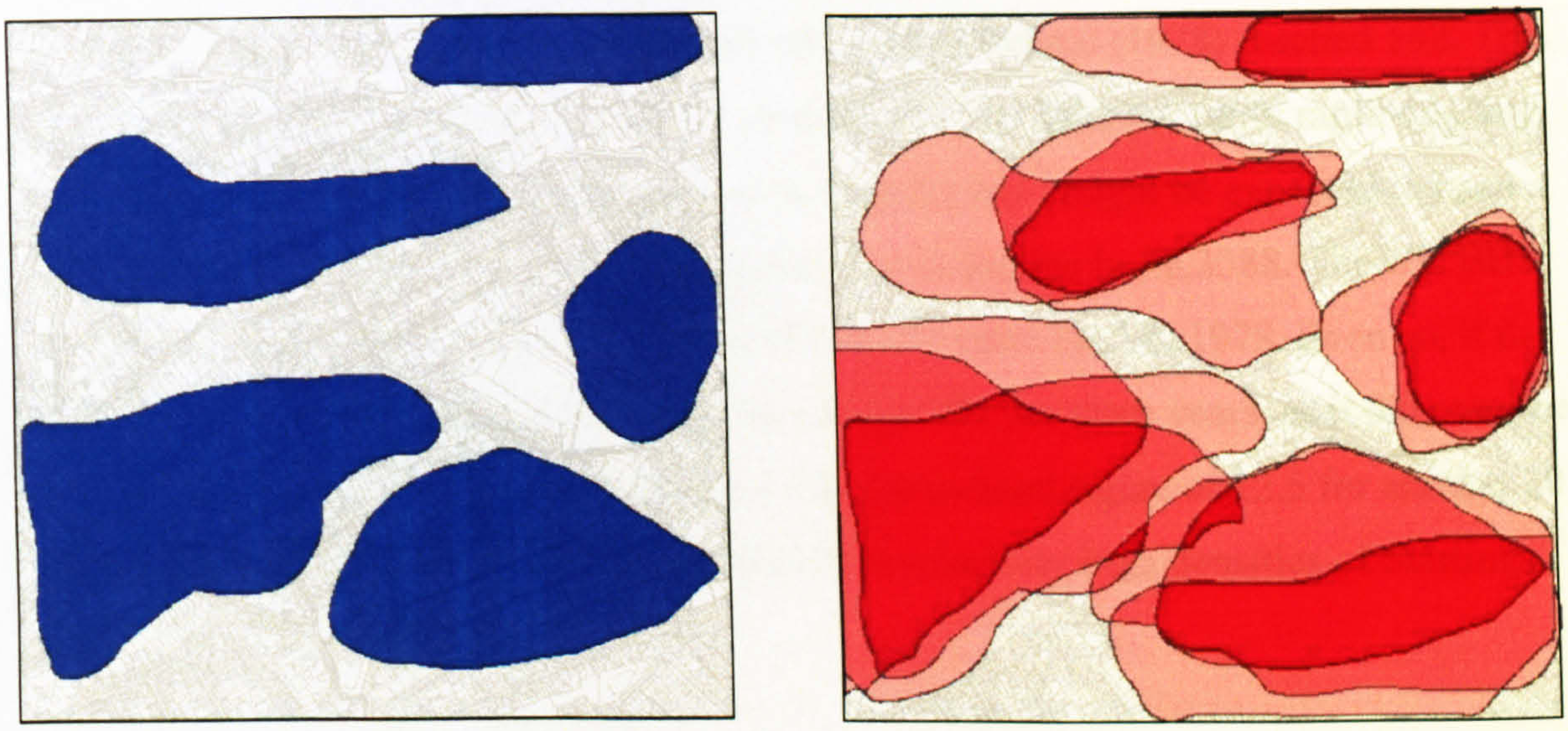
Table 7.17. Comparison of territory densities for Starling

Study location (all in Cramp et al. 1977 - 1994 unless stated)	**Density (territories km^{-2})**
BTO CBC other habitats (Gates et al. 1993)	3.5
Warsaw 1971-73, city centre (Luniak 1977).	6
BTO CBC farmland (Gates et al. 1993)	6.3
BTO CBC woodland (Gates et al. 1993)	12.5
THIS STUDY mean ± SE	**26.33 ± 1.76 N =3**
Predicted from compiled urban data (figure 7.20.)	28.1
UK BBS	90
Garden-poor area in Bristol 1978 (Bland 1979)	101
Rural human habitats, central east England 1994 - 2000 (Robinson et al. 2002a)	102.5 ± 16.7
Garden-rich area in Bristol 1978 (Bland 1979)	117
Urban central east England 1994 - 2000 (Robinson et al. 2002a)	245.9 ± 33.9
Warsaw 1971-73, allotments at city edge (Luniak 1977).	360



a. estimated activity areas: 2002

b. estimated activity areas: 2003



c. estimated activity areas: 2004

d. activity areas 2002 - 04 overlaid

🟥 = area occupied in 1 season
🟥 = area occupied in 2 seasons
🟥 = area occupied in 3 seasons

Figure 7.21. a – d. Starling
Estimated areas of semi-colonial breeding activity for Starling, 2002, 2003 and 2004. Estimated numbers of pairs; 2002: 27, 2003: 29, 2004: 23 Area mapped: 1 km × 1 km, SK3388 study area.

7.4. General Discussion

7.4.1. Relative density of breeding birds in SK3388

Of the nine species mapped, only Great Tit and Starling have breeding densities in SK3388 lower than those predicted by linear regression of urban density/plot area data from other locations and both their observed densities are within the 95% confidence limits of the regressions (figures 7.14 and 7.20). Great Tit mean density of 10.3 (all density figures in this section are pairs km^{-2}) is marginally lower than the predicted figure of 12 but still higher than the BTO CBC farmland density of 9.7. The figure for UK BBS is 82.5 and density in the garden-rich area of Bristol (1978) reached 142. This is clearly a dynamic population with only 6 pairs km^{-2} in 2002 but fairly rapid ongoing colonisation since. In contrast, Starling at 26.33 pairs km^{-2} might be expected to have a lower density than the 28.1 predicted because it is in decline in SK3388. The UK BBS figure is 90 and garden-rich areas of Bristol had 101 pairs km^{-2} in 1978. Even so, if the population in SK3388 continued to drop at a linear 7% per three years, as it did over the survey period, it would not reach the BTO CBC woodland figure of 12.5 for another 20 years; built habitats remain important refuges for relatively high densities of Starlings (Robinson et al. 2002a).

The other seven species mapped all have higher densities in SK3388 than predicted by their regression lines. The estimated figure for House Sparrow (121) is slightly higher than the predicted 101.6, and is a minimum estimate that should be treated with caution. Despite this species' general decline, the SK3388 density probably still compares quite well with that of garden-rich areas in Bristol in 1978 (142) although it is well short of the suburban central-east England figure of 444. The remaining six species all occur in SK3388 at much higher densities than the values predicted by other surveys, which for Robin was only 8.7, similar to that of garden-poor Bristol (7.2) but below the SK3388 density of 23.3 which is not far off the rural average of 30 although garden-rich Bristol supported a much higher 90 pairs km^{-2}. Dunnock too had a predicted value (8.8) similar to that of garden-poor Bristol (7.2) but much lower than the SK3388 density of 20.7 which approaches that of BTO CBC woodland (26.6). Magpie predicted density was only 5.05 whereas that in SK3388 (21.0) was very similar to that of Polish rural villages in 1992 (21.3 but probably increased since) although still short of the urban northern

England maximum of 32. Wren density at 22.3 pairs km^{-2} was also much higher than the predicted 6.0 and slightly higher than that of Suffolk farmland (20.7), Blue Tit density though was considerably lower than that of garden-rich Bristol (91); at 43.0 the SK388 density was closer to the 50 of garden-poor Bristol and very much lower than densities in oak woodlands (136 – 590). Finally, SK3388 is a productive habitat for Blackbirds; their observed breeding density was twice that predicted from the international data, although the population fell by 15% between 2003 and 2004.

In general, SK3388 supports denser breeding populations of individual species than would be expected from other urban studies and, with the exception of species undergoing rapid change in their local population, densities are closer to those of garden-rich and/or rural habitats than those of garden-poor urban environments. One shortcoming of predicting territory densities for a given plot area from the regressions is that the negative relationship between survey area and observed density is likely to be particularly strong in urban habitats because small urban survey plots are typically 'habitat islands' that support very high densities of breeding birds, particularly if nests are clustered within them because they provide the only suitable nesting habitat within the larger area over which the nesting pairs' territories actually extend. Conversely, breeding densities over large urban study plots may well be low, because such areas include large tracts of core urban habitat that supports few birds. Hence it is not surprising that a density/plot area regression for urban sites should have a steep negative slope and predict lower densities than are in fact found in a medium-sized plot of uniform residential habitat with many gardens.

7.4.2. The complete breeding avifauna and its relative density

In order to compare the overall bird density of the survey area with other urban habitats, it is necessary to estimate the entire breeding avifauna; as shown in table 7.18, which also shows theoretical maximum zero-mortality post-breeding numbers of birds in the study area to provide some insight into mortality and emigration rates. Estimating the total breeding avifauna in SK3388 is problematic due to the visibility issues that limit accurate territory mapping to singing territorial species, nonetheless other species can be estimated during territory mapping fieldwork with reasonable accuracy (Tomialojc 1980) by a combination of mapping, incidental observations and informed estimation, taking into account known nesting locations. Transient species observed during census visits but with no indications of breeding activity were Grey Heron, Sparrowhawk, Whitethroat, Willow Warbler, Pied Wagtail, Grey Wagtail, Redpoll, Jay and Rook.

Table 7.18. Estimated breeding avifauna of SK3388, 2002 -2004 (pairs) with zero mortality maximum post-breeding population (individuals) of resident species (**N_{pb}**), calculated as (number of pairs) × (maximum theoretical annual productivity per pair (**P**)) + (number of pairs) × 2. Figures for maximum productivity **P** from Robinson (2005). ** = numbers of pairs censused with confidence from territory mapping.
* = numbers of pairs estimated from cumulative mapping of breeding activity.
† = known exactly. No superscript = from supporting and incidental observations, with confidence except for Swift and Feral Pigeon which are estimates only.

Year:		2002		2003		2004	
Species	**P**	**Pairs**	**N_{pb}**	**Pairs**	**N_{pb}**	**Pairs**	**N_{pb}**
Feral Pigeon	10	15	180	15	180	15	180
Stock Dove	6	2	16	4	32	2	16
Woodpigeon *	4	12	72	24	144	23	138
Collared Dove *	8	15	150	19	190	17	170
Tawny Owl†	2	1	4	1	4	1	4
Swift	2	25	100	20	80	15	60
Wren **	4	20	120	25	150	22	132
Dunnock **	8	13	130	24	240	25	250
Robin **	9	17	187	32	352	21	231
Blackbird **	12	81	1134	80	1120	68	952
Song Thrush	12	1	14	1	14	1	14
Mistle Thrush	8	2	20	2	20	2	20
Blackcap	8	1	10	2	20	1	10
Goldcrest	14	0	0	1	16	3	48
Long-tailed Tit	7	3	27	2	18	2	18
Coal Tit	8	1	10	2	20	4	40
Blue Tit **	8	42	420	41	410	46	460
Great Tit **	8	6	60	10	100	15	150
Nuthatch†	5	0	0	0	0	1	7
Magpie **	4	18	108	22	132	23	138
Carrion Crow†	4	2	12	2	12	2	12
Starling *	4	27	162	29	174	23	138
House Sparrow *	10	138	1656	120	1440	106	1272
Chaffinch	4	2	12	2	12	3	18
Greenfinch *	8	12	120	18	180	15	150
Goldfinch	8	4	40	4	40	5	50
Bullfinch	8	0	0	1	10	1	10
Totals:	191	460	4764	503	5110	462	4688

Feral Pigeon numbers in SK3388 (an estimated 15 pairs, more or less constant 2002 - 04) are lower than in core urban habitats in Sheffield and confined to a few taller buildings; these primarily determine the distribution of this species as they provide the high nesting and loafing sites required (Cramp et al. 1977 - 1994). Very high densities are possible in core urban habitats, hence across urban areas as a whole mean densities tend to be higher than in SK3388, from 72 pairs km^{-2} upwards in Warsaw (Luniak 1996) and 58 pairs km^{-2} in Lvov (Bokotey 1996), for example. One of the most interesting of the scarcer breeding species of SK3388 is Stock Dove, nesting unobtrusively in pollarded street trees and chimneys, overlooked by most bird spotters who disregard anything similar to a Feral Pigeon. This is not a typically urban species, it's small-scale colonisation of SK3388 may be a reflection of an overall national population increase and is not necessarily secure; the birds were less visible in 2004 than in 2003 when at least four pairs were easily seen and heard; no casual records were acquired in 2005, disturbance of trees and buildings may have displaced them.

In SK3388, Woodpigeons are more numerous and visible than Collared Doves, the former increasing notably from 2002 to 2003 (although stable in 2004) while the latter, smaller species appears stable despite its high productivity and observed ability to breed as early as February in SK3388. In 2002, Woodpigeon nestlings in SK3388 were regularly predated by a large, non-resident, female Sparrowhawk; breeding numbers doubled in 2003 when this predator was not observed, perhaps more closely reflecting the increasing national population and general urbanisation of Woodpigeons (Crick et al. 2004; Mead 2000). Several casual observations of Woodpigeons' first occurrences at feeding stations were received in 2005; this species may be responding in a similar way to the Magpie to the maturation of street trees, which provide increasing numbers of nest sites, and to a superabundance of anthropogenic food. Successful ongoing urbanisation of the larger, native species might have negative implications for the smaller non-native Collared Dove, which uses similar resources and has remained largely dependent on human habitats throughout its recent colonisation of Great Britain. Collared Dove breeding density in SK3388 is around half that in Lvov (Bokotey 1996).

A single pair of Tawny Owls breeds in or close to SK3388; in 2002 fledged young were found within the study area, in 2003 and 2004 adults were regularly observed and extremely vocal. It is not unusual for this species to breed in large urban parks with densities as high as five (Biadun 1994) or six (Tomialojc & Profus 1977) pairs km^{-2}, but the SK3388 pair does well to persist given the absence of mature parkland and the relative paucity of Starlings, a favoured urban prey species. It may be that they are controlling the SK3388 population of the Grey Squirrel which casual observations suggest is around ten pairs km^{-2} and surprisingly stable, given the superabundance of anthropogenic food. Brown Rat and Wood Mouse are also abundant potential prey.

Swift numbers could only be estimated but declined noticeably over the three year survey period, mirroring a national decrease in numbers (BBS -22% 1993 – 2004, (Raven et al. 2005)). Across Warsaw overall breeding density was 10 – 11 pairs km^{-2} (Luniak 1996), in Lvov, 27 pairs km^{-2} (Bokotey 1996); these populations may also have declined if Swifts elsewhere face similar problems. Historically, much higher urban densities have been recorded (Mead 2000). Neither Swallow nor House Martin occur in SK3388 and are extremely scarce in Sheffield as a whole. The red-listed (Baillie et al. 2005) Song Thrush is very scarce in SK3388 with only one pair at most, very few juveniles were observed and all nests located were destroyed by predators. In contrast, the larger, stronger Mistle Thrush is notably successful in SK3388 with at least two broods reared in all three years. At least one pair of Blackcap bred successfully in all three years and the number of singing Goldcrests increased notably over the study period with families observed in 2003 and 2004. The numbers of Long-tailed Tit pairs in table 7.18 are probably underestimates as breeding pairs of this species are hard to observe without good and sustained visibility into gardens; however, the productivity estimate is probably a maximum as nest predation rates are high. The estimated mean density of 2.5 pairs km^{-2} lies between the 1.74 pairs km^{-2} in BTO CBC farmland plots and 7.02 pairs km^{-2} in woodland (Gates et al. 1993) but is much lower than breeding densities of 12 -13 pairs km^{-2} reported from a woodland site located on the edge of Sheffield only 6 km away from SK3388 (Hatchwell et al. 2001).

Coal Tits became more common in SK3388 over the study period, and the national population is generally stable (Baillie et al. 2005) although BBS suggests a recent decline (Raven et al. 2005). Increased use of urban garden habitat may be linked to the recent adoption by garden bird feeders of more suitable food, notably black sunflower seeds which are extremely popular with this species. Two pairs of Carrion Crow nested successfully in the study area in all three survey years. Urban populations of corvids generally appear to be increasing (Marzluff et al. 2001c; Vogrin 2003; Vuorisalo et al. 2003) and the national population is increasing steadily (Baillie et al. 2005) but numbers in SK3388 are probably constrained by the limited availability of tall trees for nesting. Residents of SK3388 report that the crows are a recent arrival in the area. Very few Chaffinches bred in SK3388 during the study period, the small numbers estimated are maxima based on singing males, not all of which may actually have bred successfully. This is surprising considering the much higher densities reported elsewhere (e.g. Bland 1979; Huhtalo & Järvinen 1977; Kocian et al. 2003), that this species is a frequent visitor to feeding stations in suburban and rural gardens around Sheffield (pers. obs.) and that it is known to breed readily in "the interiors of large cities" (Snow et al. 1998). Furthermore, the average GBW reporting rate for April – June was 76% of gardens (Toms 2003). Greenfinches, in contrast, use feeders year-round in SK3388 and although it is not meaningful to map their territories as they only defend small areas around nests, the males do sing from regular song-posts (Snow et al. 1998) and hence the densities in table 7.18 were derived from cumulative registrations with reasonable confidence. This species frequently nests in 'neighbourhoods' of 4 – 6 pairs (Snow et al. 1998) so densities are often uneven, varying between 45 – 59 and 184 pairs km^{-2} in Krotoszyn (Kosinski 2001). The more or less constant small number of breeding pairs of Goldfinch in SK3388 fails to reflect a steady increase in use of the site by post-breeding and winter feeding flocks during the survey period. Finally, Bullfinch is a regular user of garden feeders in suburban Sheffield but appears to be a new arrival in SK3388 during the study period (pers. obs.), with at least one pair breeding in 2003, 2004 and 2005.

Total breeding species richness was 27 species (table 7.18). Of the 25 species reported in 10% or more of GBW gardens between April and June (Toms 2003), five did not breed in SK3388. The only Great Spotted Woodpeckers (22% of GBW gardens, Toms 2003) seen were transient juveniles, one caught and ringed in 2003 and a casual observation in 2005. Jays (12% of GBW) were occasionally seen in all three census years but did not breed; Jackdaws (29% of GBW) were absent. Single Pied Wagtails (10% of GBW) were seen in transit but were not observed to feed, let alone breed. Rooks (12% of GBW) are colonial breeders and there is no colony in SK3388; they commute over the site between a colony elsewhere and a large refuse tip to the north but very rarely land. The seven SK3388 breeders with average GBW April – June national reporting rates of less than 10% of gardens were Blackcap (6% of GBWgardens, Toms 2003), Bullfinch (8%), Goldcrest (4%), Mistle Thrush (9%), Tawny Owl (2%), Stock Dove (negligible in GBW) and Swift (not surveyed in GBW).

Table 7.19 compares the total breeding density in SK3388 with that of other sites. This shows that the total breeding density compares well with that found over entire large cities (Berlin) and with that of small cities (Leghorn, Lvov) but is much lower than that typical of the centres of large cities where there are high densities of feral synanthropes. Nonetheless, a residential study area of a small town in northern Finland of almost identical area (95 ha) and the same species richness (Tornio) had overall breeding density 60% higher, suggesting that although the gardens of SK3388 support a breeding bird density that is within the normal range for urban habitats, it falls between the higher densities found in both core urban and suburban habitats.

Table 7.19. Total breeding densities for all species in urban study sites, from literature, with that for SK3388 shown for comparison.

Study location	Breeding pairs km^{-2}
Olsztyn (Poland): industrial areas with high species richness (Dulisz & Nowakowski 1996).	300
Tornio (northern Finland) (30 ha built-up area, 14 spp) (Huhtalo & Järvinen 1977)	326
Berlin – entire city area (Witt 1984 in (Luniak 1996)	225 - 337
Leghorn (Italy) (Dinetti et al. 1996).	419
SK3388- this study	**mean 475**
Central Lvov (Ukraine) 1993-1995 (Bokotey 1996).	500 - 550
Olsztyn (Poland): overall mean (Dulisz & Nowakowski 1996).	540
Warsaw 1986 – 1990 (Luniak 1996).	392 - 762
Warsaw 1986 – 1990 old central parks (Luniak 1996).	500 - 1000
Tornio (northern Finland) (95 ha residential area, 27 spp) (Huhtalo & Järvinen 1977)	758
Olsztyn (Poland): old town tenements, low species richness (Dulisz & Nowakowski 1996).	800
Warsaw 1986 – 1990 new housing estate (Luniak 1996).	1280
Warsaw 1986 – 1990 built-up city centre (Luniak 1996).	1180 – 2380
Berlin – 30 ha around zoo (Lenz 1971 in Tomialojc & Profus 1977)	2310
Wroclaw (Poland) 1970-73, 23 ha urban parks (Tomialojc & Profus 1977).	2422

7.4.3. Changes in density and distributions

There were some interesting changes in densities and distributions over the survey period. Robin density varied quite dramatically, almost doubling from 2002 to 2003 then dropping back by a third to 2004. Dunnock and Magpie, in contrast, showed a very similar pattern of change, increasing substantially from 2002 to 2003 then remaining more or less the same in 2004. Wren numbers were comparatively stable, up 25% in 2003 then down 12% in 2004. Blackbird numbers were remarkably consistent between 2002 and 2003 (which suggests that low numbers for other species in 2002 are not an artefact of fewer census visits but accurate) yet dropped by 15% in 2004. Great Tits appeared to be actively colonising the study area during the study period, increasing by

66% in 2003 and another 50% in 2004 while Blue Tit numbers were comparatively stable. House Sparrow and Starling are declining, House Sparrow more consistently. Table 7.20 compares SK3388 densities with BTO/CJ Garden BirdWatch (GBW) mean reporting rates and UK BBS population changes in the same three years. The drop in Robin numbers in 2004 is reflected in a -6% drop in BBS index but the same BBS decline in Dunnock has not impacted the SK3388 population, although as actual Dunnock numbers cannot be directly calculated from territory numbers, due to their complex breeding system, the very small change in the number of territories in SK3388 between 2003 and 2004 may not reflect actual population change. The increase in Magpies in SK3388 appears to oppose declining BBS indices; the GBW reporting rate varies inconsistently. All three measures are consistent for Wren and Great Tit but the increase for Great Tit in SK3388 is faster than that in either of the other two measures.

Table 7.18 Numbers of breeding pairs in SK3388 in 2002, 2003 and 2004, for species censused by territory mapping, with Garden BirdWatch (GBW) mean quarterly reporting rates and BBS population changes for England shown for comparison. Figures in bold type indicate species/year combinations in which the directions of all three measures were consistent.

[†] GBW values are means of the 13 weekly reporting rates in the second quarter of each year i.e. week numbers 14 – 26 (April – June), for urban gardens only.

[‡] BBS values are percentage population changes with respect to the previous year for England, all habitats (Raven et al. 2003; Raven et al. 2004; Raven et al. 2005).

Year:	**2002**			**2003**			**2004**		
Species	**SK3388**	**GBW[†]**	**BBS[‡]**	**SK3388**	**GBW[†]**	**BBS[‡]**	**SK3388**	**GBW[†]**	**BBS[‡]**
Robin	17	0.610	+ 5	**32**	**0.645**	**+ 2**	**21**	**0.642**	**- 6**
Dunnock	13	0.598	+ 4	**24**	**0.653**	**+ 5**	25	0.660	- 6
Magpie	18	0.435	- 2	22	0.40	- 1	23	0.436	- 4
Wren	20	0.267	- 3	**25**	**0.315**	**+ 3**	**22**	**0.308**	**- 3**
Blackbird	81	0.930	+ 3	80	0.938	+ 3	**68**	**0.928**	**- 3**
Great Tit	6	0.67	- 2	**10**	**0.68**	**+ 4**	**15**	**0.685**	**+ 8**
Blue Tit	42	0.829	+ 4	41	0.831	+ 6	46	0.826	- 2
House Sparrow	138	0.779	- 1	120	0.803	+ 2	106	0.765	+ 1
Starling	27	0.718	- 5	29	0.704	- 17	**23**	**0.676**	**- 9**

The apparent decline in SK3388's Blackbirds in 2004 is reflected in decreasing values for both GBW urban reporting rate and BBS index, whereas the SK3388 Blue Tit population seems to be decoupled from national population changes, rising in a year with falling BBS index (2004) and falling slightly in a year with rising index (2003). House Sparrows appear to be staging a small recovery nationally, according to BBS, but this is not reflected in the declining SK3388 population; also, the GBW urban reporting rate is down overall over the study period, although variable. An increase in SK3388 Starling numbers of only two pairs from 2002 to 2003 is well within likely census error;

both GBW and BBS figures are declining in line with the overall observed trend in SK3388 (there were strikingly few casual observations of this species in 2005). Overall, the correspondence between SK3388 populations and national data are mixed. Robins and Wrens may be less protected from winter conditions in SK3388 than the more omnivorous, feeder-exploiting tits, Blackbird and Magpie.

The different colours (2002 red, 2003 green and 2004 blue) of the mapped core activity areas in figures 7.5.e., 7.7.e., 7.9.e., 7.11.e., 7.13.e., 7.15.e., 7.17.e., and the overlaid breeding activity zones in figures 7.18.d. and 7.21.d show the positions of the territories varied over the three years, in addition, figures 7.22 and 7.23 summarise the proportions of the study area occupied by breeding territory in different numbers of years.

Dunnock and Wren have similar numbers of territories but Dunnocks appear to be more mobile, re-using a lower proportion of their mapped territory than Wrens. Mapped areas of breeding activity for Starling are remarkably consistent in position; sedentary House Sparrows also have high re-use percentages although for House Sparrow, comparing figures 7.19.a. and 7.19.c., the areas of mapped breeding activity have clearly shrunk between 2002 and 2004, despite the fewer census visits in 2002. In contrast, proportions of re-use in Blue Tit and Blackbird may be partially explained by increasing density.

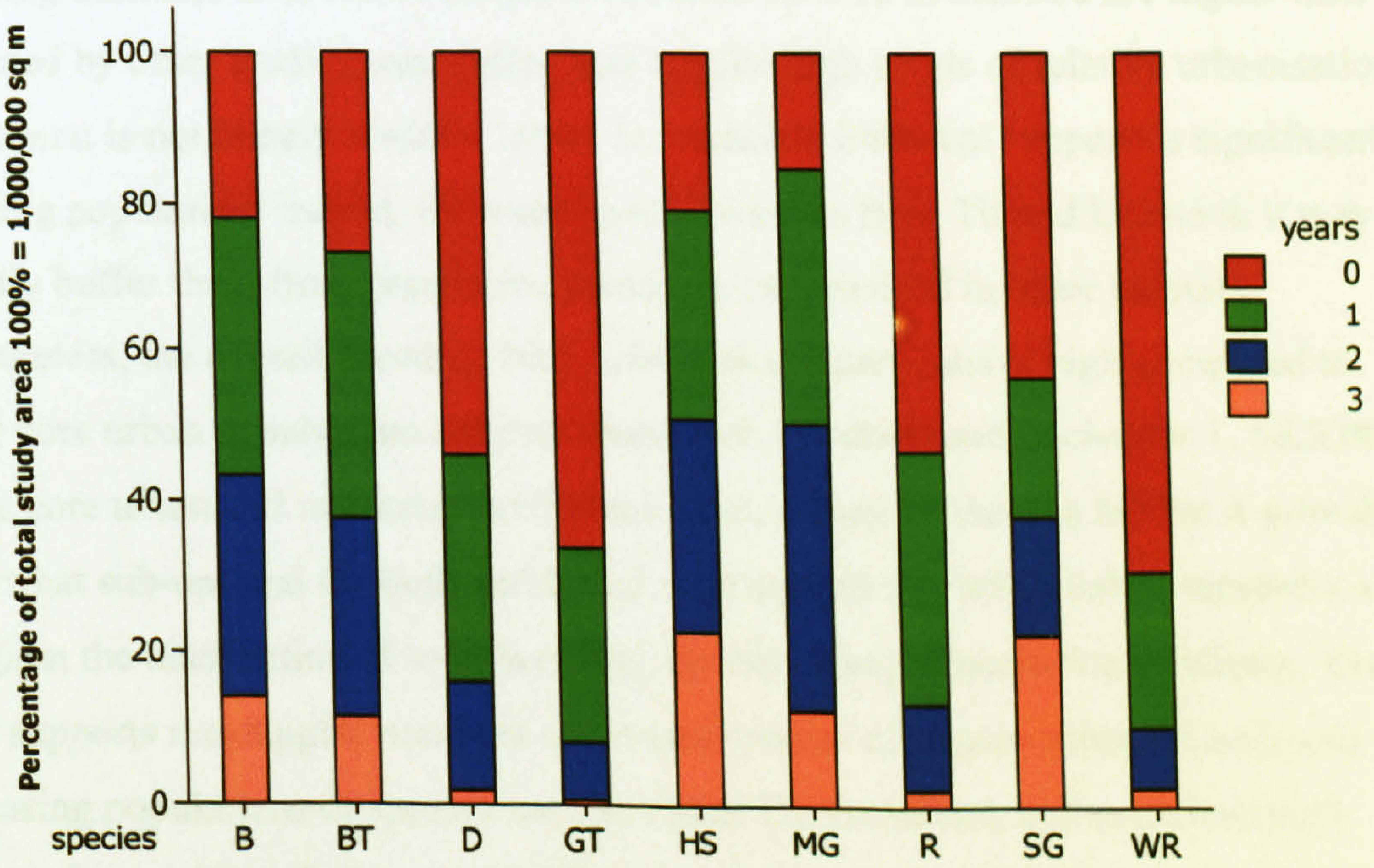


Figure 7.22. Percentages of the total area of SK3388 (1×10^6 m^2) occupied by mapped territory in zero, one, two and all three of the years 2002, 2003 and 2004 for the seven territorial and two semi-colonial mapped species. B = Blackbird, BT = Blue Tit, D = Dunnock, GT = Great Tit, HS = House Sparrow, MG = Magpie, R = Robin, SG = Starling, WR = Wren.

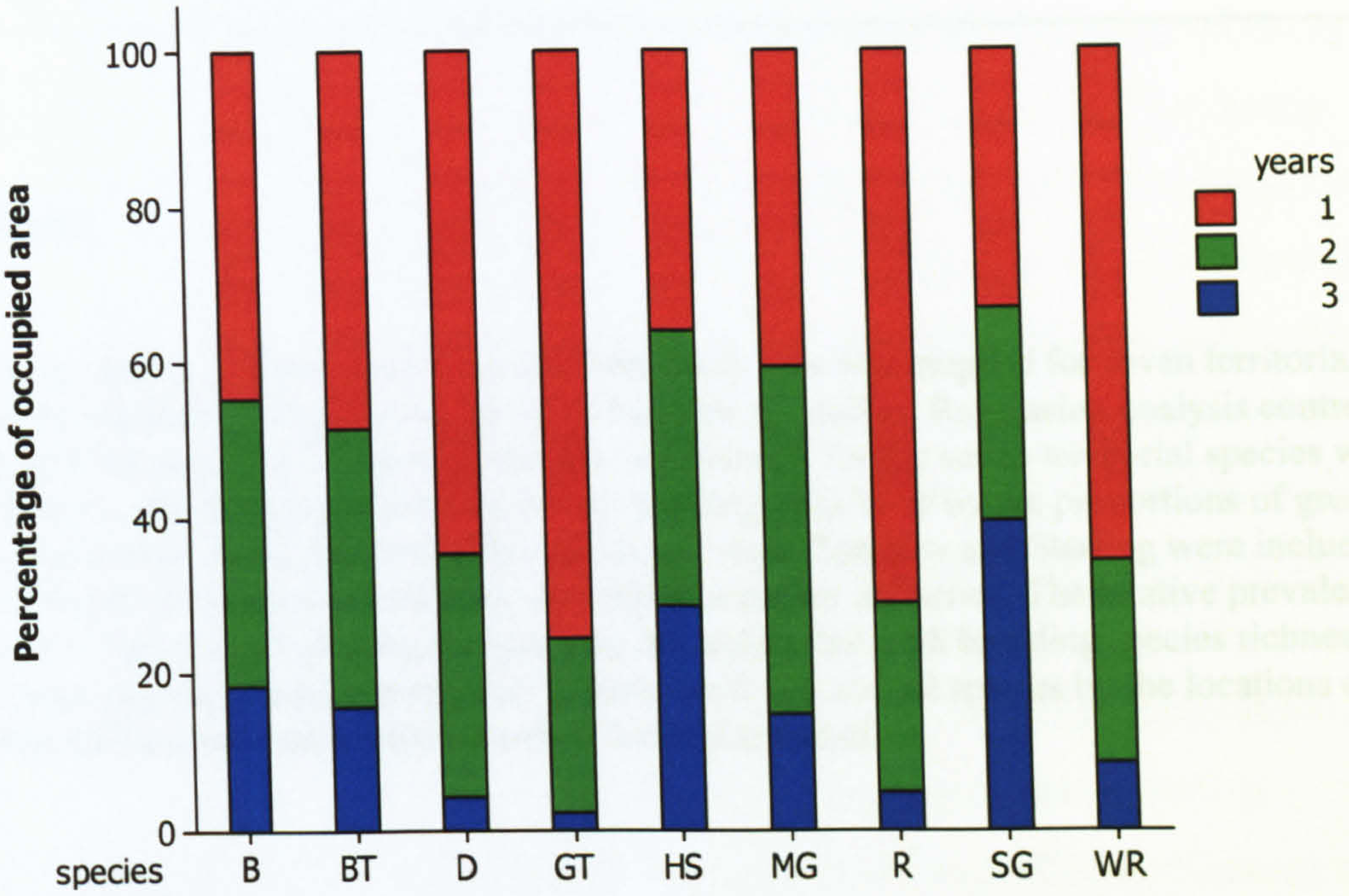


Figure 7.23. Percentages of the areas of SK3388 occupied by mapped territories for each species that were occupied in one, two and all three of the years 2002, 2003 and 2004. Species codes as figure 7.22.

7.5. Conclusions

Breeding densities of seven of the most common species in SK3388 are higher than predicted by other studies, suggesting that despite high levels of relative urbanisation this habitat is not merely a winter larder for transient birds but supports a significant breeding population; indeed, for some species such as Blue Tit and Dunnock it may actually buffer them from population pressures experienced in other habitats. Nonetheless, the overall breeding bird density is not particularly high compared to either core urban or suburban habitats elsewhere. As discussed in chapter 1, SK3388 is where core urban and non-urban avifaunas meet; it may be that the habitat it provides is somewhat sub-optimal for both and hence such second-tier urban habits represent a trough in the distribution of total breeding density along urbanisation gradients. Even so, it supports meaningful numbers of several species of conservation concern and increasing populations of species such as Great Tit, Goldfinch and even Bullfinch suggest that positive changes within the area are increasing its hospitality to species atypical of core urban environments.

8. Associations between breeding bird distribution and habitat variables

Abstract

Breeding species richness across the SK3388 study area was mapped for seven territorial and two semi-colonial bird species to 25 m grid square resolution. Regression analysis controlling for spatial autocorrelation showed that species richness for the seven territorial species was not significantly predicted by either tree cover, building density or by the proportions of green space or garden habitat in the squares, although when House Sparrow and Starling were included proportion of garden had a small but significant negative influence. The relative prevalence of Domestic Cats in each grid square was also not associated with breeding species richness which was, however, significantly predicted in both territorial and all species by the locations of feeding stations providing supplementary food year-round.

8.1. Introduction

Despite the generally lower species richness, productivity and perhaps overall sustainability of urban avifaunas compared to bird communities of non-urban habitats (Chapter 1), there are nonetheless large parts of the urban environment, especially those characterised by numerous small private gardens, which rather than just supporting a few core urban bird species and provisioning winter transients, actually sustain breeding bird communities of appreciable diversity and integrity (Chapter 7). As urbanisation continues to increase, the proportional contribution of such habitat to supporting wild bird populations increases accordingly and it will become increasingly important to understand the habitat variables that allow resident avifaunas to persist among such high levels of landscape modification and human activity. Such knowledge is also of increasing public and research interest with growing general and professional engagement in urban wildlife ecology (e.g. Bowman & Marzluff 2001; Collins et al. 2000), promotion (e.g. Baines 1986; Vandruff et al. 1990) and conservation (e.g. Barker & Graf 1989; Beebee 2001). There is also increasing realisation that it is unhelpful to attract birds to urban residential habitats with, for example, nestboxes and feeders without at the same time ensuring that the general environment enables them to sustain viable populations (Boal 1997; Vines 2005). Therefore, greater understanding is required of which habitat variables within urban residential environments most directly determine birds' ability to sustain diverse breeding communities.

In this chapter, the relationship between habitat variables and bird diversity is investigated by mathematically modelling variation in spatially mapped breeding species richness in the SK3388 study, as determined in chapter 7, against habitat variables. The exploration of any such mapped dataset using correlational techniques encounters the issue of spatial autocorrelation; a modelling method which controls for this is applied for the first time to a detailed habitat analysis over a relatively small area in which animal breeding distributions have been accurately mapped. Species richness was chosen as the measure of habitat utilisation because correlating habitat variables with relative bird abundance could be misleading as built patches supporting only core urban bird assemblages could have high abundances of commensal species, yet offer the lowest habitat quality to the species of interest here. Also, as observed by Bock & Jones (2004), bird counts are particularly likely to fail to predict habitat quality in anthropogenically altered habitats, due to the ecological trap effect; settlement to breed is likely to be a more reliable measure of habitat quality, particularly if aggregated over a number of species and over three seasons, as in this study. Also, given that species richness of avifaunas characteristically declines with urbanisation (Chapter 1), it follows that breeding species richness reflects the extent to which an area of urban habitat approaches or emulates non-urban habitat quality.

The habitat structure variables used were green space, garden area, building density and tree cover. Breeding season species richness was correlated with green space in Örebro, Sweden (Sandström et al. 2005) and in Harwich (Mason 2004) although in the latter study it was independent of garden area which was nonetheless included in the analysis as it forms the majority bird habitat in SK3388 and garden size was related to probability of occurrence in 25 GBW species (Chamberlain et al. 2004). Green space is also informative in that it is a surrogate (negative) measure of human population density (r = -0.64 in US cities, according to Nowak et al. 1996). Cowie & Hinsley (1987) found a significant association between tree density and productivity in garden Blue Tits, while Lancaster & Rees (1979) showed that urban bird species richness increased with tree cover, as did Palomino & Carrascal (2005) in Tenerife, where it was also negatively associated with building density, which Thorington & Bowman (2003) found positively predicted urban nest predation rates. As urban areas have both street trees and treeless green spaces, tree cover and greenspace are complementary habitat metrics.

Two other measure of anthropogenic influence on habitat quality were also included in the analysis, the provision of supplementary food and the prevalence of cats. The general ecological impact of the Domestic Cat remains little understood and, in particular, its effect on birds' breeding distribution is unknown but it is one of the most visible predators of urban birds. Cats occur at higher densities in urban areas (Lepczyk et al. 2003b) and they predate both young and adult birds (Leopold & Dedon 1983 in Adams 1994b; Churcher & Lawton 1987; Kawakami & Higuchi 2002; Kosinski 2001), hunting behaviour in cats being decoupled from hunger (Calhoon & Haspel 1989). Cat predation may particularly impact colonisation (and consequently diversity) as they have been shown to select rarely encountered prey when food density is generally high (Church et al. 1994). However, predation rates vary greatly between individual cats (e.g. Tabor 1983) and are very hard to quantify as not only is the ratio of kills discovered to kills attempted impossible to ascertain but many birds injured in cat encounters die of septicaemia from even small puncture wounds (Cousquer 2003). In terms of influencing the spatial distribution of nesting birds, however, the deterrent effect of cat activity may be as important as actual levels of predation.

Another striking characteristic of urban residential bird habitats is the availability of anthropogenic food. Supplementary food can boost breeding diversity and attract new species, particularly range-expanding granivores such as Mourning Dove, House Finch, American Goldfinch and Northern Cardinal in North America (Brittingham & Temple 1989; Bolen & VanDruff 1987 in Morneau et al. 1999). Of 17 Montréal park species whose reporting rates increased between 1981 and 1994, 10 were feeder users; between the two censuses many new feeding stations had been established, including some in the parks themselves (Morneau et al. 1999). The recent adoption of thin skinned oilseed Sunflower varieties for garden bird feeding has assisted northwards range expansion of wintering Greenfinch and Blue Tit in Finland (Jokimäki & Suhonen 1998). It can also affect breeding behaviour and success. Carrion Crows with supplementary food produced nine times as many young as pairs with only natural food (Richner 1992 in Soh et al. 2002) and supplementary food increased clutch size in Nutcracker (Swanberg in Lack 1954) and advanced mating in Robins (Tobias 1997) and Red-winged Blackbirds (Ewald & Rohwer 1982), although the effect depends on food quality. High-protein food brought forward laying in Magpie (fish, Hogstedt 1981)), Carrion Crow (eggs and chickens, Yom-Tov 1974) and Great Tit (mealworms, Källander 1974) yet sunflower seeds failed to advance Great Tit laying dates (Jones 1973 in Hogstedt 1981) and whereas supplementary cooked egg increased egg volume in Blue Tits, fat had no effect (Ramsay & Houston 1997). In SK3388, households feeding year-round tended to provide *ad lib* high-quality food, in line with conservation organisation guidelines. In contrast, winter-only feeders often provided just intermittent poor quality food such as bread and scraps in hard weather. Also, supplementary feeding during the breeding season will increase the energy available, which could predict breeding species richness in the same way that it is predicted better by summer than winter energy availability measured by temperature (Lennon et al. 2000). Hence, all-year provision was the feeding variable used for this analysis.

8.2. Methods

The Geographic Information System (GIS) ESRI® ArcMap™ 8.3 was used to calculate breeding bird distribution dependent variables and habitat covariates for the spatial regression analysis based on the 1600 cells (each 625 m^2) of a 25 m × 25 m square grid generated using ET Geowizards 8.6. First, the maps of breeding territories (and of the circular core activity zones for the vocal territorial species, see Chapter 7) were converted from feature layers to raster data using ArcMap's Spatial Analyst, the output cell size was set to 1 m^2. The Zonal Statistics feature, also in ArcMap's Spatial Analyst, was then used to assign values of 1 for 'breeding species present' and 0 for 'breeding species absent' to each of the 25 metre grid squares according to the overlaid breeding territory data. This procedure also produced counts of the numbers of 1m squares out of the 625 within each 25 m grid square that were occupied by breeding territory but due to the indicative nature of the initial territory drawing procedure, this finer level of analysis would have represented a spurious degree of mapping accuracy. The 1's and 0's for each 25 × 25 m square were then summed to give a numerical score for breeding species richness for each square, having values between 0 and 7 for the seven vocal territorial species and between 0 and 9 when zones of breeding activity for the semi-colonial House Sparrow and Starling were included. Summing the three annual values of breeding species richness for each square gave the overall breeding occupancy per 25m square, having values between 0 and 21 based on the mapped territories and the circular core activity zones respectively of the territorial species, and values between 0 and 27 based on mapped territories of all nine species.

Data on the occurrence of cats and bird feeding were collected through an intensive field survey of private homes in SK3388 conducted mostly in 2003, with some supplementary data collection in 2004 and 2005. An attempt was made to interview an occupant of every accessible home and to collect a small amount of deliberately simplified information, primarily the number of domestic cats associated with the household and whether food was provided for birds, either year-round or in winter only. The full data collection protocol and results of this survey will be presented elsewhere, the present analysis uses only the records obtained of cats and of year-round bird feeding. Where householders were not at home, the simplicity of the survey meant that in virtually all cases reliable data could be obtained from neighbours or from visual inspection of gardens. The 337 households with cats that were identified in the field survey (approximately 10% of households in SK3388) were mapped as point features in the GIS. In order to spatially map relative cat activity in a systematic way circular core activity zones were drawn around each cat-occupied home with a radius of 50 m (area 0.78 ha). This is a reasonable approximation to a 'typical' home range radius for domestic cats (Barrette 1997; Calhoon & Haspel 1989) but actual range size of cats varies with age, sex and season and the degree of territoriality of urban cats remains unknown so it is, at best, an estimate. Each circular zone was weighted with the number of cats associated with the household, most commonly 1 but in a few cases as high as 9. The superimposed and weighted cat activity zones were rasterised to 1 m^2 resolution and the union and dissolve functions within ArcGIS used to calculate an index of relative cat activity in cat m^2 for each 25 × 25 m grid square (variable *cats*).

The locations of the 345 surveyed households at which food was provided throughout the year were mapped in ArcGIS. To more accurately represent the influence of feeding stations over their immediate area, rather than using merely counts of their point locations within grid squares as the spatial covariate, neighbourhood counts of feeders (variable *feeders*) were calculated using 3 × 3 neighbourhoods of 25 × 25 m (0.5625 ha) grid squares. Other habitat variables for SK3388 were available as spatial covariates by courtesy of J.Tratalos (pers. comm). Variable *greenspace* is the proportion of each 25m square classified as 'natural' in the Ordnance Survey (OS) Mastermap dataset (Ordnance Survey of Great Britain 2005). Private gardens are not included in this classification. Variable *gardens* is the proportion of the area of each 25 m square consisting of private gardens, which are classified by Mastermap as 'multiple'. These two variables were coded as numbers of square metres per square, i.e. having values between 0 and 625. Variable *trees* is the proportion of each 25 m square that was covered by tree canopy and was obtained by hand digitisation of visible tree cover on Cities Revealed aerial photographs (The Geoinformation Group 2001). Variable *buildings* is the number of building centroids (from the OS Mastermap dataset) located within each 25 m square; this provides a simple index of relative housing density.

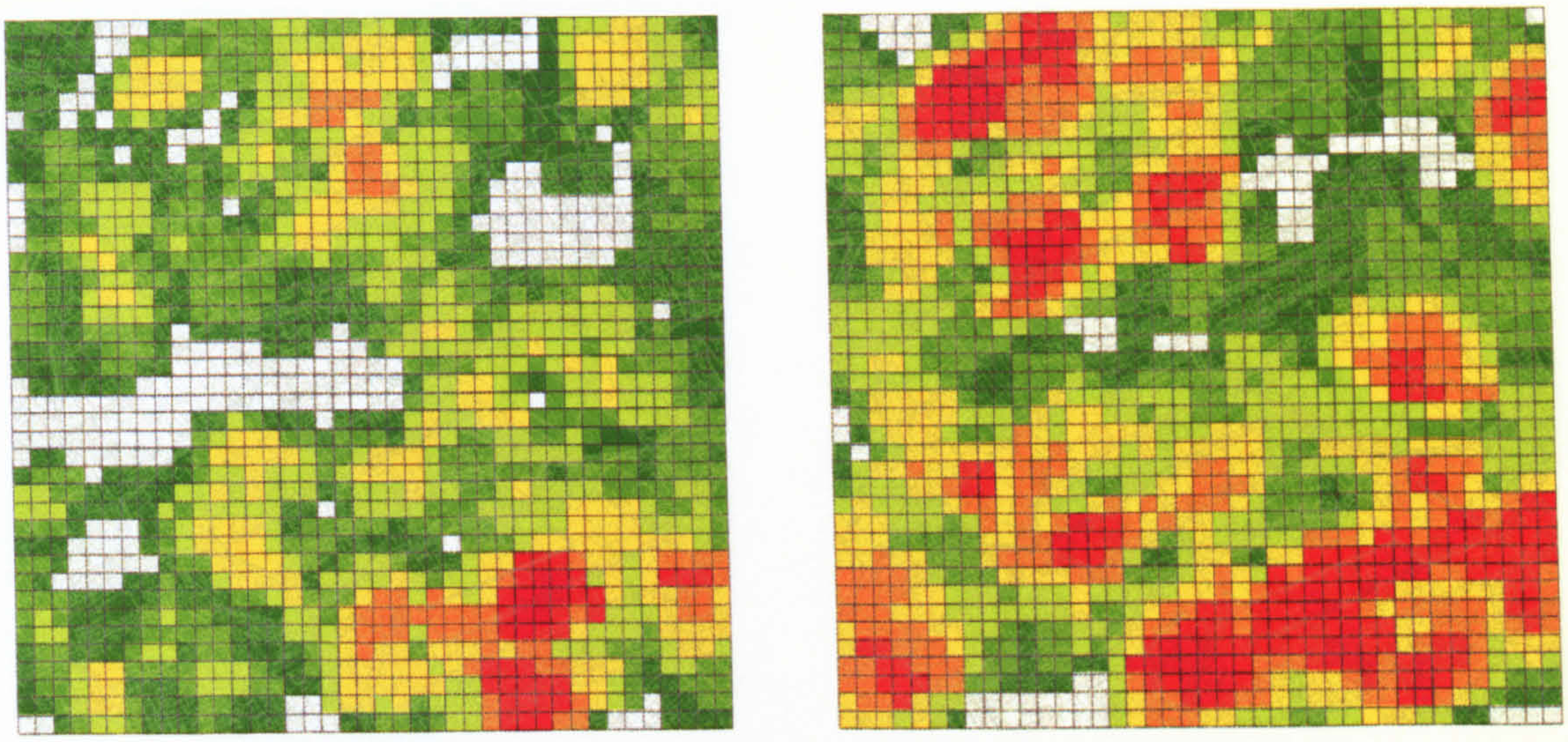
The relationship between breeding bird species richness and the predictor variables *feeders*, *cats*, *greenspace*, *buildings*, *trees*, and *gardens* was modelled using a generalised linear mixed model with spatial covariance as a random effect, Poisson errors and pseudo-likelihood estimation (PROC GLIMMIX in SAS). The model range parameter ρ was estimated by eye from the asymptote of a semi-variogram plotted for the 40 × 40 grid cell dataset using the residuals of a non-spatial model (using PROCs MIXED and VARIOGRAM in SAS) and was held fixed. The sill parameter s^2 was not fixed but set to a starting value, also from the semi-variogram, and allowed to converge to an estimate in each model. Exponential spatial covariance structure was chosen based on visual assessment of the semi-variogram following Legendre & Legendre (1998); for low distance values the semi-variogram appeared to be rather linear, lacking the sigmoidal trajectory that would suggest a Gaussian covariance structure. The change parameter was set to 1×10^{-5}. GLIMMIX option random _residual_ was set to correct for overdispersion via residual-side random components, as appropriate for a smooth-scale environmental effects model as opposed to block effect designs (SAS Institute Inc. 2005a), and option subject = intercept instructed the model to consider all observations as correlated. Backwards stepwise model selection was used based on type 3 P values; covariates were successively removed until all remaining effects were significant. Collinearity of predictors was tested by measuring tolerance as $1 - r^2$ in OLS multiple regression of each single predictor against all others; following Quinn & Keough (2002) it was deemed acceptable overall as no predictors had tolerances less than 0.1.

8.3. Results

Figures 8.1, 8.2 and 8.3 show the spatial distributions across SK3388 of breeding species richness for the three survey years separately (a – c) and the composite values as used in the analysis (d). For the seven vocal species, Robin, Magpie, Dunnock, Great Tit, Blue Tit, Blackbird, and Wren, figure 8.1 maps the estimated hand-drawn territories while figure 8.2 maps the circular ‘core activity zones’ systematically calculated from territory centroids (Chapter 7). The general distribution patterns are very similar, as expected, but there are some differences in detail, mostly in 2002 when hand-drawn territories were smaller, again, this is as expected. There is clearly an area of high species richness in the southeast corner and two interesting ‘holes’, in the centre and towards the northeast. In figure 8.3, breeding activity zones for two colonial species, House Sparrow and Starling have been added to the composite species richness mapping; some of the less-used areas are filled in somewhat but the general pattern of figure 8.3. d is similar to that of figure 8.2.d.

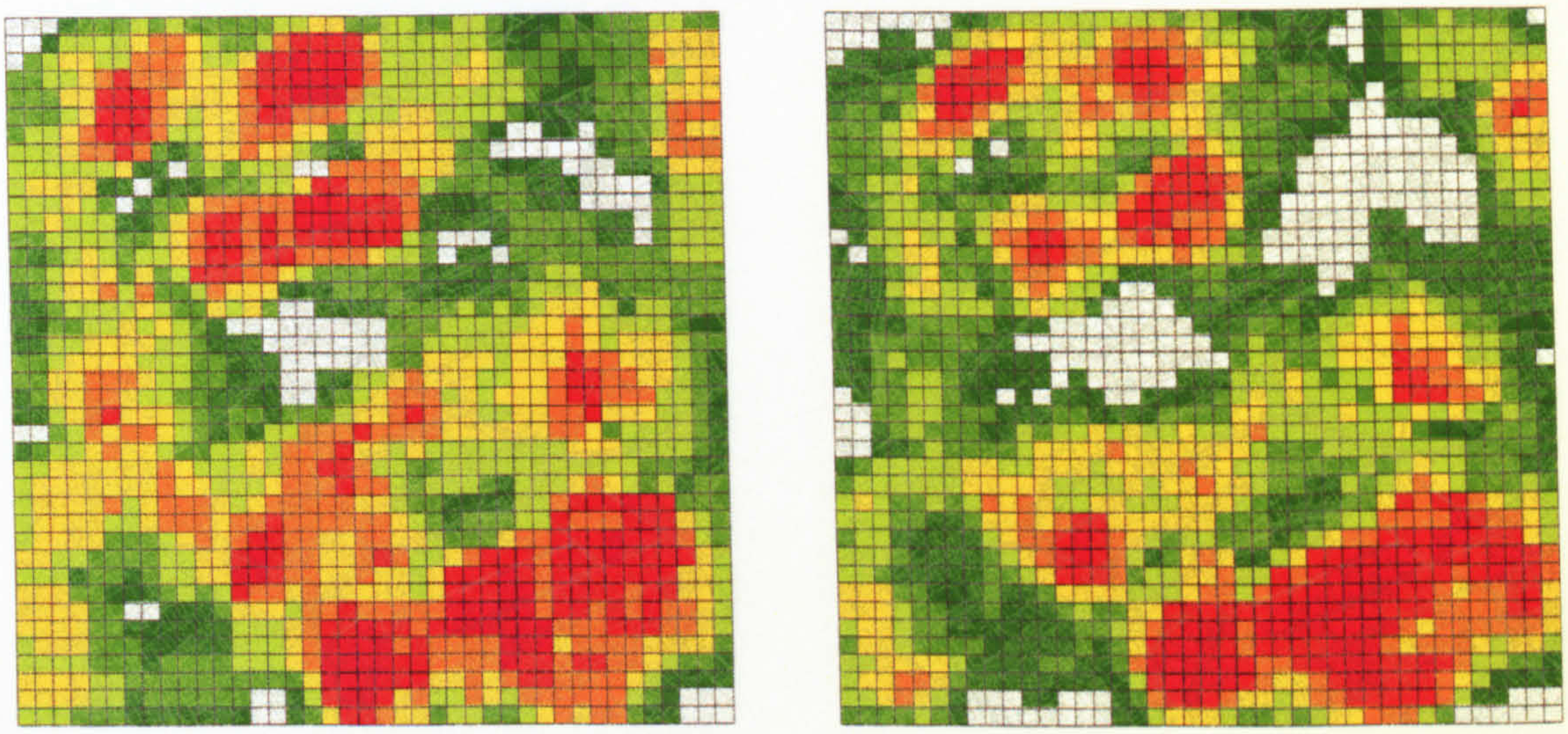
Figure 8.4 shows the spatial distributions of the four habitat structure variables, as calculated with reference to the 25 × 25 m square grid. The proportion of squares covered by gardens (figure 8.4.a) is relatively uniform across the area, reflecting the uniform residential character of SK3388, apart from two clear gaps (green) corresponding to the park and the grassed recreation area which also show up as red patches in figure 8.4.c (green space); as mentioned above, these two measures were not unacceptably collinear despite their apparent complementarity when mapped. Figure 8.4.b maps the amount of tree cover in each square; both this and the numbers of buildings (figure 8.4.d) show an apparent correspondence (positive and negative respectively) with the area of high species richness to the southeast, but patterns elsewhere across the study area are less visually apparent.

Figure 8.5 a and b show the derivation and figure 8.5.c the final mapping of relative cat activity, an obvious ‘hot spot’ coincides with one of the two ‘holes’ in the bird distributions but the second of these has no obvious matching cat concentration although cat activity is clearly low in the southeast where diversity is high. Figure 8.5.d shows feeder locations and figure 8.5.e the neighbourhood statistics, showing low feeder counts in open spaces, as expected, but also a low count in the high-diversity southeast. Evidently, these patterns are insufficiently simple for visual assessment, underlining the value of the mathematical modelling approach used.



a. 2002

b. 2003

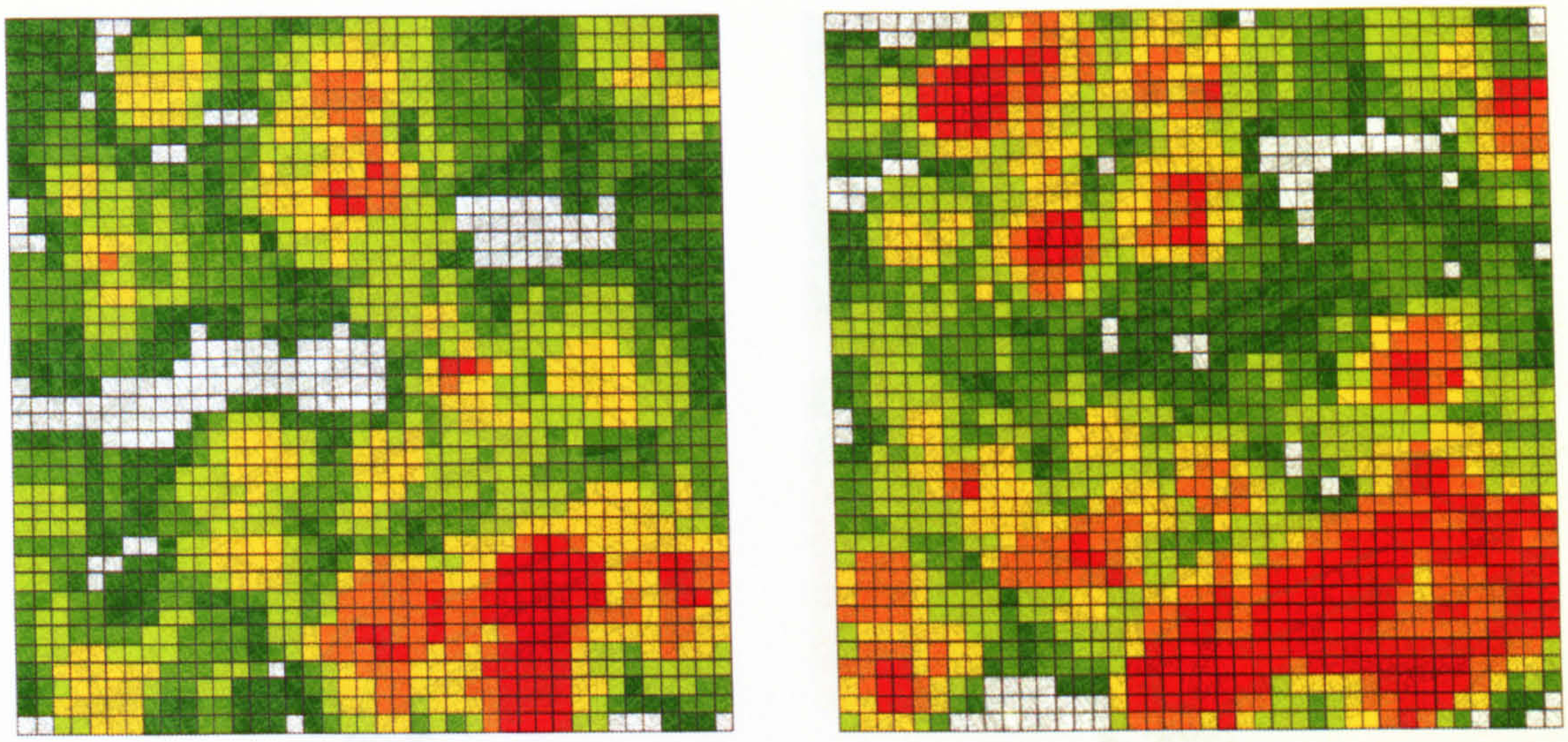


c. 2004

d. Total species-years 2002 -2004

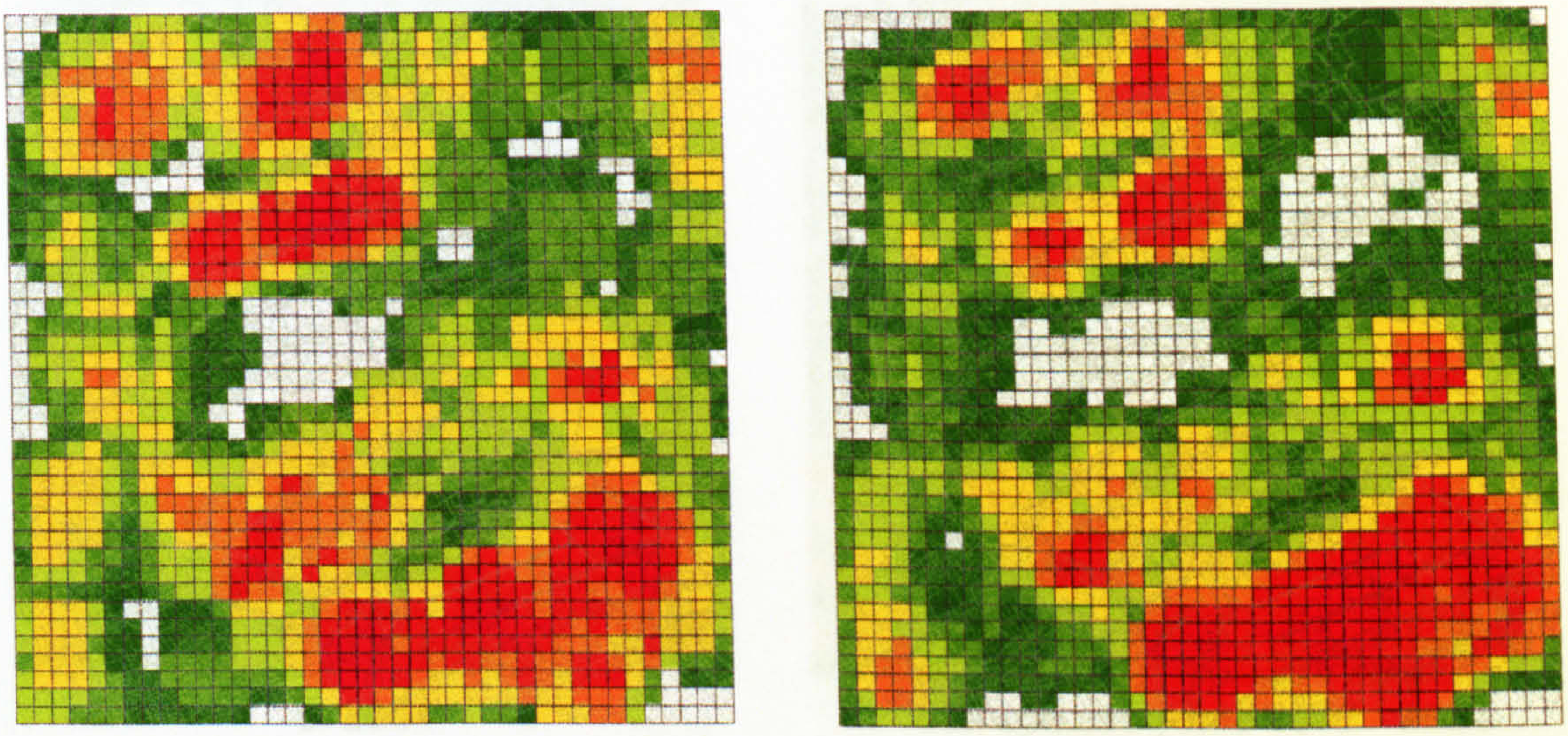
a. - c. number of species		**d.**species-years
⬜	= 0	0 - 3
🟩	= 1	4 - 6
🟩	= 2	7 - 8
🟩	= 3	9 -10
🟨	= 4	11 - 12
🟧	= 5	13 - 14
🟥	= 6	15 - 17
🟥	= 7	18 - 21

Figure 8.1. (a – c). Estimated breeding species richness for seven vocal territorial bird species in SK3388, 2002 – 2004, expressed as the number of species with their hand-drawn mapped territories occurring within each grid square. Mapped area: 1 km × 1 km. Grid: 25 m × 25 m. Species: Robin, Magpie, Dunnock, Great Tit, Blue Tit, Blackbird, Wren.
(d). Summed estimated breeding species richness for 2002 - 04, seven species, three years i.e. each 25 m square is scored between 0 and 21.



a. 2002

b. 2003

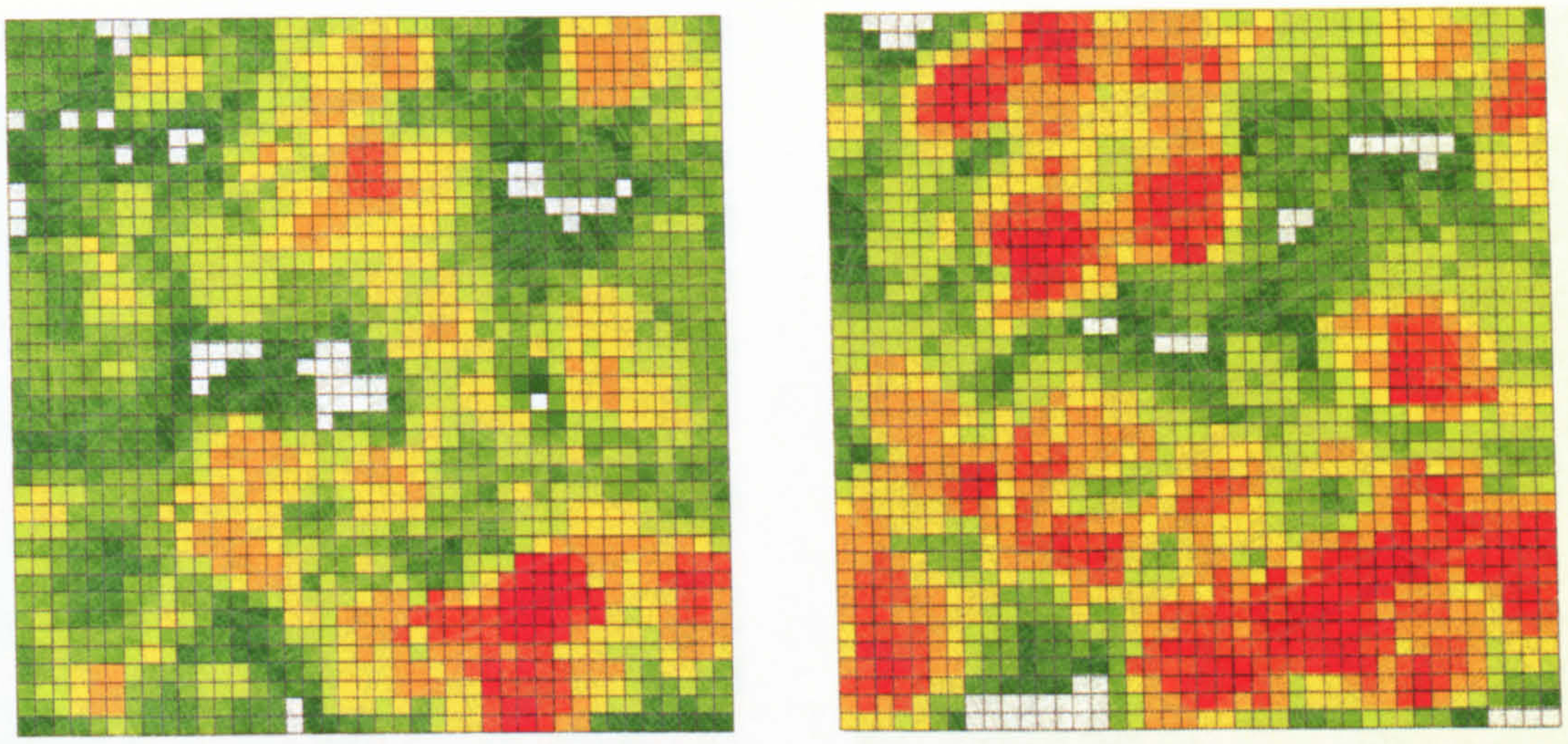


c. 2004

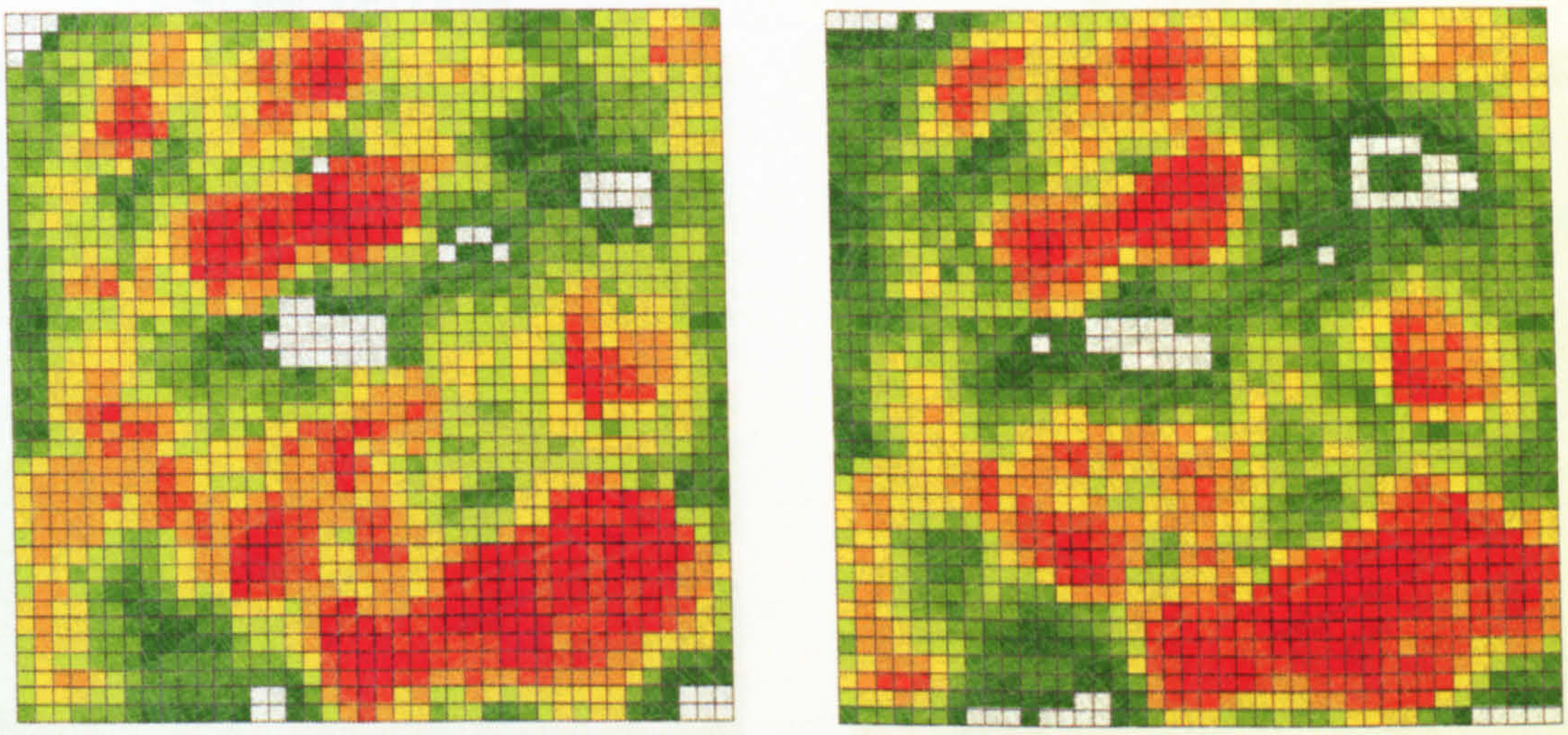
d. Total species-years 2002-2004

	a. - **c.** number of species	**d.**species-years
⬜	= 0	0 - 3
🟩	= 1	4 - 6
🟩	= 2	7 - 8
🟩	= 3	9 -10
🟨	= 4	11 - 12
🟧	= 5	13 - 14
🟥	= 6	15 - 17
🟥	= 7	18 - 21

Figure 8.2. (a – c). 'Systematic' breeding species richness for seven vocal territorial bird species in SK3388, 2002 – 2004, expressed as the number of species with their circular core breeding activity zones occurring within each grid square. Mapped area: 1 km × 1 km. Grid: 25 m × 25 m. Species: Robin, Magpie, Dunnock, Great Tit, Blue Tit, Blackbird, Wren.
(d). Summed systematic breeding species richness for 2002 - 04, seven species, three years i.e. each 25 m square is scored between 0 and 21.



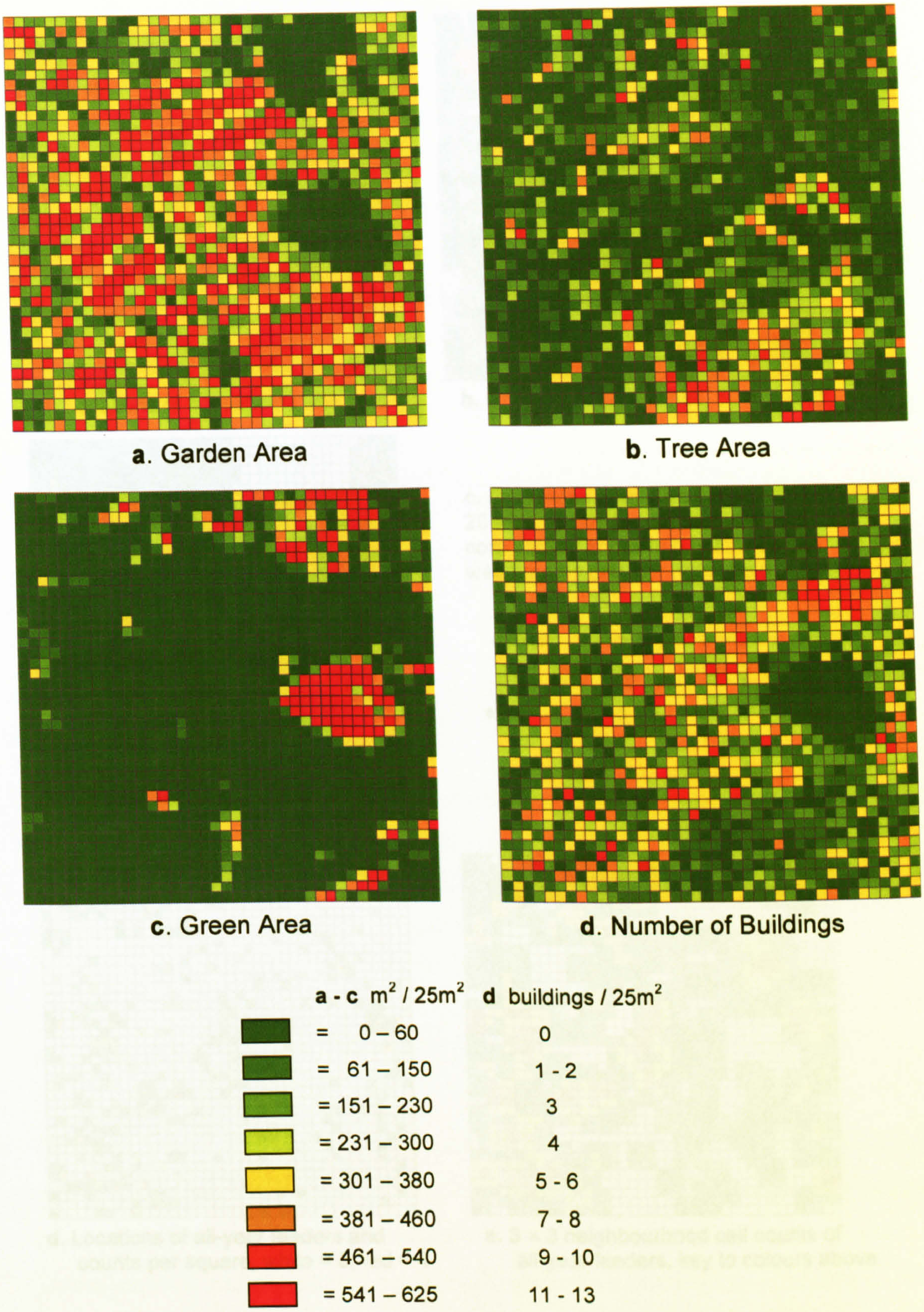
a. 2002 **b**. 2003



c. 2004 **d**. Total species-years 2002 - 2004

	a. - c. number of species	**d.** species-years
⬜	= 0	0 - 3
🟩	= 1	4 - 6
🟩	= 2	7 - 9
🟩	= 3	10 - 11
🟨	= 4	12 - 13
🟨	= 5	14 - 15
🟧	= 6	16 - 17
🟥	= 7	18 – 20
🟥	= 8	21 - 23
🟥	= 9	24 - 27

Figure 8.3. (a – c). Estimated breeding species richness for nine bird species, seven vocal territorial and two semi-colonial, in SK3388, 2002 – 2004, expressed as the number of species with their hand-drawn mapped areas of breeding activity occurring within each grid square. Mapped area: 1 km × 1 km. Grid: 25 m × 25 m. Species: Robin, Magpie, Dunnock, Great Tit, Blue Tit, Blackbird, Wren (territorial), House Sparrow, Starling (colonial).
(d). Summed estimated breeding species richness for 2002 - 04, nine species, three years i.e. each 25 m square is scored between 0 and 27.



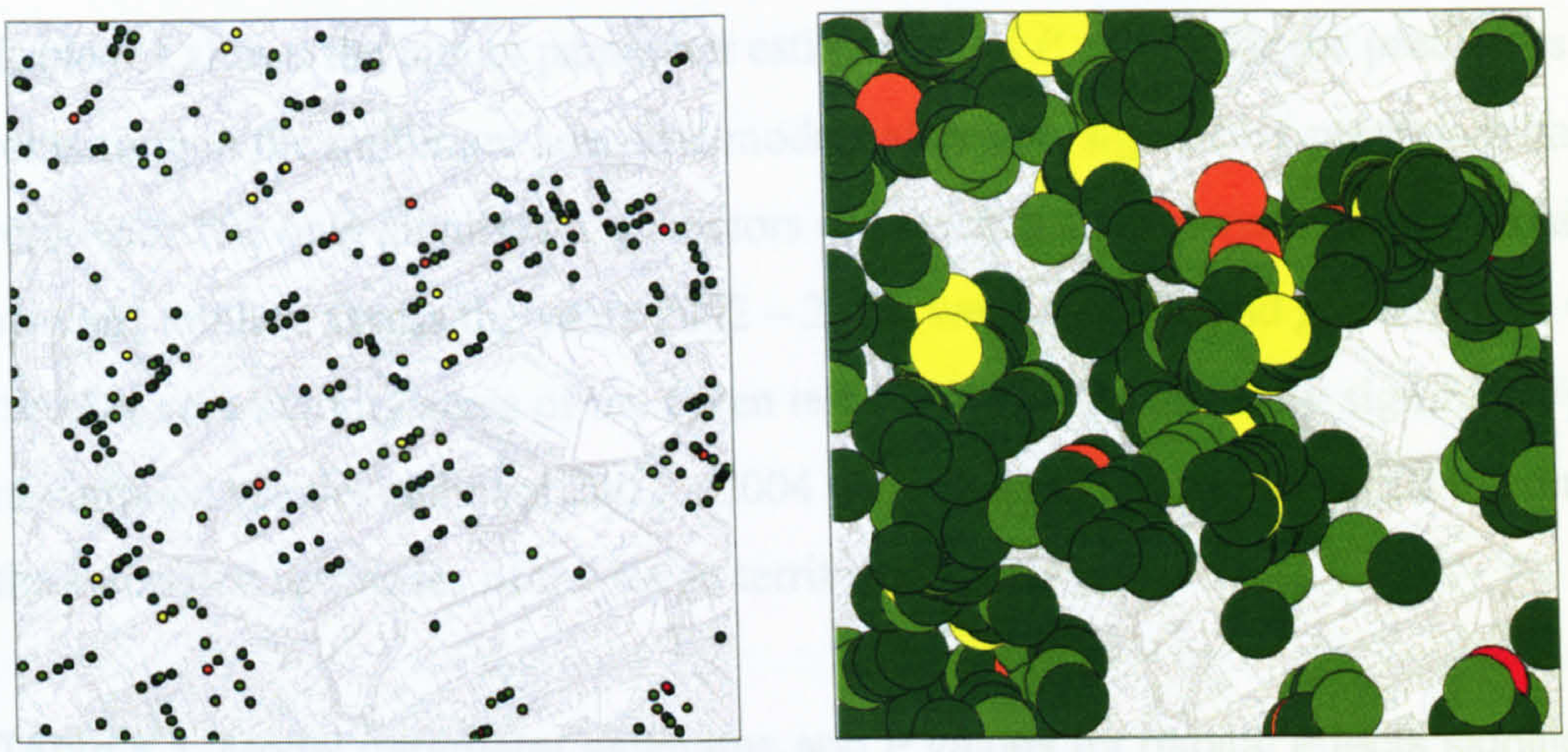
a. Garden Area

b. Tree Area

c. Green Area

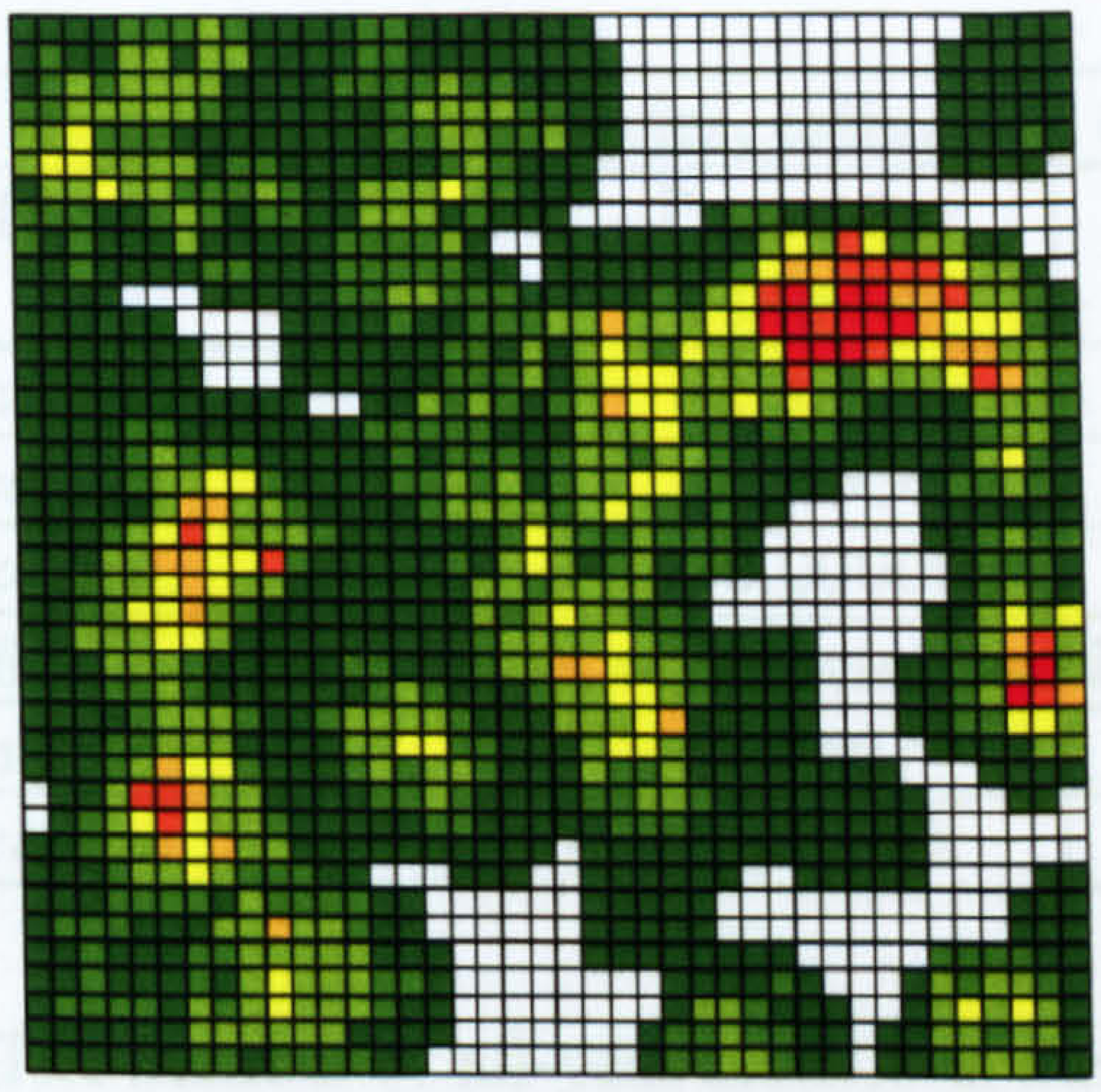
d. Number of Buildings

Figure 8.4.a. – d. Spatial distributions of habitat predictor variables *gardens*, *trees*, *green* and *buildings*.



a. Locations of households with cats.

b. Core cat activity zones, 50 m radius.

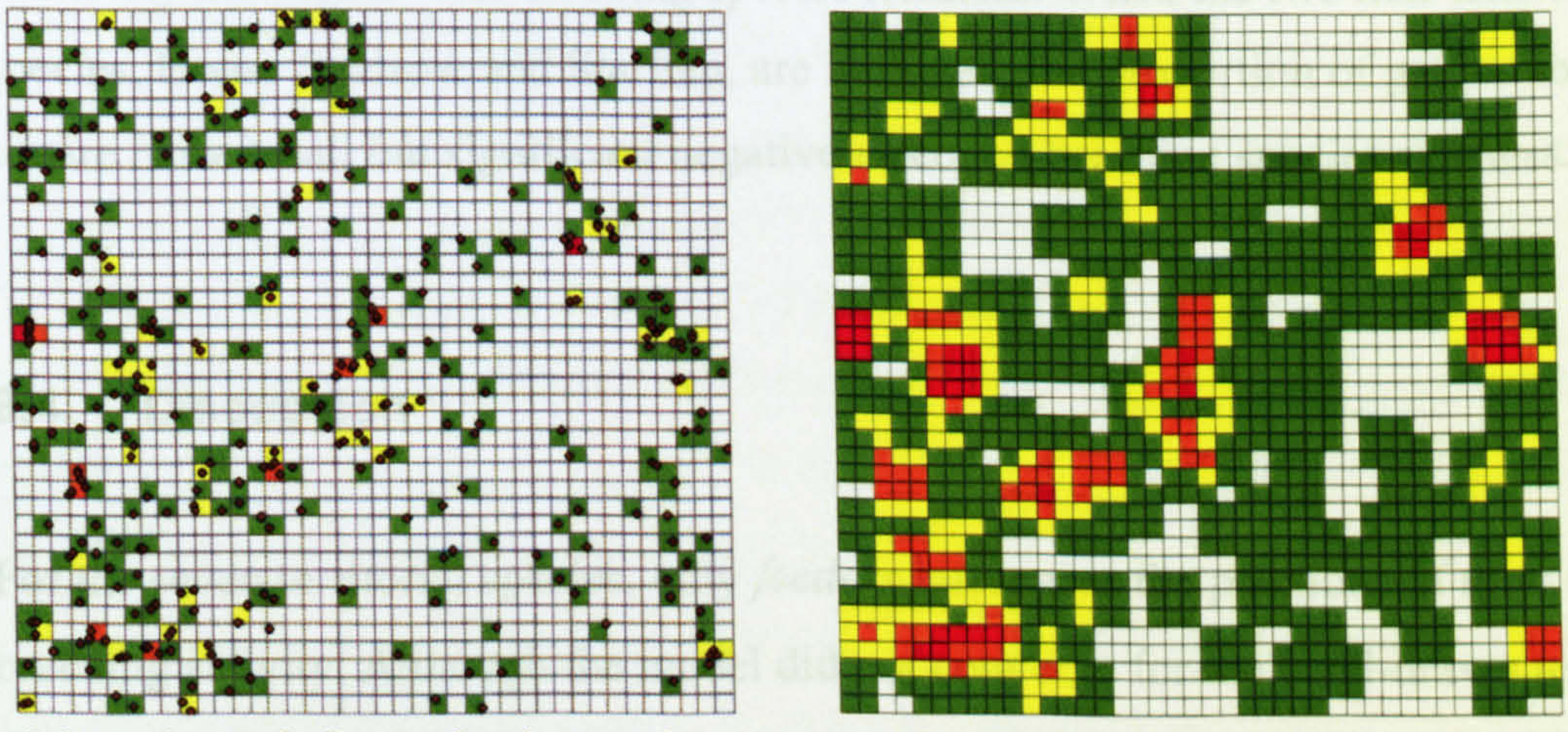


c. (left) Index of relative cat activity per 25 × 25 m grid square, derived from core activity zones in b. summed and weighted by cats per household.

c: 0 cats increasing cat activity →

⬜ 🟩 🟩 🟨 🟧 🟥

e: 0 1-3 4-5 6-7 8-9 10-11 feeders



d. Locations of all-year feeders and counts per square, white = 0, red = 4

e. 3 × 3 neighbourhood cell counts of all-year feeders, key to colours above

Figure 8.5.a. – e. Spatial distributions of cat activity and year-round provision of supplementary bird food within SK3388. c. and e. show values of the predictor variables *cats* and *feeders* in the spatial regression analysis.

Table 8.1 shows the model parameter estimates and *P* values for the predictors remaining in the minimum adequate models after non-significant predictors had been removed. The only significant predictors of breeding species richness for all nine species, totalled across the years 2002 – 2004, were *feeders*, and *gardens*. For the circular core activity areas of the seven territorial species, the only significant predictor of summed species richness 2002 – 2004 was *feeders*. The model failed to converge for the estimated territories of the seven territorial species.

Table 8.1. Model parameter estimates and *P* values for habitat effects significantly predicting summed breeding species richness of 25 m squares 2002 – 2004 in SK3388

i. Response: Nine species, estimated territories $\rho = 12$ $s^2 = 0.842$					
Effect	Parameter estimate	± SE	DF	t	$P_r > \|t\|$
Intercept	2.3754	0.05643	0	42.09	–
feeders	0.01066	0.00361	1597	2.95	0.0032
gardens	– 0.00005	0.000025	1597	-2.24	0.0252
ii. Response: Seven territorial species, circular core activity zones $\rho = 21$ $s^2 = 1.69$					
Intercept	1.7457	0.163	0	10.71	–
feeders	0.01083	0.0054	1598	2.01	0.0449

The number of all-year feeders in the immediate surrounding neighbourhood is positively associated with breeding species richness. When the two non-territorial species, House Sparrow and Starling, are included, the proportion of garden in each square has a small but significant negative effect on breeding species richness.

8.4. Discussion

For the seven territorial species, only *feeders* influences the positions of their centres of breeding activity. Although the model did not converge for the hand-drawn territories; (these complex models take many hours to run and consequently scope for further investigation is limited), modelling the systematically-derived species richness is nonetheless useful as the circular core activity zones are meaningful in terms of both their total area occupied and the positions of their centroids. Furthermore it is reasonable to assume in this relatively low density and unsaturated habitat (Chapter 7) that breeding pairs may be predominantly 'central-place foragers' (Hatchwell et al. 2001) rather than being most active in defending territory edges. If birds were adjusting the shapes of their actual territories to include strategic resources, these might be expected to include feeders, in which case the model of the estimated spatial distributions against feeder locations would be more likely to converge than that of the circular zones, not less likely. In fact, the relative performance of the two models suggests that feeders play a central, not peripheral, role in territory positioning. Nonetheless, this approach fails to accommodate variations in individual and/or pair quality and in resource density, which might vary territory size, as well as constraint or expansion of territories into irregular shapes due to roads, sectors of unsuitable habitat or positions of suitable nest sites with respect to food sources; such variations undoubtedly occur in reality.

When hand-drawn, estimated territories were used and the two non-territorial species were added, the model did converge and indeed the *P* value for the association with *feeders* improved. Feeders clearly play an important role in determining the location of territories, however they may be mapped, which is perhaps unsurprising as they represent a considerable resource. Average annual US expenditure on bird food in 2001 was $68 per person (US Fish & Wildlife Service 2001) equating to approximately 61 kg of sunflower seeds or 102 kg of mixed seed per household. Moss & Cottridge (1998) estimate that more than15,000 tons of peanuts are presented to birds annually in Britain, more than the annual energy intake of the entire breeding population of Greenfinches (Kirkwood 1998). The field survey (this chapter) found that around 25% of households in SK3388 provide food, 15% year-round. Globally, this is not a high proportion. In Rennes, 33% of people fed birds regularly (Clergeau et al. 1997), the US average in 1972 was 20% (DeGraaf & Payne 1975 in Brittingham & Temple 1988a) and 34% of Wisconsin households fed birds regularly in 1983(Brittingham & Temple 1988a). More recently, 37% of survey respondents in both Michigan and Brisbane fed birds or wildlife (Lepczyk et al. 2003a; Rollinson et al. 2003). These figures suggest that feeding stations may have an even more profound influence on bird ecology elsewhere; in northern Finland Great Tits depend on them for winter survival (Orell 1989).

The small negative effect of *gardens* introduced by House Sparrow and Starling corresponds with the findings of Chamberlain *et al.* (2004) who showed that although 25 GBW species were more likely to occur in larger gardens, House Sparrow and Starling (as well as Collared Dove and Black-headed Gull) were more prevalent at smaller sites. It is also supported by survey data from Bristol, where House Sparrows and Starlings were more prevalent in less affluent neighbourhoods with denser housing than in suburbs with larger gardens (J.Tully, 2004, pers. comm) and follows logically from the observation of Fernandez-Juricic (2001) that in Madrid parks synanthropes were denser at edges, species with more 'natural' habits were denser away from them.

Although the landscape variables almost entirely fail to predict the distribution of centres of breeding activity across the entire 100 ha study area their influence is clearly scale-dependent. At smaller scales, hotspots of species richness map onto the park (but not the recreation area, which has no shrubberies) and the patch of larger gardens and tree cover to the southeast. Clergeau et al (2001a) found that local habitat features influenced species richness in French, Finnish and Canadian urban bird communities, which were substantially independent of the bird diversity of adjacent landscapes but other studies have found that either landscape scale habitat variables are more important than local (Chamberlain et al. 2004) or that both should be considered (Bolger et al. 1997; Hostetler & Holling 2000; Mason et al. in press) particularly if landscape-scale habitat quality is non-uniform (Melles et al. 2003). However, a recent multiscale study in Phoenix found that land use was not a good predictor of urban bird occurrence even at multiple scales (Hostetler & Knowles-Yanez 2003).

Scale-dependence may also apply to the influence of cats; the correspondence of a cat density hotpot and a bird density 'hole' to the northeast of the study area is apparent in the field (pers. obs.) and well-known to local residents. One possible explanation is a threshold effect; birds may tolerate a certain range of cat activity levels but leave an area when it becomes too high. It may be that cat density in SK3388 has in fact dropped to a historically low level, enabling birds to colonise. In old, high-density residential areas of Cardiff in 1944, around 60% of households had cats (Matheson 1944), compared to around 10% currently in SK3388.

Although numerous studies have shown that birds optimise nest site details to minimise predation in general (e.g. Burger 1987; Liebezeit & Luke 2002) and even from learned experience of predation (Hatchwell et al. 1999), as Burger (1987) pointed out, territory and nest site selection are different stages in the breeding process and may be influenced by different factors. Evidence of a direct effect of relative predator prevalence on territory location is scarce. Some studies do show territory-scale site selection related to general avoidance of predation (e.g. Hoover & Brittingham 1998; Throgmartin 1999; Whittingham et al. 2002) and local variations in predation pressure do influence settling

(Forstmeier & Weiss 2004). The presence of Red Foxes alters breeding density but not species richness of farmland birds (Tryjanowski et al. 2002), but in other species territory-scale habitat selection and predation seem quite unrelated (e.g. Chase 2002). There seems no reason to doubt the prediction of the model that the birds of urban gardens are little influenced by moderate levels of cat activity in their breeding territory selection, which begs the question of whether this lack of clear avoidance is adaptive. If birds are failing to judge the significance of cat predation in reducing their breeding productivity, it may amount to an ecological trap in urban garden habitats, especially where feral cats are present in addition to household animals (none were known in SK3388). However, preliminary field data from SK3388 (V.Sims, 2005, pers. comm.) suggests that most cats in the study area predate mostly mammals with only a few individuals specialising on birds. Also, unlike the Grey Squirrels and Magpies which are abundant in SK3388, Haskell et al. (2001) found that most cats did not eat eggs, even when presented in their food bowls and when urban nest predation in Italy, France and Spain was compared, only in Italy was it related to cat numbers (Jokimäki et al. 2005). Cat density did not influence recruitment of Blackbirds in Madrid parks (Fernandez-Juricic & Telleria 1999) and both Gering & Blair (1999) and Shochat (2004) considered the effect of cats on nest mortality to be negligible.

The general lack of significant associations between the habitat structure variables and breeding species richness in this analysis does not necessarily mean that birds ignore such variables in SK3388; the habitat variables may influence other measures of breeding performance such as abundance, or it may be that other measures of habitat are more influential. Vegetation volume has been shown to influence urban bird distributions (Goldstein et al. 1986; Mills et al. 1989) and shrub cover and height predicted recruitment of urban Blackbirds (Fernandez-Juricic & Telleria 1999), a species for which Hatchwell et al. (1996) considered an index of habitat complexity ('cover score') to represent a key defensible resource. Shrubby areas were occupied first by urban Blackbirds in Szczecin, whereas tree canopy, the variable used in this analysis, predicted late occupancy (Wysocki et al. 2004). Other studies found relationships with the proportion of native plants (Borgmann & Rodewald 2004; Day 1995; Green 1984; Mills et al. 1989; Rosenberg et al. 1987; White et al. 2005) although such results tend to be found where there are dramatic differences between natural and planted vegetation, such as in arid climates and Parsons et al. (2003) found remnant native vegetation had no influence on suburban bird species richness. A particular issue with multiple predictors is that different species within an urban assemblage may respond differently to the same habitat variables, for example in Breznice (Czech Republic), urban Redstart territories contained larger proportions of trees than those of urban Black Redstarts, which contained more buildings (Sedlacek et al. 2004).

However, the result of Chamberlain et al. (2004) that birds use of individual gardens was influenced substantially by surrounding habitat but very little by garden habitat supports the overall lack of influence of the habitat structure variables demonstrated in this analysis as SK3388 is actually rather homogenous on a 'surrounding habitat' scale and the 25 m resolution of the variables used in this analysis is more akin to the less influential single-garden scale of variation. Above all, this analysis supports the opinion of Shochat (2004) that it is high predictability of food above all else that influences bird population structure in urban habitats.

Acknowledgement

The field survey of cats and feeders was conducted jointly with V.Sims. C.E.Gascoigne and volunteers acted as field assistants.

9. A ringing study of urban garden birds: i. Birds caught

Abstract

Trends and patterns over the three years 2002-2004 in the use of feeding stations by wild birds in SK3388 were investigated by systematically trapping feeder-using species with mist nets. From 1785 catches of 29 species the overall re-trap rate was 11.6% and increased slightly over time suggesting long-term persistence of some individuals. Winter catch rate and diversity peaks suggested use of the feeders by transient foragers but for the ten most-frequently ringed species, total numbers of breeding adults caught correlated with numbers of breeding adults known to be present in 2002 and 2003. This suggests that in the breeding season the feeder-using avifauna is representative of a stable breeding avifauna and that in general this habitat is exploited by birds in a similar way to larger suburban and rural gardens, despite the study area being highly urbanised. Inter-specific variation in diel patterns of feeder use were observed, with Coal Tits in particular visiting feeders earlier than other species.

9.1. Introduction

Territory mapping successfully quantified the breeding avifauna of SK3388 and showed that its size, composition and spatial distribution were relatively stable between 2002 and 2004 (Chapter 7). However, this method is unable to determine the extent to which this avifauna is either self-sustaining or dependent on annual immigration from other habitats and provides no data on the winter bird community. To assess the persistence from year to year of the breeding birds in SK3388 required the marking and subsequent recognition of individuals. Although some expert observers have visually identified individual birds at feeders from plumage variation within single species (e.g. Fitzpatrick 1997a; Fitzpatrick 1997b), marking individuals with uniquely-recognisable combinations of coloured leg rings is a well-established, safe and productive way of achieving this on a larger scale (e.g. Milligan et al. 2003). Colour-ringing can encompass a wider range of the species using the gardens and the data/effort ratio can be greatly improved by the acquisition of supplementary re-sighting records from relatively unskilled volunteer observers.

A programme of mist-netting and colour-ringing was undertaken in order to trap and uniquely mark a sample of individual birds within and in the immediate area of SK3388. Trapping was undertaken all year round to maximise the proportion of the avifauna subsequently identifiable. This year-round sampling enabled the study to additionally address issues of seasonal stability in the composition of the avifauna by examining whether relative numbers of different species caught corresponded with their representation in the breeding avifauna. A distinctive feature of British private residential gardens, typified by those of SK3388, in their role as wild bird habitat is the availability of point sources of *ad lib* anthropogenic supplementary food, some seasonal (typically winter-only) but increasingly year-round. Focusing the trapping and marking of birds at these feeding stations maximised catch rates. The dominant habitat feature, as far as winter birds are concerned, was effectively monitored and some important additional questions concerning the ecological impact of such food provision on an urban garden avifauna could be addressed. The fidelity of individuals and/or species to certain feeders or their mobility between them could help elucidate the effects of garden feeding on territoriality and foraging behaviour. The degree of correspondence of year-round patterns of relative activity at the feeders with national patterns should suggest the extent to which the small urban gardens of SK3388 support birds in similar ways to larger suburban and rural gardens. Daily patterns of relative activity at the feeders might indicate whether some species are more constrained than others in their exploitation of this habitat

In this chapter, data obtained from year-round catching and ringing of wild birds at feeding stations in residential gardens within the SK3388 study area between February 2002 and November 2004 are presented and summarised. Section 9.2 describes the trapping programme and reports the numbers of birds caught, their trends and patterns. In section 9.3, the species caught are reported, temporal patterns in diversity examined and the composition of the sampled feeder-using assemblage compared with that of the breeding avifauna. Section 9.4 considers the pattern of daily activity at the feeders, as reflected in catch rates and reports inter-specific variation in the timing of daily feeder visits. The trapping data presented in this chapter include repeated catches of the same individuals (designated 're-traps'). The data on survival and mobility obtained from re-sightings of colour-ringed birds and recoveries of dead birds, as well as re-traps (all three henceforth referred to collectively as 're-encounters') are reported in chapter 10. Biometric and condition data obtained through the mist netting programme are reported in chapter 11.

9.2. Trapping method, numbers of birds caught, trends and patterns

9.2.1. Introduction

In this section, overall temporal trends and patterns in the mist-net catches, including re-traps, of all species are examined for information on the way birds use the feeding stations at which they were trapped and how that usage varies with time of day and with the seasons. The seasonal pattern of activity is compared with national garden bird reporting rate data to determine whether the urban birds of SK3388 differ in their seasonal use of this resource from the general garden bird population.

9.2.2. Methods

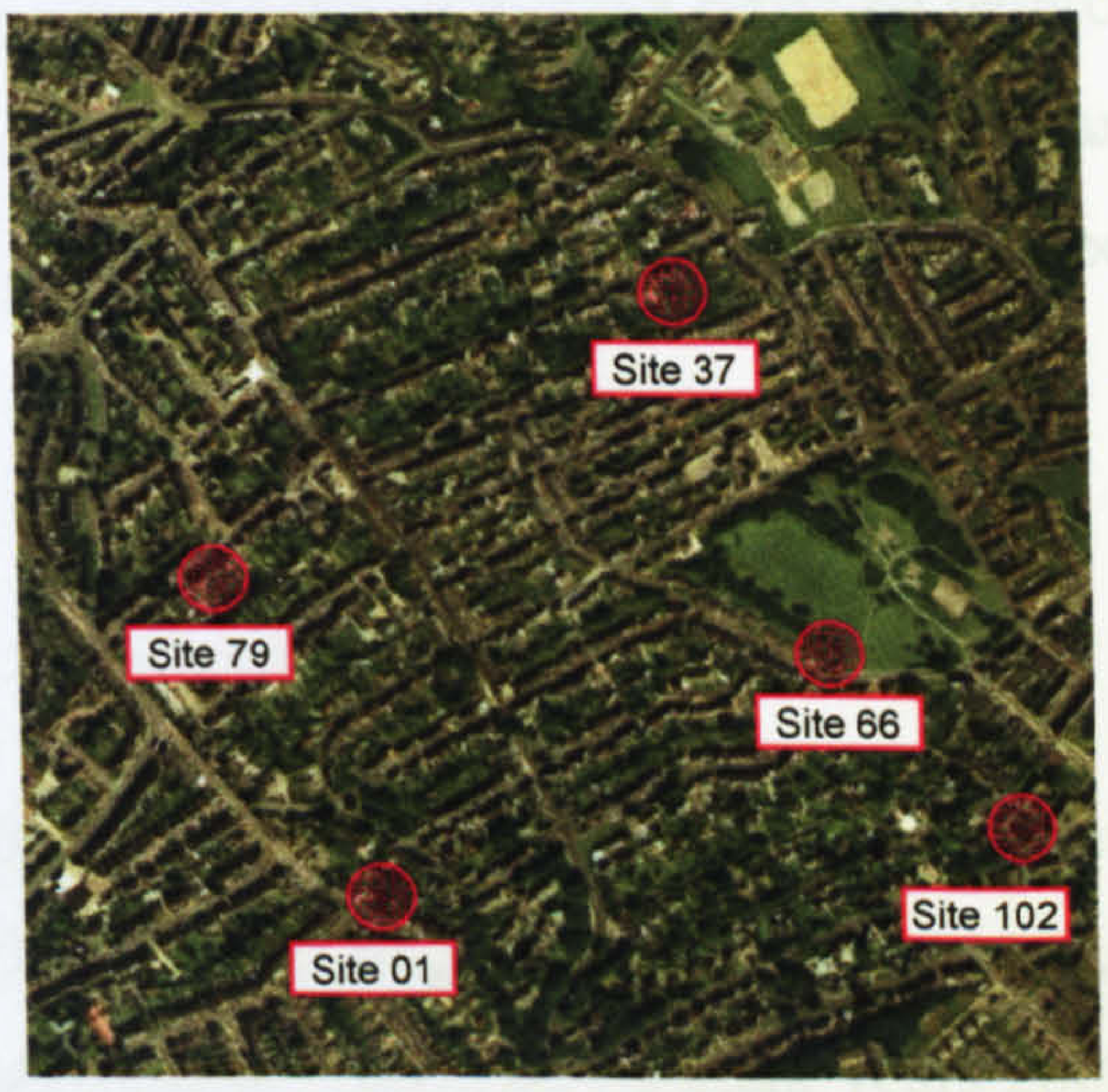
Birds were caught using mist-nets in private residential gardens. Initially, an attempt was made to catch birds at as many sites as possible within and adjacent to the study area, in order to saturate the area with marked birds and generate data secondarily through numerous re-sightings from the public. However, it became clear that due to very low catch rates, uneven distribution of suitable and/or accessible gardens, weather-dependence and consequent unpredictability of catching and a general lack of interest among local residents in re-sighting birds, a more systematic trapping programme that maximised primary data acquisition from the mist-netting *per se* was required. Accordingly, in 2003 and 2004 effort was focused on the five most productive sites, with the objective of catching birds at each site once per month using the same nets in the same positions; a form of 'constant effort' protocol. Constant effort mist-netting has been implemented widely and successfully by national ringing schemes, enabling bird ringing to generate survival rate and productivity data in addition to biometric and movement information (deSante & Nott 2001; Peach et al. 1998; Spina 1999). It was envisaged that sampling a smaller number of sites more systematically in this way would enable more information to be gathered on the persistence of individual birds at feeding stations. Locations of these five primary sites are shown in figure 9.2.1. The SK3388 study area, its location and characteristics are described in chapter 7. Details of the mist-netting technique for trapping live birds are provided by Bub (1995), Redfern & Clark (2001) and Gosler (2004). Trapping and colour-marking of birds was performed under a licence (A4754) issued by the British and Irish Ringing Scheme administered by the British Trust for Ornithology (www.bto.org/ringing) and subject to the bird welfare, health and safety regulations of that scheme (Redfern & Clark 2001).

Bird feeders were installed at the five primary sites and replenished regularly with pre-shelled sunflower seed ('sunflower hearts', donated by CJ Wildbird Foods Ltd). Other foods such as peanuts and scraps were also provided by the garden owners at each site and at all five sites there was additional anthropogenic food available in adjacent or nearby gardens, resulting in effectively a year-round *ad lib* food supply at each site. 'Superfine' (75 denier 2-ply, 1.25 inch mesh) four shelf polyester mist-nets approximately 4 m high and of varying lengths according to site were used; these retain species up to the size of Magpie. Larger species such as pigeons and doves are rarely retained by such nets and are therefore under-sampled with respect to their actual prevalence at the ringing sites. It was necessary for an observer to remain within sight of the nets at all times to prevent domestic cats from attacking restrained birds, this probably reduced the catch rate somewhat compared to that typical of garden mist-netting at safer sites. Every bird caught was fitted with a uniquely-numbered butted aluminium alloy BTO leg ring and Blue Tit, Great Tit, Blackbird, House Sparrow, Dunnock, Robin, Greenfinch and Chaffinch were additionally colour-ringed with three single-colour DARVIC (PVC) rings; a total of four rings per bird in unique combinations of colours and positions, enabling individual birds to be identified upon re-sighting at feeders and elsewhere. Colour-rings were heat-sealed with a portable butane gas soldering iron to prevent loss or removal. Mist-net lengths and times open were recorded for each session.

The five primary sites were different in character, the aim being to sample as far as practicable a representative selection of the garden types in the study area. Site 102 was a sloping garden entirely planted with decorative perennials, no lawn but a pond, and typically a single 12 m net was used, sloping above stone steps adjacent to a large feeding station. Site 37 was a level garden, relatively undeveloped with fruit trees and bushes and semi-wild vegetation, and typically one 18m and one 6 m net were erected either side of feeders. Site 66 was a small, level, square garden with central feeders, a small pond, conifers and a park adjacent, two 6 m nets were used along two sides. Site 79 was a long, level, narrow garden laid to lawn with tall hedges either side, typically 27 m of netting was placed in a single line with feeders distributed along the length. Site

01 was a large, steep, terraced garden entirely planted with decorative perennials and vegetables, with a pond and trees within the plot and to either side, feeders at several locations and typically around 18 m of net in various configurations. Site locations were determined primarily by availability, the observed presence of appreciable numbers of birds and suitability for mist-netting. Capture data were computerised using the BTO standard ringing database program *Integrated Population Monitoring Reporter* (IPMR) and submitted to the national ringing scheme. IPMR uses standard BTO five-letter species codes; these codes appear in some figures in this chapter that are derived directly from that database (see Appendix A).

Figure 9.2.1. Locations of the primary ringing sites within the SK3388 1 km^2 study area



Monthly new bird and re-trap numbers were corrected for variation in monthly catching effort by dividing monthly totals by the total number of mist-net metre hours (metres of net multiplied by hours nets were open) for the month then multiplying by the mean value of the monthly mist-net metre hours over the three years 2002 – 2004 to give standardised figures. Monthly re-trap ratios were calculated by dividing the numbers of re-traps (including repeats) each month by the numbers of new birds each month (standardised and actual re-trap ratios are equal). Cumulative monthly re-trap ratios were calculated from the cumulative monthly figures for re-traps and new birds, standardised to control for catching effort. Monthly catch/effort ratios were calculated as total birds caught divided by total number of mist-net metre hours for each month.

To examine whether monthly catch rates were related to national garden reporting rates for the same species a monthly national garden usage index was calculated for the years 2002 – 2004. Geometric means of the BTO/CJ Garden BirdWatch (chapter 4) weekly reporting rates for the eleven most-frequently caught species (Blackbird, Blue Tit, Coal

Tit, Dunnock, Goldfinch, Great Tit, Greenfinch, House Sparrow, Long-tailed Tit, Robin and Wren) were calculated to compile an index (see chapter 6) and the means of the four or five weekly index values optimally corresponding to each calendar month were calculated to produce 34 values of *GBWindex* (month 2 – month 35). The winter-visiting Siskin was excluded. The total numbers of these eleven species that were caught by mist-netting in each month (*catch*) were then regressed against *GBWindex* with minimum monthly temperature (*mintemp*, for location 4339E 3872N, 131 metres amsl, from UK Meteorological Office www.metoffice.com/climate/uk/stationdata) and monthly catching effort in net metre hours (*effort*) as covariates using PROC REG in SAS following Der & Everitt (2002). Variance inflation factors were examined to check for multicollinearity. Examination of residuals revealed heteroscedasticity, log transformation of *catch* over-compensated; therefore the square root of *catch*, for which residuals were symmetrically distributed, was used as the dependent variable.

9.2.3. Results

Over the three years 2002-04, 1785 birds were caught by mist-netting, of which 207 were re-traps (including repeat re-traps), an overall cumulative re-trap proportion of 11.6%. Re-trap proportions for individual calendar years 2002, 2003 and 2004 were 10.2%, 11.2% and 14.7% respectively. Table 9.2.1 details the overall catch and re-trap rates at the five primary sites and at all other sites combined. Some variation in the proportions of birds re-trapped is apparent but is not significant, neither considering just the five primary sites ($\chi^2 = 2.37$, DF = 4, $P = 0.67$), nor when the overall re-trap proportion at all other sites was included ($\chi^2 = 2.55$, DF = 5, $P = 0.77$). Monthly totals for 32 months, February 2002 (month 2) to November 2004 (month 35), are plotted cumulatively in figure 9.2.2. The mean monthly trapping effort in net metre hours ± SE was 342 ± 29 m hr, which in traditional mist-netting parlance equates approximately to a single 'sixty-foot' (actually 18 m) mist-net open for 19 hours. The mean number of new birds caught per month was 49.3 ± 5.7. Linear regression of cumulative standardised new birds against month predicts a linear catch rate of 48.9 ± 0.73 new birds per month ($r^2 = 99.3\%$, $P < 0.001$).

Table 9.2.1. Total numbers of new birds (unique) and re-traps (including repeat re-traps) caught by mist-netting at each of the five key sites over the three years 2002-04, with the proportion of re-traps among all captures at each site.

Site code:	102	37	66	79	01	all others	Totals
New birds:	323	181	233	218	147	476	1578
Re-traps:	39	29	25	27	21	66	207
Total:	362	210	258	245	168	542	1785
Re-trap proportion:	10.8%	13.8%	9.7%	11.0%	12.5%	12.2%	11.6%

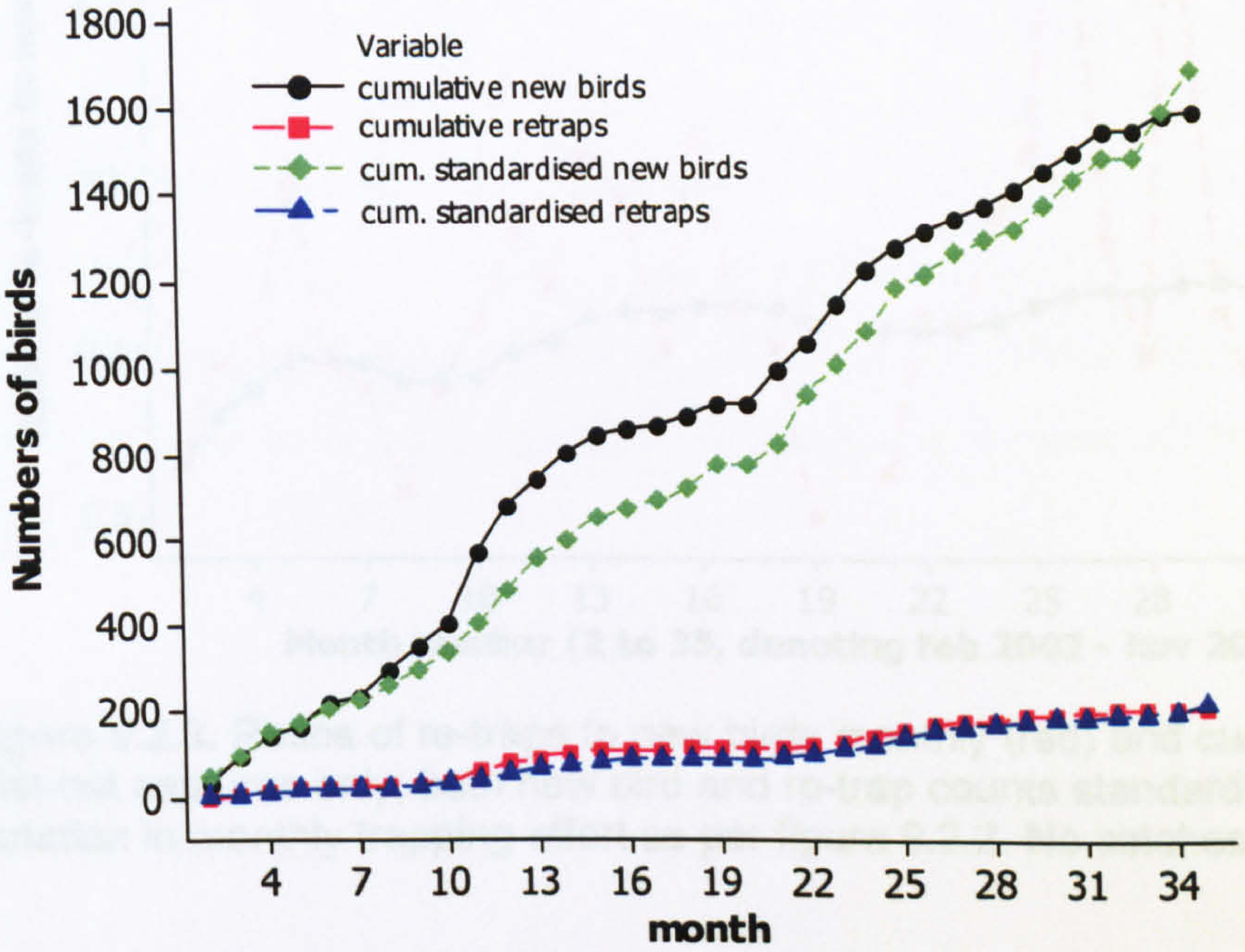


Figure 9.2.2. Cumulative monthly totals of new birds and retraps mist-netted. Black and red plots are actual monthly totals. Green and blue plots are standardised to control for variation in monthly trapping effort: monthly numbers caught and re-trapped were divided by actual mist-net metre hours for the month, then multiplied by the mean number of monthly mist-net metre hours (342 net m hrs ± 29 N = 32).

In figure 9.2.3, the plot of cumulative re-trap ratios (black), standardised for catching effort suggests a slow increase in the proportion of captures that were re-trapped. The plot of actual ratios (not shown) is almost identical and their mean not significantly different (t-test, $t = -0.51$, $P = 0.613$, DF=65). Linear regression of cumulative monthly re-trap ratio against month ($r^2 = 63.9\%$, $P < 0.001$) predicts a monthly increase in the re-trap ratio of 0.00186 ± 0.00025, i.e. if 49 birds are caught per month with zero re-traps in month one, the number of re-traps in month 12 would be two, in month 24, three and in month 36, four. Re-trap ratios are highest in May 2002 (month 5), April 2003 (month 16) and May 2004 (month 29), when only territorial breeding adults, most of which are already ringed, would be expected to visit the feeders, and in January 2003 (month 13) and February 2004 (month 26) when most of the winter visitors to the feeders have already been ringed but are still using the feeders. Re-trap ratio minima occur in July —

September 2002 (months 7 – 9), July — September 2003 (months 19 – 21) and June — October 2004 (months 30 – 34), when unringed juveniles were using feeders.

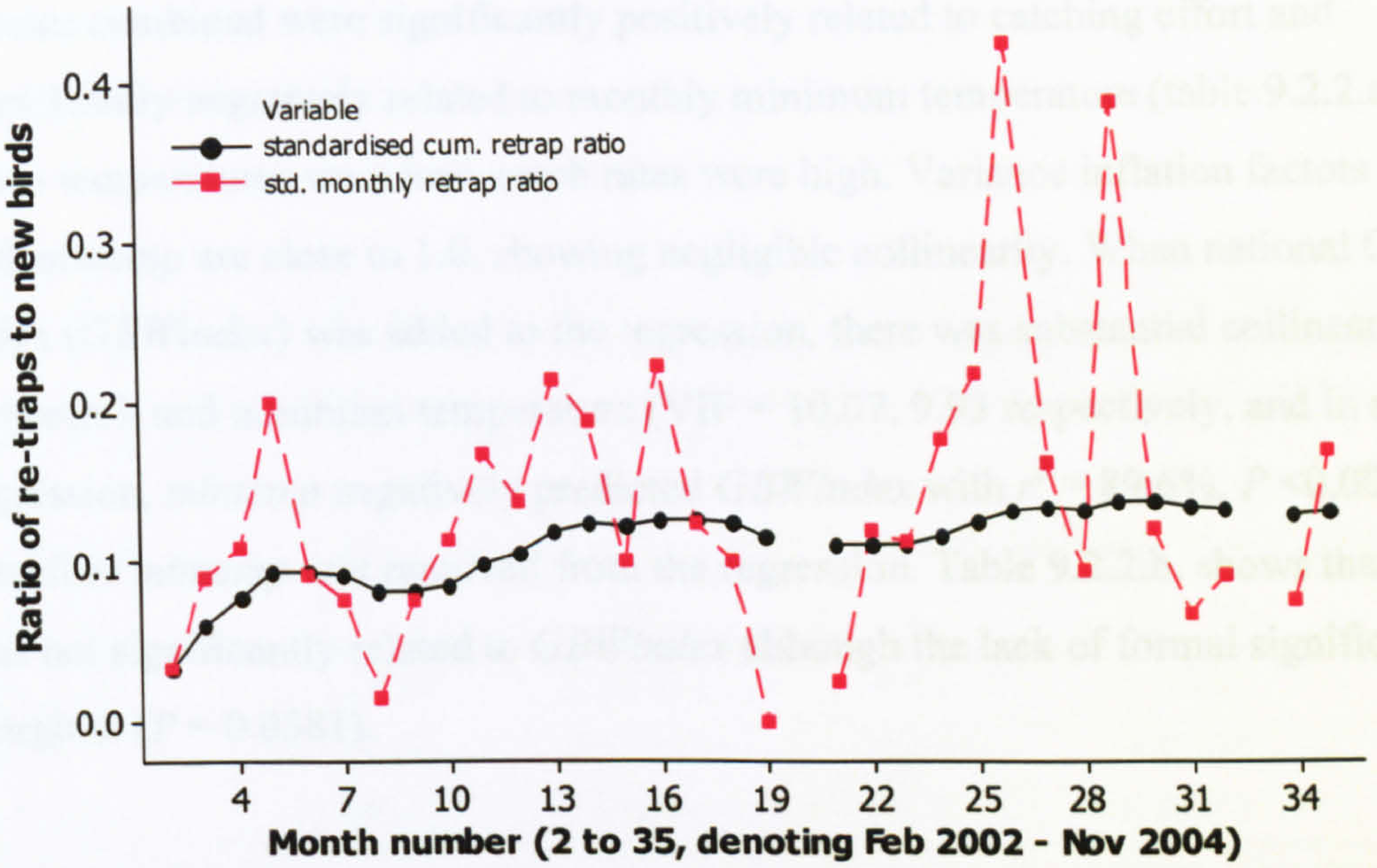


Figure 9.2.3. Ratios of re-traps to new birds monthly (red) and cumulatively (black), mist-net captures only, both new bird and re-trap counts standardised to control for variation in monthly trapping effort as per figure 9.2.2. No catches in months 20 or 33

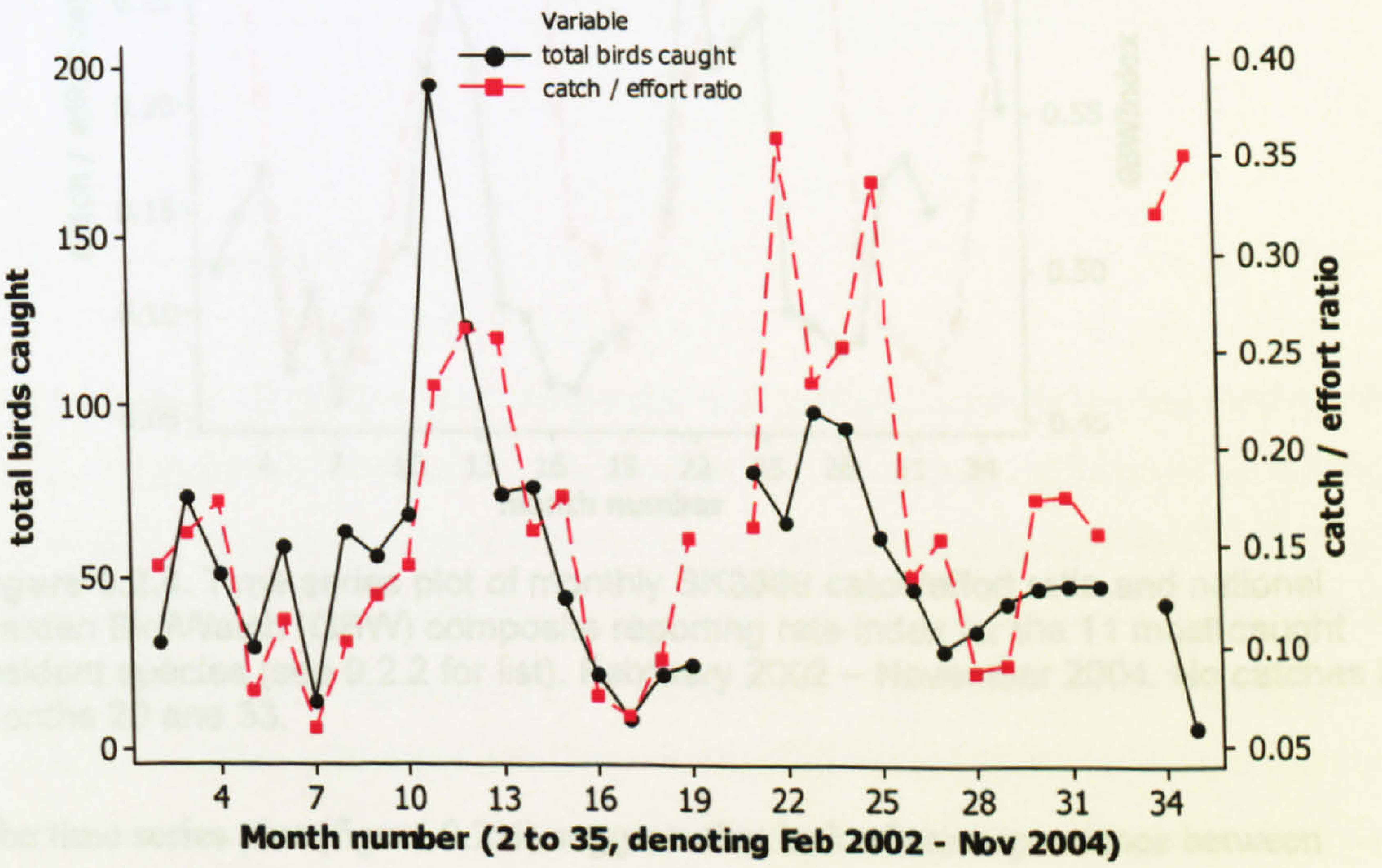


Figure 9.2.3. Total monthly mist-net catches (new birds and re-traps combined), 2002 – 2004 (black plot, primary Y axis), with monthly catch / effort ratios (total catch / net metre hours for the month, red plot, secondary Y axis). All species (*cf* catch-effort ratios in figure 9.2.4. which are for the 11 most-caught resident species only).

Corresponding patterns can be seen in the monthly total numbers of birds caught (figure 9.2.3., black) which attain maxima in November — December 2002 (months 11 – 12) and November — December 2003 (months 23 – 24). Low catch and high catch/effort ratio in month 35 was due to anomalously low effort. Monthly catches of the 11 major species combined were significantly positively related to catching effort and significantly negatively related to monthly minimum temperature (table 9.2.2.a.), i.e. when temperatures were low, catch rates were high. Variance inflation factors for *effort* and *mintemp* are close to 1.0, showing negligible collinearity. When national GBW index (*GBWindex*) was added to the regression, there was substantial collinearity between it and minimum temperature (VIF = 10.07, 9.93 respectively, and in a separate regression, *mintemp* negatively predicted *GBWindex* with $r^2 = 89.6\%$, $P < 0.0001$), therefore *mintemp* was removed from the regression. Table 9.2.2.b. shows that $\sqrt{catch}$ was not significantly related to *GBWindex* although the lack of formal significance is marginal ($P = 0.0581$).

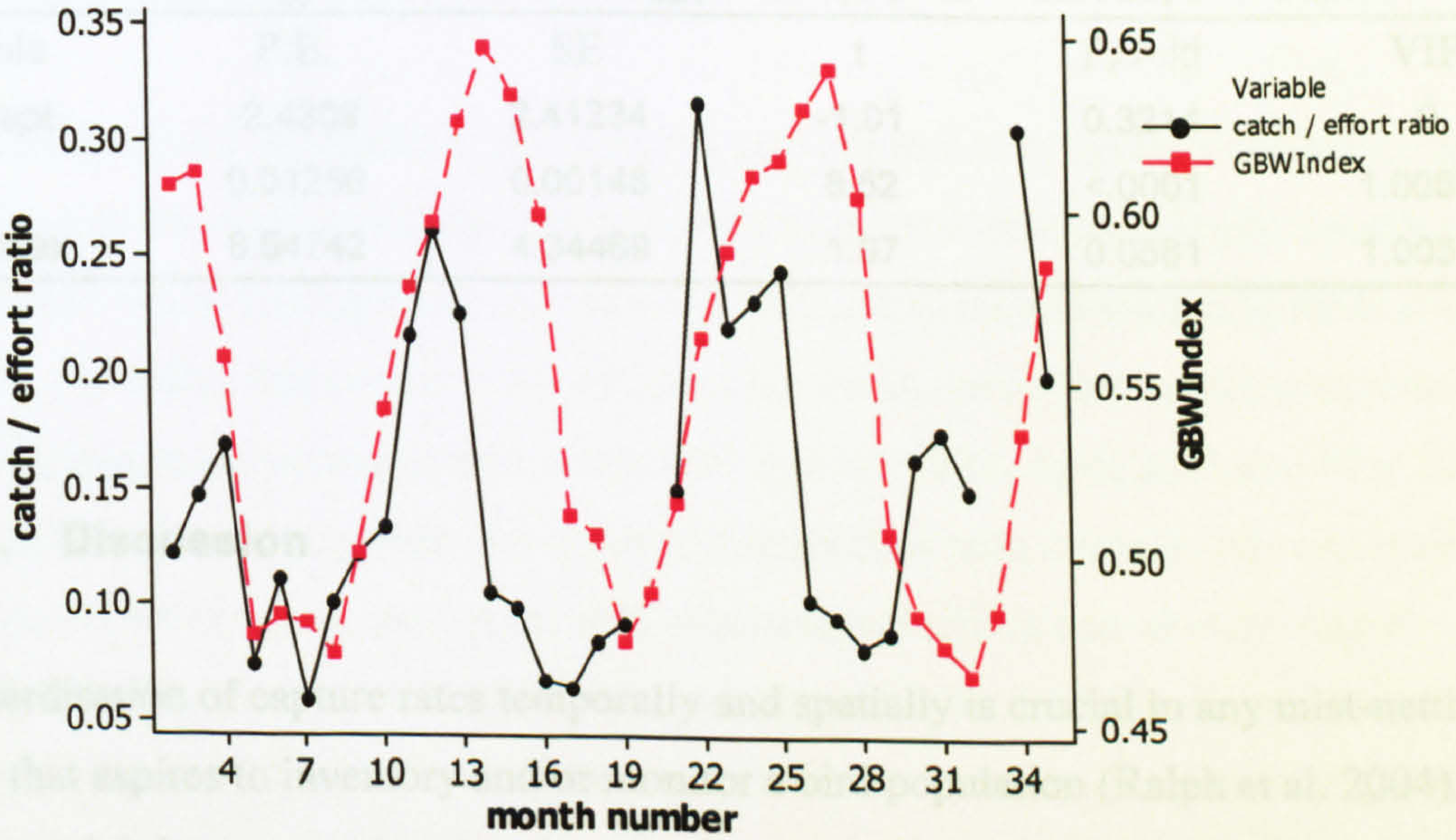


Figure 9.2.4. Time series plot of monthly SK3388 catch/effort ratio and national Garden BirdWatch (GBW) composite reporting rate index for the 11 most-caught resident species (see 9.2.2 for list). February 2002 – November 2004. No catches in months 20 and 33.

The time series plot (figure 9.2.4) suggests that lack of correspondence between SK3388 catch rate and national *GBWIndex* values is most pronounced in months 30, 31 and 32. If values of *catch* and *effort* for these three months were set to values similar to those for the same months in the preceding year, the *P* value for *GBWIndex* in the multiple regression model with *effort* improved to $P = 0.0055$. Comparing catches for weeks 30, 31 and 32 with those for weeks 18, 19 and 20, this variation could be accounted for by increased catches of Great Tits (mean monthly catch 10.7 ± 3.8 vs 0.33 ± 0.33, adoption of nestboxes) and substantially more Blue Tits (20.0 ± 4.7 vs 5.7 ± 2.9, increased numbers and box use) and Goldfinches (2.3 ± 2.3 vs 0, increased breeding numbers). Otherwise, the main source of lack of correspondence appears to be an earlier peak and a faster decline in winter catch rates in SK3388 with respect to the national garden reporting rate index (figure 9.2.4).

Table 9.2.2.a – b. Results of multiple regression analysis of monthly catch rates against monthly catching effort, monthly minimum temperature and national monthly average garden reporting rate. P.E. = parameter estimate, SE = standard error of parameter estimate, VIF = variance inflation factor.

a. Model: $\sqrt{catch} = effort\ mintemp$. $F_{2,31} = 42.7$, $P_r > F < 0.0001$, $r^2 = 73.4\%$

Variable	P.E.	SE	t	$P_r > \lvert t \rvert$	VIF
Intercept	3.50987	0.76106	4.61	<.0001	0
effort	0.01228	0.00145	8.48	<.0001	1.02148
mintemp	-0.15641	0.06526	-2.4	0.0228	1.02148

b. Model: $\sqrt{catch} = effort\ GBWindex$. $F_{2,31} = 39.7$, $P_r > F < 0.0001$, $r^2 = 71.9\%$

Variable	P.E.	SE	t	$P_r > \lvert t \rvert$	VIF
Intercept	-2.4309	2.41234	-1.01	0.3214	0
effort	0.01256	0.00148	8.52	<.0001	1.00586
gbwindex	8.54742	4.34469	1.97	0.0581	1.00586

9.2.4. Discussion

Standardisation of capture rates temporally and spatially is crucial in any mist-netting study that aspires to inventory and/or monitor a bird population (Ralph et al. 2004). In this regard, it is encouraging that the monthly new bird acquisition rate plot (figure 9.2.2) is reasonably linear and there was no systematic variation between the sites in the likelihood of re-trapping a ringed bird. However, the first comment of any experienced garden mist-netter with respect to these data would be that 49 new birds per month is a remarkably low mean catch rate for mist-netting at garden feeding stations, it would be commonplace to catch more than that number of birds in a single morning at a suburban or rural garden ringing site (pers. obs.). This reflects not only the practical difficulties of mist-netting in small, cat-infested urban plots but also the generally low numbers of birds in the study area; the breeding population is relatively low by general urban/suburban standards (chapter 7). The roving winter feeding flocks of small woodland passerines, notably tits, that are typical of non-urban habitats were absent (pers obs), with the exception of small winter Siskin flocks in the early months of 2003 and 2004; such flocks are generally smaller and less diverse in more fragmented (Telleria et al. 2001) and urban (Yaukey 1996) habitats. After a slow start, trapping and re-trap rates improved at the start of 2003 (month 12) when the revised program of ringing at just the five primary sites was implemented.

The slow increase in the cumulative monthly re-trap ratios, corrected for trapping effort (figure 9.3.2, black) and considered against the high linearity of the overall monthly marking rate for new birds, might suggest a positive annual survival rate overall, lending support to a hypothesis that the bird population of SK3388 is not dependent on annual net immigration for its persistence. However, three years' data are insufficient to assess this definitively. Over this short timescale, the regression that suggests a linear increase in re-trap ratios could be unduly influenced by the relatively steep initial slope as re-traps rise from zero, the plot does appear to level off somewhat in 2004.

The timings of the catch/effort ratio maxima and minima vary between the years, which suggests that there is more to the use of these feeding stations than simply a resident population regularly supplementing its daily diet. Transient and wintering birds could well be exploiting this resource as well, possibly on an annual basis; this is explored further using re-encounter data in chapter 10. In May 2002, April 2003 and May 2004 there are notable correspondences between catch/effort ratio minima and re-trap ratio maxima, as winter transience in the bird assemblage declines and already-ringed breeding adults become most prevalent at the feeders. Catch/effort ratio maxima in months 4, 12 and 25 are followed one month later by re-trap ratio maxima, suggesting persistence of trapped birds at the feeding stations; interestingly, the winter catch/effort ratios behave very differently in 2003 and 2004. 2003's January peak (month 12) is sustained into February, whereas the January peak in 2004 (month 25) is followed by a sharp dip in February (month 26), when the re-trap ratio attains an all-time high in contrast to the re-trap ratio in February 2003 which is lower than that in January 2003. This suggests significant inter-year variation in how the feeder-using birds in SK3388 respond to varying winter conditions.

The overall form of the seasonal variation in mist-net catches supports the general result that urban bird densities are higher in winter (DeGraaf 1991; DeGraaf & Wentworth 1986; Yaukey 1996), particularly as feeders attract tits into provisioned areas (Graber & Graber 1979) and decrease their winter mortality (Brittingham & Temple 1988b; Jansson et al. 1981), but also that the feeder-using bird assemblage in SK3388 is at least partly composed of an established breeding population. The general form of figure 9.2.4. suggests a strong correspondence between patterns of seasonal variation in feeder use by common species in SK3388 and nationally, although the winter peaks (months 12 and 22) in activity occur earlier than those in the national index (months 15 and 27) and decline more quickly. Possible reasons for this include the typical later winter reporting rate maxima for Greenfinch in GBW gardens nationally (Cannon 2000) not being reflected in the generally low and steady SK3388 catch rates (although catches in late winter of 2002–03 were higher than in 2003–04). This might indicate that SK3388 is not recognised as a resource by large numbers of transient winter birds in the way that larger suburban and rural garden feeders are, despite an apparent superabundance of *ad lib* food. Other possible reasons include earlier commencement of breeding activity in the urban habitat and the fact that the ringing sites in SK3388 were provisioned continuously year-round, whereas national garden food provision rates may vary seasonally. Nonetheless, for the purposes of this study, the fact that the seasonal pattern of feeder usage in SK3388 can be brought into significant correlation with the national pattern after only minor adjustment for known changes in the local avifauna suggests that this second-tier urban habitat, despite its high human housing and cat density, is capable of provisioning wild birds in a similar manner to the larger suburban and rural gardens traditionally considered to be more suitable bird habitat.

Although mist-netting is a stochastic, non-selective and weather-dependent capture method for which small urban gardens are not ideally configured, it nonetheless enabled the inspection and marking of 1578 birds over three years, a reasonable sample size considering that the mean total annual adult breeding bird population in SK3388 over the same period was 950 individuals (table 7.18). The relationships between mist-net catch rates and numbers of birds present are not necessarily direct and vary between species (see section 9.3.1 for discussion), but if the proportions of the individuals of each species utilising the feeding stations that are caught in nets set at those stations do not vary significantly from month to month, seasonal variation in overall catch/effort ratios should reflect seasonal variation in feeding station utilisation. Problems with this assumption include the observation that certain species are less cautious at certain times of year, for example Mistle Thrushes are prone to capture when competing for territories in late winter but otherwise are extremely trap-shy (pers. obs.). Adults and juveniles may also have differing susceptibilities to mist-netting (e.g. Bart et al. 1999), altering the overall trapping probability of a species between seasons. However, both the problematic examples cited above involved species that do not use feeders; in the present study the great majority of the birds caught were visiting the sites specifically to feed, nets were set close to and around feeders and were constantly observed; personal observations suggest that most individual birds of feeder-using species choosing to use the feeding station on a particular morning stood a high chance of being caught at some point during a catching session.

Nonetheless, some birds will have been missed. It may be that catch rates are also influenced by the urgency with which the birds require supplementary food which in turn will be influenced by their condition and the weather. However, that factor can also be expected to influence the national prevalence of wild birds at garden feeding stations and is therefore arguably controlled to a great extent within any time series comparison of local and national feeding station utilisation through the year; Lepage & Francis (2002) showed that the numbers of birds using feeders were representative of actual winter populations for around 80% of feeder-using species in North America. Therefore, examining the degree of correspondence between feeder usage rates in SK3388 and nationally will aid better understanding of whether birds in the urban habitat are using feeders in different ways from those at the non-urban sites that make up the bulk of the national Garden BirdWatch dataset (see chapters 4 and 5) and consequently the extent to which the avifauna of SK3388 resembles that of more ostensibly bird-friendly suburban and rural garden habitats that provide the bulk of the national data.

9.3. Species caught: diversity and comparison with breeding population

9.3.1. Introduction

In this section, two aspects of the composition and ecological diversity of the subset of species caught by mist-netting during the study are examined. Firstly the ecological diversity and its seasonal patterns are examined. If SK3388 supports wild birds in a similar way to suburban and rural gardens, that is to say with a stable but relatively low-diversity breeding avifauna augmented by additional species visiting exclusively to feed in winter, the ecological diversity of the feeder-using assemblage should show a regular seasonal pattern. Conversely, if SK3388 is marginal habitat, exploited only opportunistically by transient species, ecological diversity would be relatively constant and less seasonally predictable. Secondly, breeding season catch rates of the most common resident species are compared with their actual breeding populations as determined by territory mapping (chapter 7), in order to investigate the extent to which relative degree of exploitation of feeding stations in support of breeding activity varies between species. A further benefit from the demonstration of concordance between the two measures of relative density would be that the mist-netting catch rates for the post-breeding and winter periods in the same study area could then be used to at least indicate changes in their bird population densities.

Mist-netting is not a suitable catching method for all species of bird and in most study areas only a subset of species actually present will be trapped using this technique; some are too large to be retained in the nets, some behave in ways that make them less vulnerable (see Bibby et al. 2000; Gosler 2004). In this study, species which do not use garden feeding stations are very unlikely to be caught by mist-nets placed at those stations. In SK3388, however, apart from habitat-specific and easily located exceptions such as Swift and Feral Pigeon that were consistently present across the study period, species other than garden and feeder users were relatively rare (chapter 7) and gardens with anthropogenic food are the dominant habitat (chapter 8). Furthermore no colonisations or extinctions of non-garden species were detected during either breeding censuses or winter observations over the three years. It follows therefore that there will have been little meaningful variation in diversity that would not have been reflected in the birds sampled at garden feeding stations. Hence the form of the species accumulation curve for mist-netting at these stations will indicate the relative stability of the feeder-using bird assemblage. Also, the diversity of the species caught, although perhaps not reflecting the complete avifauna of the site, should nonetheless vary seasonally in line with the diversity of the most significant and potentially variable component of that avifauna.

Silkey et al. (1999) observed that relative changes in breeding density can be inferred from mist-net catch rates for some species, but not for others. Their study and review of literature demonstrated variability in the relationship between catch rate and breeding density among studies and between species, which they attributed to behavioural differences rather than abundance differences. To some extent the present study addressed this by distributing catching effort between five very different garden types in which different behaviours might be expressed, rather than concentrating effort at a single station or in a single garden type. Also, behaviour-induced variation in relative catch rates actually provides further rationale for comparing the two measures of relative density in terms of the present study because it suggests that presence or absence of correspondence between catch rates and density will elucidate inter-specific differences in the extent to which the presence of feeders influences foraging behaviour and territoriality. For example, relative capture rates in a 12 year study did correlate significantly with relative breeding density for three out of four scrub-nesting passerines (Silkey et al. 1999) and other studies showed good correspondence in 9 out of 21 species (Peach et al. 1998) and in 47 of 64 species (Dunn et al. 2004). However, validation studies on relative abundance indexing via mist-netting are scarce in the literature (Dunn & Ralph 2004).

9.3.2. Methods

To assess variation in the ecological diversity of species trapped per month, the Shannon-Wiener diversity index (H) for each month was calculated (equation 9.1, S = number of species and p_i = proportion of total sample belonging to species i).

$$H = -\sum_{i=1}^{S} p_i \ln p_i \qquad 9.1.$$

This is a type I diversity index that signals changes in relative abundance of rare species; it was used rather than a type II index that signals changes in relative abundance of common species (Krebs 1999) because the question of interest is whether a known and relatively stable breeding assemblage is augmented by scarcer visiting species at certain times of year.

Breeding populations were estimated between April and June (chapter 7), therefore, for comparison, numbers of unique individual adult birds, assumed to be breeding or at least capable of breeding, ringed in months 4 –6, 16 – 18 and 28 – 30 were totalled and divided by the total trapping effort (net metre hours) for the three month period. Same-year re-traps were not counted. Ratios of adults ringed per net metre hours are multiplied by 10^3 for easier comparison (figure 9.3.3).

9.3.3. Results & Discussion

Of the 29 species that were mist-netted during the three year study period, 27 species had been caught by September 2003 (month 21), 28 by November 2003 and 29 by April 2004. All 18 of the relatively mobile breeding passerine species likely to be caught without specially targeted effort had been trapped by February 2003, one year after project commencement. Figure 9.3.1 plots the rate of accumulation of trapped species with catching effort in mist net metre hours; a plot against date had a very similar form (not shown) showing signs of converging towards an aysmptotic limit of the number of catchable species but with occasional new species still occurring after three years.

Figure 9.3.2 shows a general pattern; both diversity and species/effort ratio are higher in winter and lower during and just after the breeding period. This is probably accounted for by winter visits to feeders by non-breeding species such as Siskin (72 birds, all in months 13 – 15 and 25 – 27), Redwing (three birds, months 13, 24 and 25) and Redpoll (three birds in month 13), the late winter carelessness of the territory-disputing Mistle Thrushes (two in month 2, one in month 14) and the winter hunger of otherwise uncatchable Woodpigeons (one in month 28) and Collared Doves (one in month 11). The diversity minimum and corresponding high species/effort ratio at month 35 is due to low trapping effort.

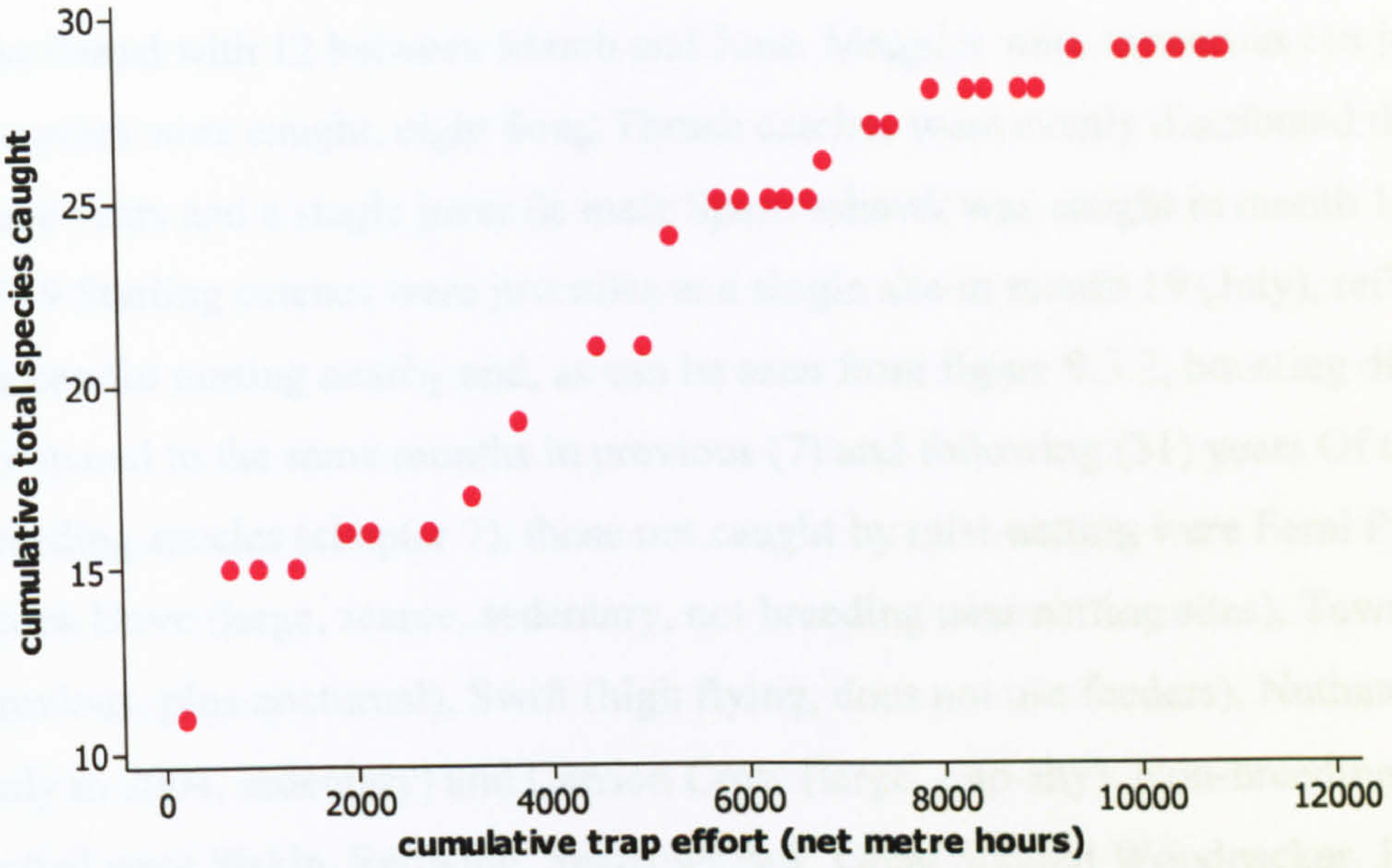


Figure 9.3.1. Cumulative total numbers of species caught with increasing cumulative total trapping effort (net metre hours)

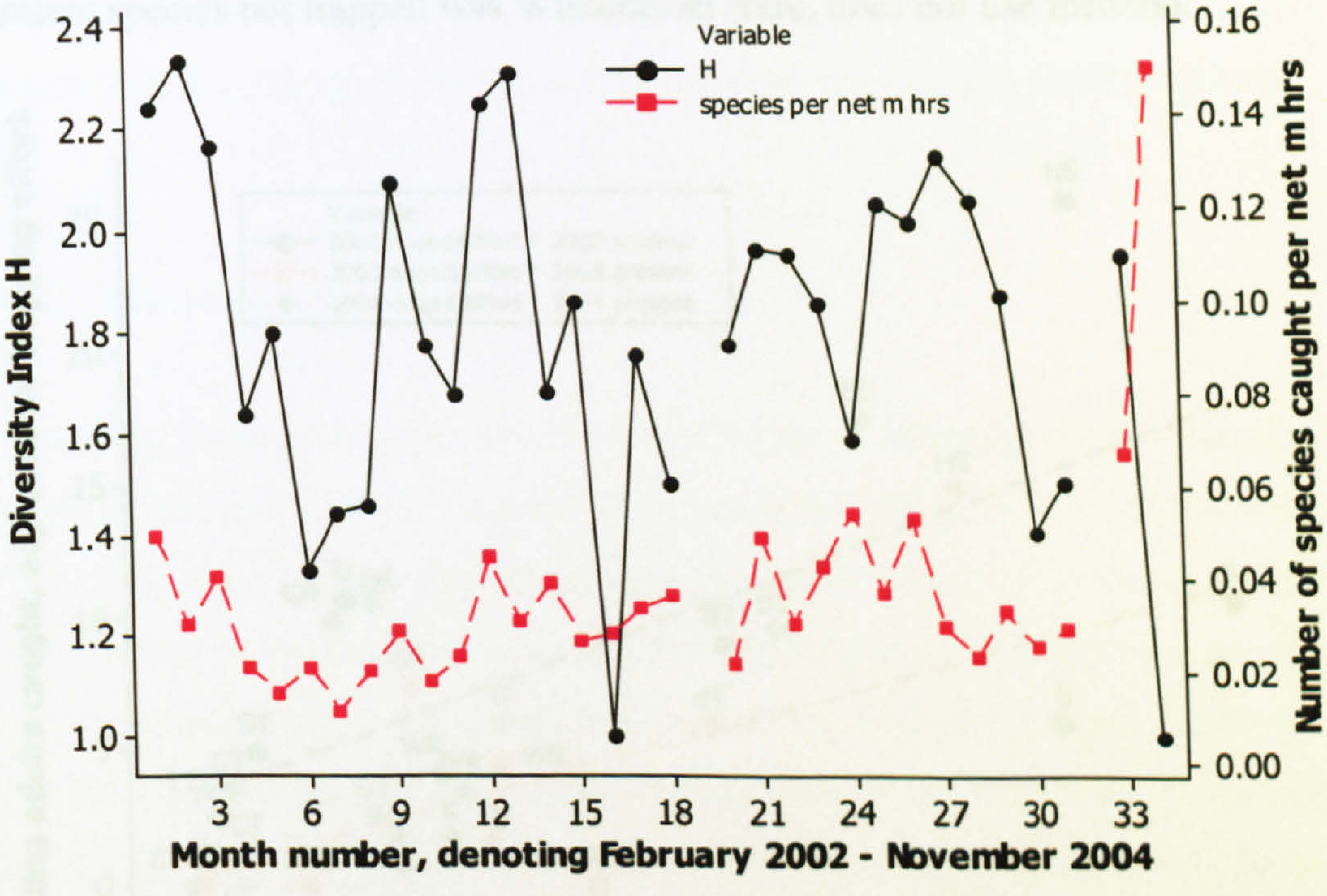


Figure 9.3.2. Shannon's Diversity Index H (black plot) for species caught by mist-netting plotted for each month, together with the ratio of number of species caught to trapping effort (net m hrs) for each month (red plot, secondary Y axis).

Among the less frequently caught species, two Willow Warblers boosted diversity in month 28 and wintering Blackcaps were caught in months 2, 3 and 24. The only Chaffinches caught were winter juveniles (months 6, 14, 24, 27 and 34); one Chiffchaff improved diversity in month 9 and an exceptional four were caught in month 21. Transient Goldcrests were caught in late autumn each year. In 2002 and 2003, Goldfinch catches were almost all in winter; in 2004 catches were more evenly distributed with 12 between March and June. Magpies were numerous but just three juveniles were caught, eight Song Thrush catches were evenly distributed through the three years and a single juvenile male Sparrowhawk was caught in month 10. Nine out of 19 Starling catches were juveniles at a single site in month 19 (July), reflecting successful nesting nearby and, as can be seen from figure 9.3.2, boosting diversity compared to the same months in previous (7) and following (31) years Of the 27 known breeding species (chapter 7), those not caught by mist-netting were Feral Pigeon and Stock Dove (large, scarce, sedentary, not breeding near netting sites), Tawny Owl (as previous, plus nocturnal), Swift (high flying, does not use feeders), Nuthatch (one pair only in 2004, sedentary) and Carrion Crow (large, trap-shy). Non-breeding species mist-netted were Siskin, Redwing, Sparrowhawk, Great Spotted Woodpecker, Jay, Goldcrest, Willow Warbler and Chiffchaff. Known wintering species not trapped were Waxwing *Bombycilla garrulus* and Fieldfare (scarce, do not use feeders). The only known transient species not trapped was Whitethroat (rare, does not use feeders).

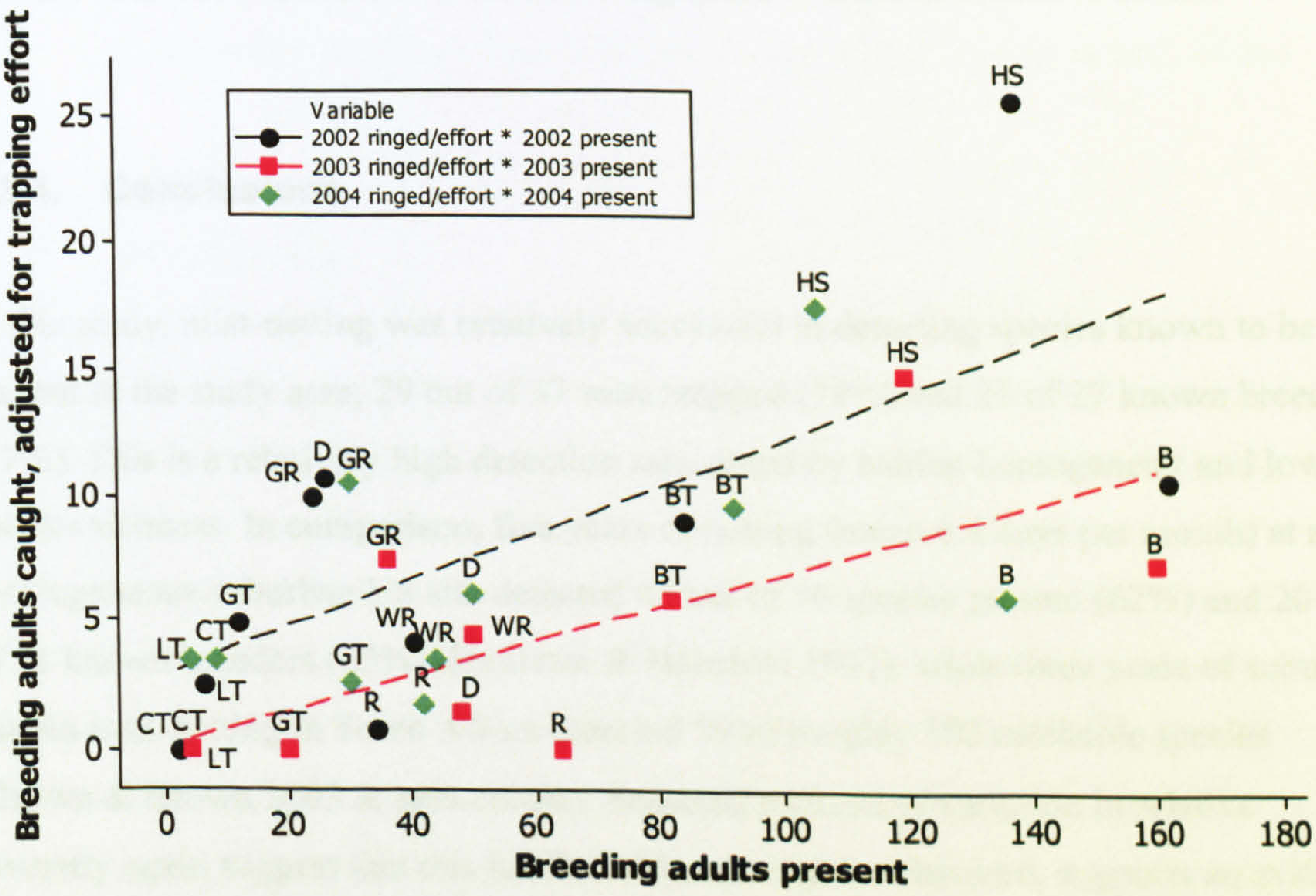


Figure 9.3.3. Adjusted numbers of adults ringed against actual numbers of breeding adults (individuals) in the study area (from census data, chapter 7) April – June, linear regression lines shown for 2002 (black) and 2003 (red), regression for 2004 (green) was not significant. Numbers of birds ringed in each season are divided by trapping effort in that season (2002, 1208; 2003, 674; 2004, 1141 net m hrs) and multiplied × 10^3 for easier comparison. WR = Wren, D = Dunnock, R = Robin, B = Blackbird, BT = Blue Tit, GT = Great Tit, LT = Long-tailed Tit, HS = House Sparrow, GR = Greenfinch, CT = Coal Tit.

For the ten most-ringed species, OLS linear regression indicated that the numbers of breeding adults caught per year were correlated with the numbers of breeding adults present in 2002 ($F_{1,8} = 8.02$, $r^2 = 50.1\%$, $P = 0.022$) and 2003 ($F_{1,8} = 8.16$, $r^2 = 50.5\%$, $P = 0.021$). (figure 9.3.3), but the correlation for 2004 was not significant ($F_{1,8} = 3.41$, $r^2 = 29.9\%$, $P = 0.102$). From examination of the residuals between actual numbers of breeding season adults trapped and those predicted by breeding populations (figure 9.3.3), some species show consistent variation. Fewer breeding adult Blackbirds and Robins were trapped than might have been expected from relative breeding numbers; this perhaps reflects high territoriality and relatively low dependence on feeding stations, although residuals for Wren and Dunnock, for which similar factors might apply, are inconsistent. In contrast, numbers of mobile, feeder-using Greenfinches ringed are consistently higher than predicted, as are those for House Sparrows which are notoriously immobile but localised populations were resident at four of the five primary sites. Residuals for Blue and Great Tits are inconsistent and reverse between years; in 2002 more Great Tits and fewer Blue Tits were trapped than predicted, the opposite was the case in 2003. Numbers of Coal and Long-tailed Tits are too small to assess.

9.3.4. Conclusions

In this study, mist-netting was relatively successful in detecting species known to be present in the study area; 29 out of 37 were trapped (78%) and 21 of 27 known breeders (77%). This is a relatively high detection rate, aided by habitat homogeneity and low species richness. In comparison, five years of netting (mean 6.8 days per month) at a heterogeneous suburban US site detected 47 out of 76 species present (62%) and 20 out of 31 known breeders (65%) (Hansrote & Hansrote 1991), while three years of suburban garden mist-netting in South Africa detected 59 of roughly 100 catchable species (Brown & Brown 2003 & pers.comm). Seasonal patterns of variation in relative diversity again suggest that this habitat, although highly urbanised, supports an avifauna more typical of suburbia rather than a core urban avifauna; in the latter, seasonal variation in diversity is characteristically low (e.g. Mulsow 1980 in Bezzel 1985).

Some aspects of the interspecific variations in correspondence between numbers of breeding adults trapped and present are unsurprising, particularly the contrast between granivorous and semi-colonial Greenfinch and House Sparrow (higher than predicted trapping rates at feeders) and territorial, invertebrate-feeding Blackbird and Robin (lower than predicted). Silkey et al (1999) suggested that the least territorial species had the poorest correspondence between catch rate and breeding population. This might suggest that this correspondence could be particularly poor if dependence on point sources of high-quality, *ad lib* food at feeding stations induced the birds of SK3388 to forage in a less conventionally territorial way than conspecifics in a habitat with more uniform food distribution. It seems that in none of the most-trapped species does the presence of these particular feeders obviously over-ride normal territorial behaviour, suggesting that availability of food within territory is not a serious constraint on breeding season adults. An alternative hypothesis might be that if feeders draw all the breeding individuals within an area to a point source of food at some time during each day, catch rates at those feeders should be a good reflection of overall breeding numbers. This would depend on the extent to which the feeders attract extra-limital birds, the study area being arbitrarily delimited within a continuous population.

9.4. Differential timing of garden feeding station use in urban birds

9.4.1. Introduction

This analysis examines whether different species of bird utilise urban garden feeding stations at different times of day. If they did, this might indicate temporal resource partitioning inter-specific competition (Kronfeld-Schor & Dayan 2003). It might also reflect how species resident in and transient through the study area use feeders in different ways, and the degree to which the presence of feeding stations affects territoriality. Resident/territorial species will have access to the resource at any time of the day, whereas transient or non-territorial species might visit according to a regular daily schedule of foraging activity.

9.4.2. Method

The times after sunrise of 1785 individual mist-net catches (corrected for summer time) were obtained from the US Navy Astronomical Applications Department website (aa.usno.navy.mil/cgi-bin/aa_pap.pl) for Sheffield (longitude W1.5, latitude N53.4). One-way ANOVA of trapping time after sunrise against species was performed using MINITAB v.14, Tukey multiple comparison tests detected differences between species pairs. To normalise the distribution of the response variable, it was square root transformed and captures after 12 p.m (181 captures, 10.1% of the data) were removed (Ryan-Joiner normality statistic = 0.999, P =0.095). To focus the analysis on species with a reasonable sample size and restrict species to a tractable number for pairwise comparison, species with fewer than 30 captures were removed, leaving 1508 records of 12 species, Blackbird (68 captures), Blue Tit (529), Coal Tit (70), Dunnock (86), Goldfinch (65), Great Tit (109), House Sparrow (210), Long-tailed Tit (77), Robin (39), Siskin (67) and Wren (60 captures).

9.4.3. Results

In general, the urban garden birds of SK3388 did not differ in their general diel trapping pattern from that well-known to non-urban mist-netters, i.e. the bulk of birds are caught in the first 4 hours (0 – 14400 seconds) after sunrise and catch rates tail-off after 5 hours (18000 seconds). The boxplots for both winter (figure 9.4.2) and breeding season (figure 9.4.3) captures suggest that there is some variation between species in the timings of the use of the feeding stations, even in winter when daylength and consequently available feeding time is less. Among all captures in all months, there was highly significant variation among the 12 species in time after sunrise of capture (ANOVA: $F_{11, 1489} = 2.96$, $r^2 = 2.14\%$,. $P = 0.001$). Tukey pairwise comparisons revealed five significant differences between species pairs: Coal Tit and Blue Tit ($t = -4.11$, $P = 0.0024$), Coal Tit and Greenfinch ($t = 3.59$, $P = 0.0174$), Coal Tit and Long-tailed Tit ($t = 3.49$, $P = 0.0244$), Coal Tit and House Sparrow ($t = 4.645$, $P = 0.0002$) and Great Tit and House Sparrow ($t = 3.55$, $P = 0.0198$).

For winter captures in months October to March only (figure 9.4.2, ANOVA: $F_{11, 893} = 2.63$, $r^2 = 3.14\%$, $P = 0.003$), pairwise differences were found between Coal Tit and Blue Tit ($t = -3.7$, $P = 0.0114$), Coal Tit and Greenfinch ($t = 3.997$, $P = 0.0037$) and Coal Tit and Long-tailed Tit ($t = 3.58$, $P = 0.00178$). For breeding season captures in months April – September only (figure 9.4.3, ANOVA: $F_{10, 585} = 2.75$, $r^2 = 4.49\%$, $P =$

0.003), the only significant pairwise difference was between Great Tit and House Sparrow ($t = 4.39$, $P = 0.0006$).

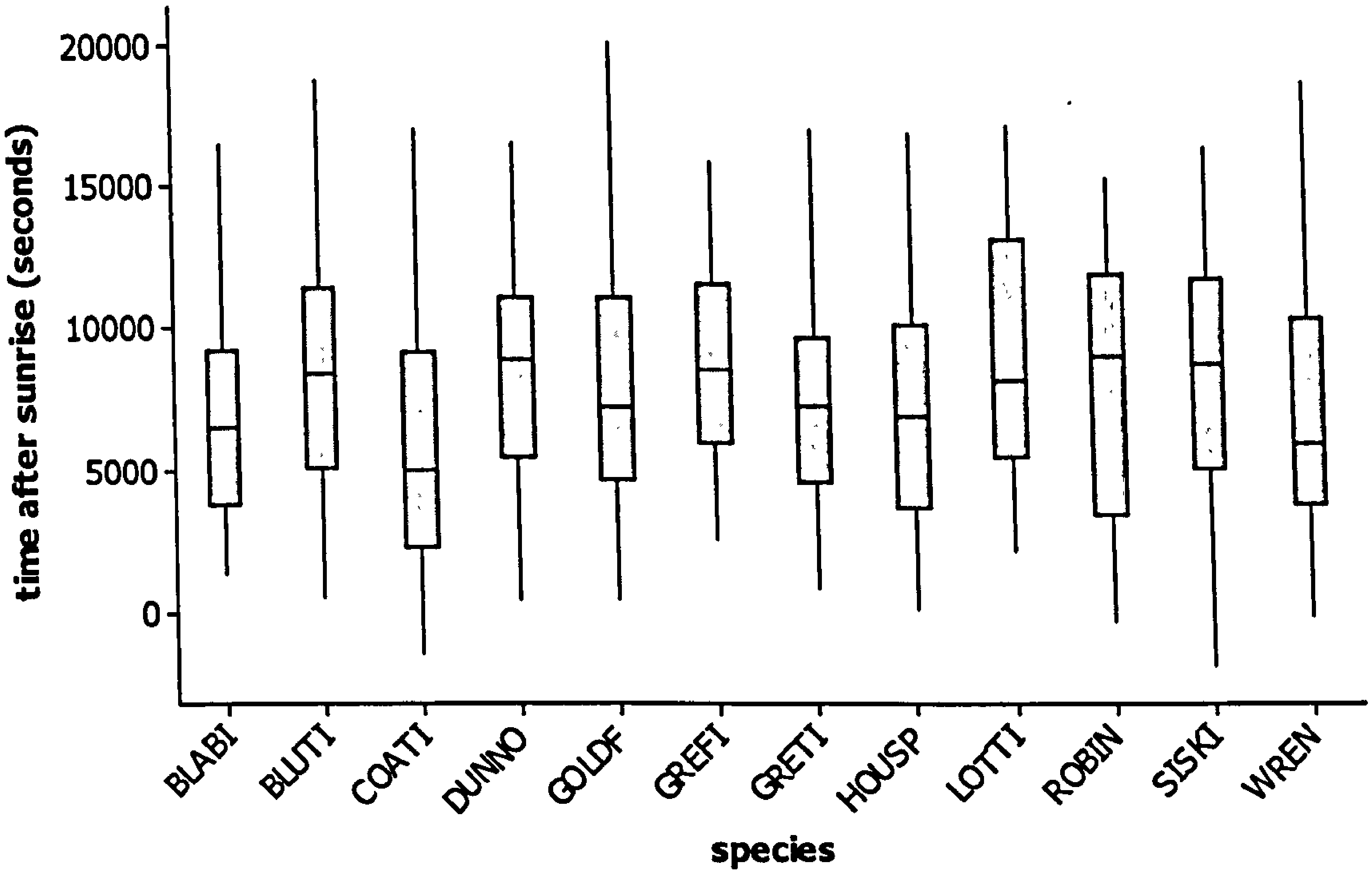


Figure 9.4.2. Winter: boxplot of time after sunrise of capture by species, 911 captures, before midday, October – March only, 2002-2004. Bar = median, box bottom= first quartile Q1 (25%), box top = third quartile Q3 (75%), upper whisker = Q3 + 1.5(Q3 – Q1), lower whisker = Q3 – 1.5(Q3 – Q1), asterisks = outliers.

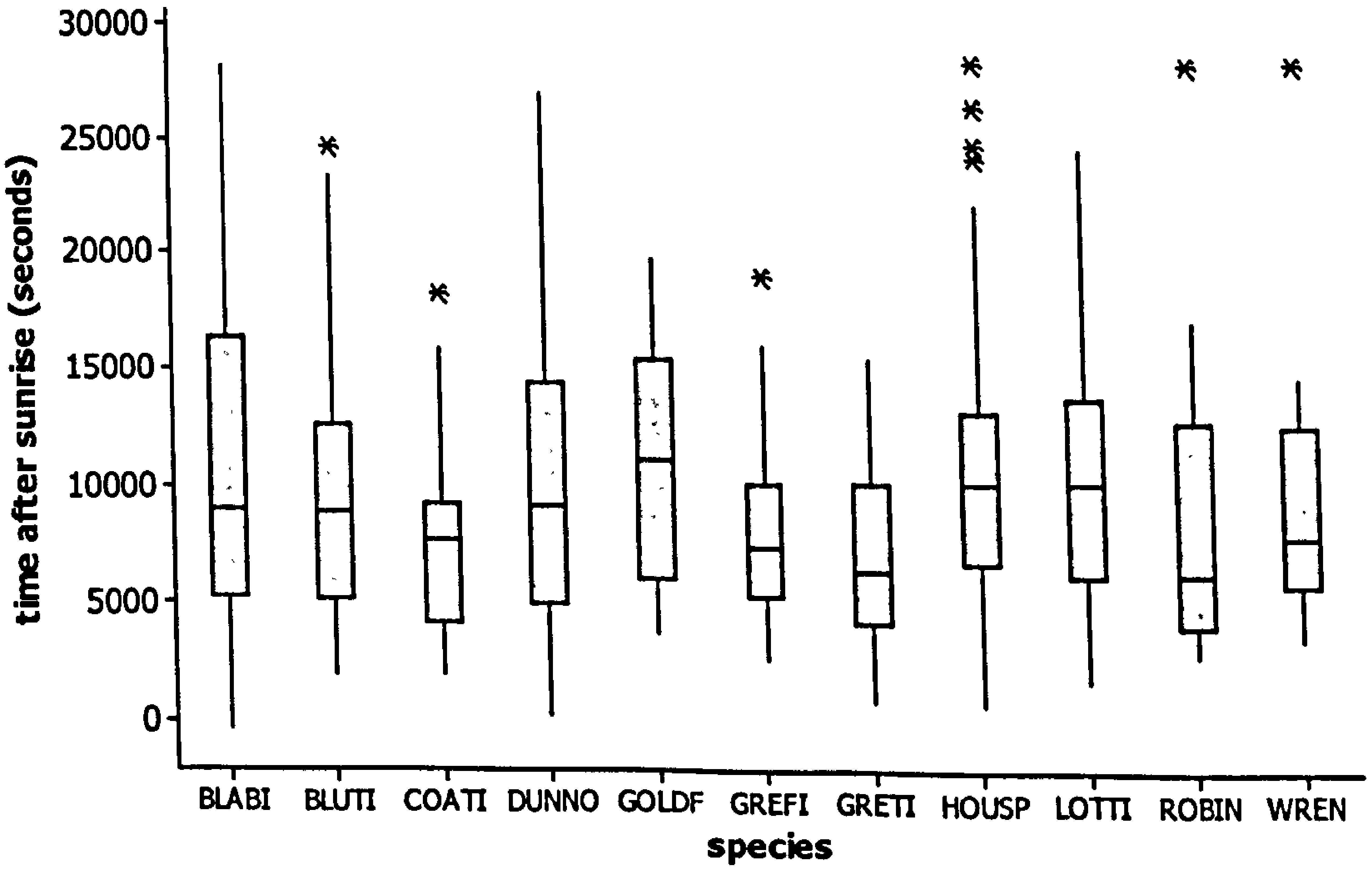


Figure 9.4.3. Breeding season: boxplot of time after sunrise of capture by species, 597 captures, before midday, April – September only, 2002-2004.

9.4.4. Discussion

It would be desirable to compare these patterns with those obtained in non-urban habitats but it would be impossible to control for catching effort; in the present study a uniform protocol was adopted, weather permitting (start at dawn, stop after 11 am as soon as no bird caught in 30 minutes) but netting durations elsewhere are generally not recorded. All that can really be said with reference to non-urban avifaunas is that the presence of *ad lib* food does not seem to grossly distort the diel activity pattern in terms of inducing birds to forage evenly throughout the day; there is still a clear early morning activity peak at the feeding stations. This observation is confounded by the increasing visibility and consequent decreasing sampling efficiency of mist-nets with increasing sunlight but anecdotal observation and field notes concur that bird feeders in SK3388 generally do go quiet by mid-morning. A post-breakfast increase in visible human (and cat) activity may contribute to birds' preference for early morning feeding.

Much of the small proportion of variation in capture time attributable to species is probably accounted for by the notably early use of the feeders by Coal Tit, which Fitzpatrick (1997b) also observed visiting feeders early in the day. This species is similar in food and feeder exploitation methods to the Blue Tit but is marginally smaller and notably less competitive at feeders, also (and perhaps associatively) it stores seed in caches rather than consuming it immediately at the time of acquisition. These differences could explain its use of feeders early in the day when it attempts to acquire and store as much food as possible before competing species become active. Coal Tits are notoriously selective and inefficient exploiters of sunflower seeds (pers. obs & comms); possibly, in this habitat, they forage as 'cream skimmers' (Kneitel & Chase 2004; Jones et al. 2001 in Kronfeld-Schor & Dayan 2003; Brown et al. 1997 in Shochat et al. 2004) with a high giving up density in the face of competition, although their singular caching behaviour may also redeem the cost of not visiting the feeders later in the day. House Sparrows, in contrast, are reputed to be 'late risers', able to dominate feeding stations and to have a relatively short 'working day' in terms of active food acquisition (Summers-Smith 1963). Once they do visit feeders they use them to obtain the bulk of their food and with low giving-up densities, according to Shochat et al. (2004) who point out that "competitive interactions play significant roles in structuring urban bird communities". In one US study, 82.6% of the food of urban House Sparrows was seed (Gavett & Wakeley 1986).

Capture times of Blackbird, Wren, Robin and perhaps Dunnock can be dissociated from feeding behaviour as these are not generally feeder users except in hard weather; resident territorial individuals of these species may be mist-netted at any time of day. In contrast, most Long-Tailed Tit captures are from flocks drawn to peanuts in winter, and they visit feeding stations significantly later than the seed-eating Coal Tit. This analysis assumes that diel variations in mist-net detectability and avoidance are similar in all the species considered. Casual observations of feeders in SK3388 suggest that further periods of activity do occur during the afternoons; a more complete investigation of diel interspecific variation in feeder use would require systematic catching effort throughout all the hours of daylight. Also, observations of diel activity patterns cannot necessarily be generalised between sites; Wilson (2001) noted that Black-capped Chickadees varied in their diel patterns of winter feeder usage between two sites.

9.5. Conclusions

In general, feeders are not used uniformly throughout the days and seasons but their usage rates are associated with early morning low temperatures, suggesting that for many individual birds in SK3388 they fulfil their traditionally-ascribed primary role of alleviating short-term nutritional stress. Nonetheless, some birds can be caught at feeding stations throughout the year, suggesting that they provide resources for a breeding population as well as winter transients. With uniform trapping effort, the re-trap rate slowly increased with time, suggesting that this avifauna is not entirely dependent on repeated immigration. Year-round patterns of feeder utilisation are generally similar to national garden patterns, suggesting that to some extent small urban gardens fulfil a similar role to larger suburban and rural gardens as bird habitat. There is some correspondence between catch rates of breeding adults and the known breeding population and departures from correspondence can be understood in terms of the species' normal breeding and feeding ecology, again suggesting that this habitat is supporting a breeding avifauna whose patterns of habitat use do not differ markedly from those in other habitats. This also suggests that the degree to which this habitat represents ecological opportunities or constraints varies between species; this is further supported by evidence that some species are more constrained that others in their diel patterns of feeder usage.

10. A ringing study of urban garden birds: birds re-encountered

Abstract

Mist-netting at feeders and re-sighting of colour-ringed birds in the SK3388 study area produced 2077 re-encounter records of 587 individuals and 17 species; 33% of birds ringed were re-encountered. Some individuals were very persistent, 26 birds (4.5%) contributing 25% of re-encounters and individuals of seven species were re-encountered more than two years after ringing. Frequency distributions of re-encounter durations showed that some species use the study area seasonally whereas others are year-round residents. Re-encounter rates of birds ringed in the breeding season did not differ between species in both adults and juveniles, suggesting the breeding avifauna is stable in composition. In winter, re-encounter rates varied between species, affected by winter visitors and transient juveniles. Very few birds were recovered dead but there was some evidence of population interchange between SK3388 and suburban gardens as well as several longer-distance movements. Within the study area, however, most birds maintained normal territoriality as evidenced by site fidelity; only Greenfinches were re-encountered at more than four sites. Despite high relative urbanisation, SK3388 supports an avifauna of stable composition and with movements and seasonal dynamics typical of more rural garden habitats.

10.1. Introduction

A fundamental question that has been little-investigated to date in urban ornithology is the extent to which the same individual birds persist at a given site through time. Many urban garden bird enthusiasts are sure that ‘their’ favourite birds visit daily for several seasons (numerous pers. comm.), yet overall mean survival rates among the species involved are in general so low as to render such longevity unlikely. The persistence and mobility of individuals and species within urban habitats are of key importance in evaluating whether they support self-sustaining avifaunas or are just either temporary resources for time-varying assemblages of transients and/or sink habitat for doomed immigrants. They are also important in terms of the wider objective of this thesis: evaluating the ecological opportunities and constraints experienced by the birds of SK3388. If birds are generally sedentary, their opportunities and constraints are those of the immediate environment; greater mobility, on the other hand, would increase the scale over which the ecological factors affecting them should be assessed. In this chapter, the persistence and mobility of individual birds using urban garden feeding stations is investigated using re-encounters of birds that were ringed in the SK3388 study area between 2002 and 2004.

Firstly, frequency distributions of re-encounter durations are compared to determine whether any particular species or age classes are exploiting the habitat differently from others. Differences in re-encounter duration patterns will indicate the degree to which species are either largely resident or exploiting the habitat seasonally or transiently.

Secondly, species' re-encounter rates are examined separately according to age class of birds ringed and season of ringing. Variation in re-encounter rates between adults and juveniles will provide insight into the overall and species-specific sustainability of the avifauna. Variation between species' winter and breeding season re-encounter rates will indicate whether the dynamics of the winter and breeding bird assemblages in SK3388 are different. If the utilisation of the study area by all species is fairly stable and the population of each species in reasonable equilibrium year to year with no anomalous influxes or emigrations, over three years the re-encounter probabilities of regularly-caught and re-sighted species should not vary greatly between species. If, on the other hand, the composition of the assemblage were unstable and irregular changes to the relative numbers of some species within it took place, significant inter-specific variation in re-encounter rates over a three year period might be expected.

Thirdly, the bird movements revealed by the ringing programme are reported and the relative mobility within the study area of the most-frequently ringed species evaluated. Movements between SK3388 and elsewhere will show whether the avifauna is isolated or part of a wider population, a key issue in urban ornithology. The degree of intra-site mobility will indicate the extent to which this highly-urbanised habitat supports a residential, territorial bird community or, conversely, to which SK3388 is a 'free for all' with mainly transient birds ranging widely over the area and little settlement.

10.2. Methods

Mist-netting and colour-ringing of wild birds at garden feeding stations in SK3388 during 2002 – 2004 (Chapter 9) produced 2077 records of 587 previously-ringed individuals of 17 species that were either re-trapped, found dead or, in the case of the eight colour-ringed species, re-sighted. All these post-ringing events in combination are referred to henceforth as 're-encounters'. In addition, 136 pulli and a few adults ringed in nestboxes contributed re-encounters; hence numbers of birds considered in this chapter differ slightly from the mist-net catch data in chapter 9. For each re-encounter, the time elapsed in days since initial ringing of the bird was designated 'duration'. Records of birds ringed at unknown age and species contributing less than 35 individuals and/or less than 5 re-encounters were removed from the sample, leaving Blackbird, Blue Tit, Coal Tit, Dunnock, Great Tit, Greenfinch, House Sparrow, Long-Tailed Tit, Robin, Siskin and Wren and a total of 1553 records. The threshold was chosen to exclude Goldcrest (30 individuals but a transient species generating only two re-encounters) and Goldfinch (66 individuals but not colour-ringed and consequently only two re-encounters) but to include Robin (only 39 individuals but a colour-ringed resident with some interesting re-encounter histories). Frequency distributions of re-encounter durations for the eleven species, listed above, together and for the seven most-frequently ringed species (Blue Tit, Blackbird, Dunnock, Greenfinch, Great Tit, House Sparrow and Robin) separately were plotted as histograms for comparison.

For the calculation of age- and season-specific re-encounter rates and their comparison between species, each record of a newly-ringed bird was allocated one of four codes according to age and season of original ringing. 'Winter' was defined as the months October – March inclusive, 'breeding season' as months April – September. Birds of EURING age code 3J (juvenile plumage) at any time or age code 3 in months April – September were coded as juveniles ringed in the breeding season. Birds of age code 3 in months October – December and birds of age code 5 in months January – March were coded as juveniles ringed in winter. Birds of age codes 4, 5 or 6 in months April – September were coded as adults ringed in the breeding season; birds of age codes 4 or 6 in months October – March plus age code 5 in months October - December were coded as adults ringed in winter.

Overall re-encounter rates were first examined for differences between birds ringed as adults and juveniles in each species; using Wilcoxon two-sample tests (SAS, PROC NPAR1WAY) as distributions of durations were significantly different from normal. Secondly, to compare the overall probabilities of winter and breeding re-encounters between age classes and species, ringed individuals were coded according to presence or absence of any winter and/or breeding season re-encounters in the dataset. Re-encounter rates were then compared separately for birds ringed as adults and juveniles and in winter and in the breeding season using χ^2 tests, including only those species with sufficient data.

To examine relative mobility, re-encounters occurring at a different location from that at which the bird was originally ringed were classified as 'movements' and their linear distance (m) measured using ArcGIS. To examine inter-specific variation in relative local mobility, the numbers of different locations within and nearby (< 500m) the study site at which individual birds were encountered over the three year study period were expressed graphically as proportional pie charts for the nine most re-encountered species.

10.3. Results

10.3.1. Re-encounter rates

Within or close to SK3388, 251 birds were re-trapped and 21 birds recovered dead, in addition two re-traps and four recoveries were more distant. Colour-ringing generated 1833 field sightings, 147 in 2002, 759 in 2003, 775 in 2004 and a further 152 in the six months after ringing ceased, all but two were from within or near SK3388. Members of the public supplied 1397 sightings, of which 95.3% were from the seven keenest regular observers; 436 sightings were obtained by the author. Figure 10.1 shows the cumulative monthly re-encounter numbers over time (orange plot) in comparison with the cumulative numbers of new birds and re-traps. The re-encounter rate mirrors the re-trap rate until November 2002 when several keen observers were recruited and re-sighting rates accelerated rapidly. Considering individual birds, figure 10.2 shows that although most of the individual birds that were ringed were not re-encountered (1173 out of 1754, 67%, all catching methods) and many subsequently contributed relatively few observations (257 (14.6%) re-encountered only once), a small number of individuals were re-sighted regularly. Of the 581 individuals that were re-encountered at least once, 26 individuals (4.5%) contributed 25% of the logged re-encounters. For example, territorial female Blackbird RK11376 was formally recorded 38 times in the garden in which she nested during two of the three study years but was actually present almost daily, according to the observer.

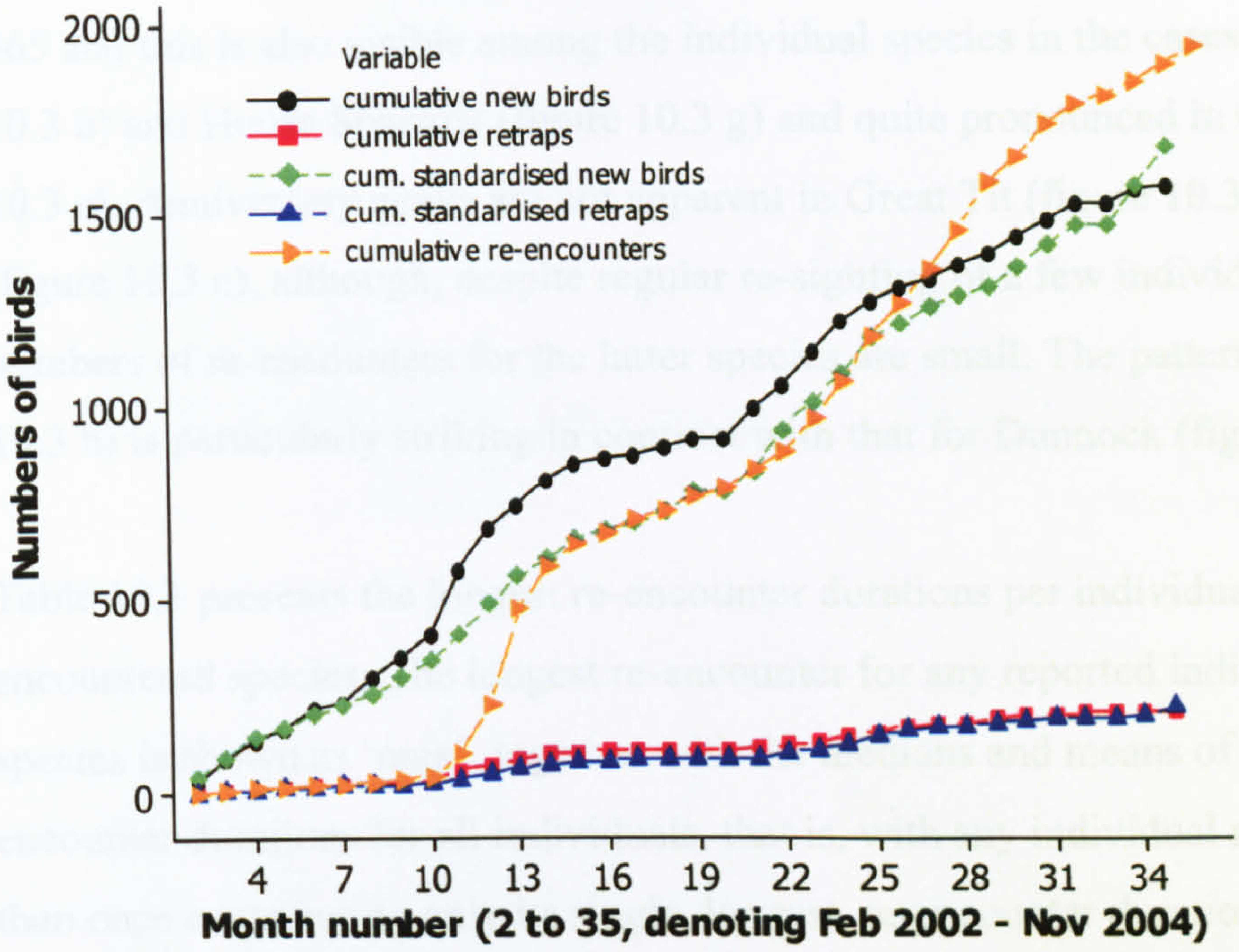


Figure 10.1. Time series plot of cumulative monthly re-encounter numbers (orange plot), superimposed on plots of monthly new birds and re-traps as in figure 9.2.2.

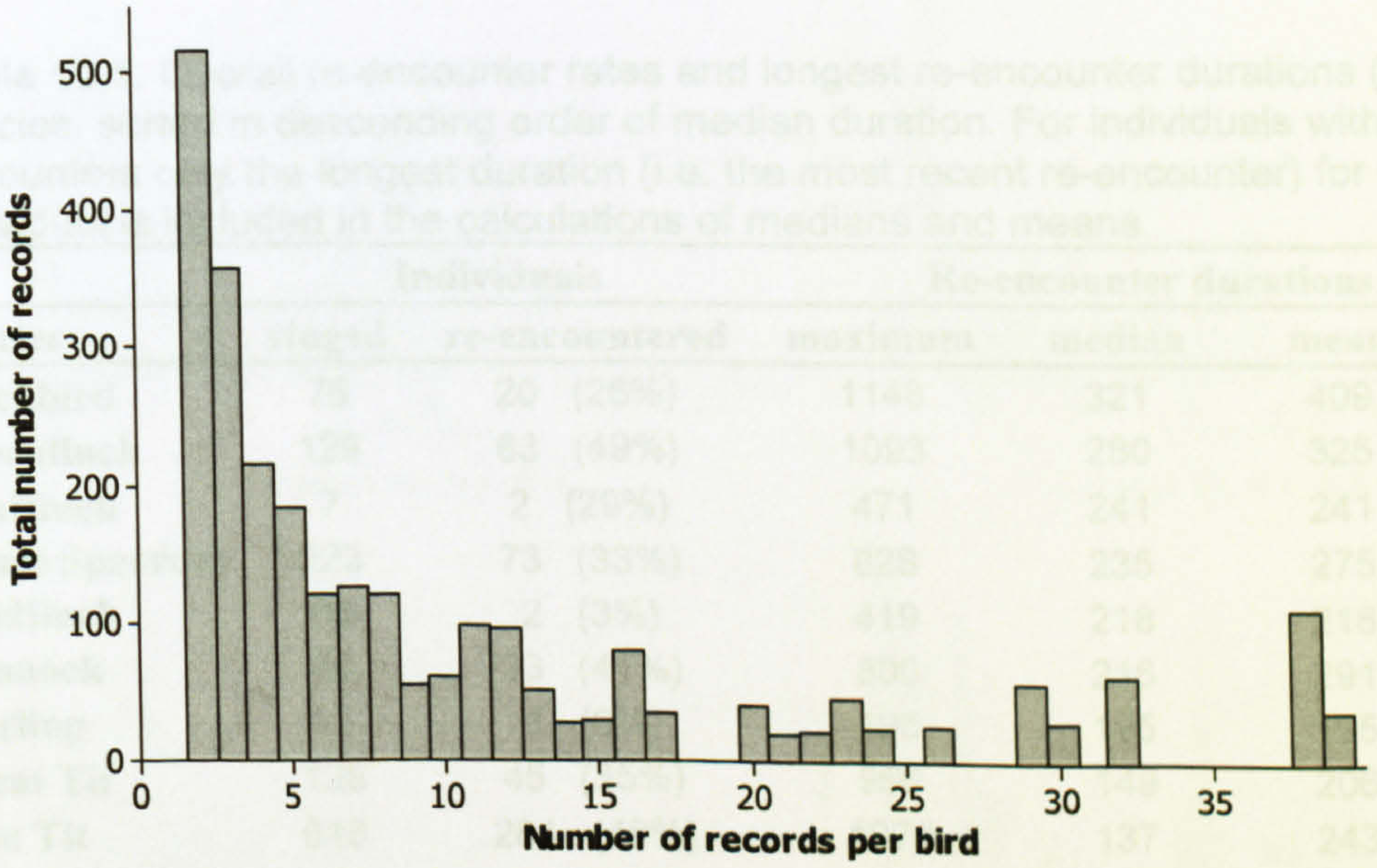


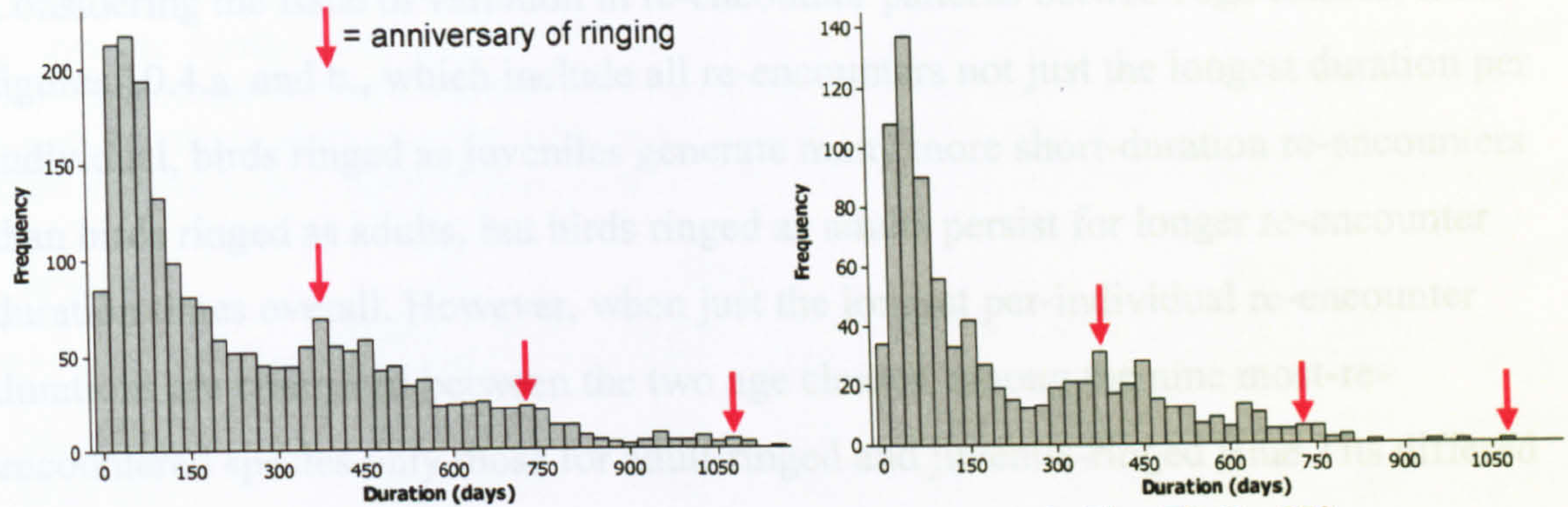
Figure 10.2. Frequency distribution of total numbers of records by number of records generated per individual bird, all species, birds contributing two or more records each.

Out of the 30 species ringed, 14 generated no re-encounters. Individuals of sixteen species were re-encountered on one or more occasions but only seven species provided more than 20 re-encounter records each over the study period. Frequency distributions of all re-encounter durations for all species combined and for these seven most-re-encountered species individually are plotted in figures 10.3 a – h. The data for all species combined (figure 10.3.a) show an anniversary peak in re-encounters around day 365 and this is also visible among the individual species in the cases of Blue Tit (figure 10.3 b) and House Sparrow (figure 10.3 g) and quite pronounced in Greenfinch (figure 10.3 e). Anniversary peaks are not apparent in Great Tit (figure 10.3 f) and Blackbird (figure 10.3 c), although, despite regular re-sighting of a few individuals, overall numbers of re-encounters for the latter species are small. The pattern for Robin (figure 10.3 h) is particularly striking in contrast with that for Dunnock (figure 10.3 d).

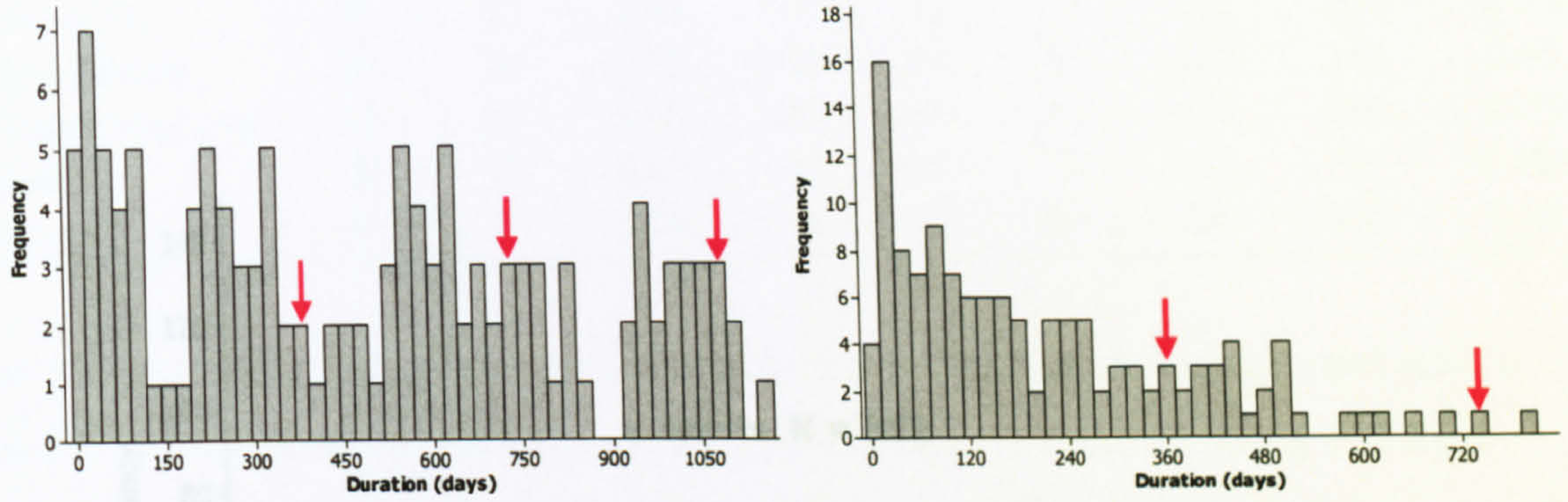
Table 10.1 presents the longest re-encounter durations per individual for each of the re-encountered species. The longest re-encounter for any reported individual of that species is shown as 'max', together with the medians and means of the maximum re-encounter durations for all individuals, that is, with any individual re-encountered more than once contributing only its single, longest, re-encounter duration. Medians are consistently less than means, as expected for right-skewed survival data, and are not correlated with numbers of birds ringed (Spearman's rank correlation $r_s = 0.32$, $P = 0.231$, N = 16).

Table 10.1. Overall re-encounter rates and longest re-encounter durations (max) , by species, sorted in descending order of median duration. For individuals with repeat re-encounters only the longest duration (i.e. the most recent re-encounter) for each individual is included in the calculations of medians and means.

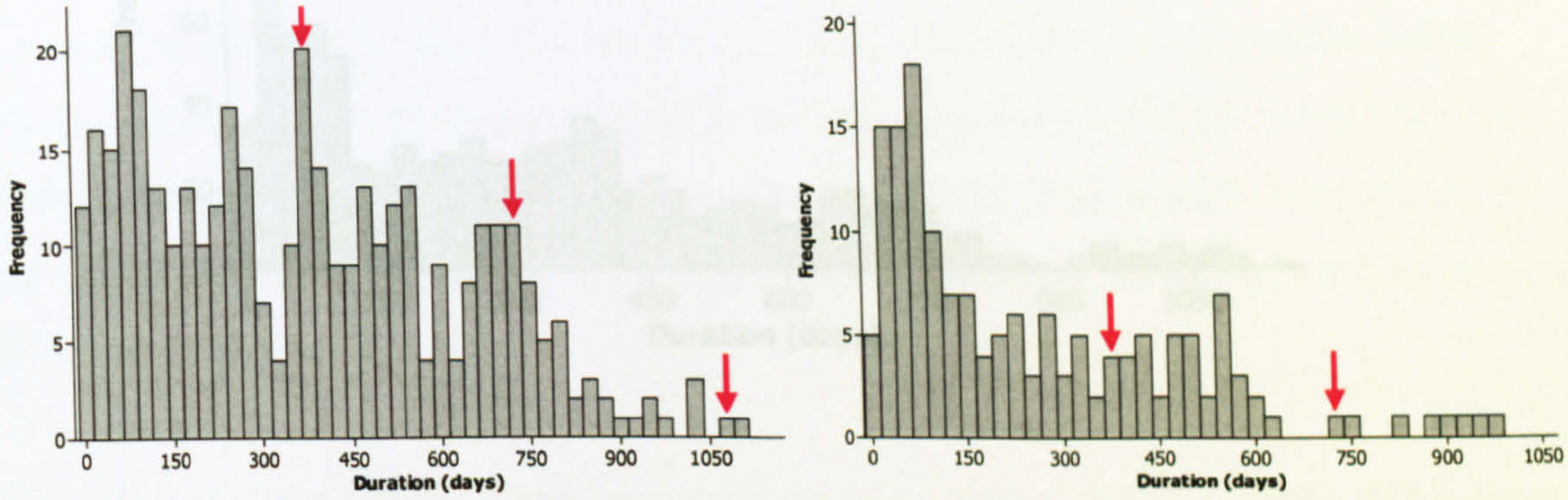
	Individuals		**Re-encounter durations (days)**			
Species	**ringed**	**re-encountered**	**maximum**	**median**	**mean**	**± SE**
Blackbird	76	20 (26%)	1148	321	409	71
Greenfinch	129	63 (49%)	1093	280	325	35
Chaffinch	7	2 (29%)	471	241	241	229
House Sparrow	223	73 (33%)	828	235	275	23
Goldfinch	66	2 (3%)	419	218	218	201
Dunnock	80	33 (41%)	800	216	291	40
Starling	18	1 (6%)	195	195	195	
Great Tit	128	45 (35%)	966	149	206	28
Blue Tit	615	284 (46%)	1070	137	243	14
Coal Tit	58	14 (24%)	561	108	136	39
Robin	39	18 (46%)	799	93	184	54
Long-tailed Tit	85	14 (16%)	676	68	177	62
Goldcrest	30	2 (7%)	105	64	64	42
Bullfinch	6	1 (17%)	59	59	59	
Wren	51	10 (20%)	378	54	114	39
Siskin	69	5 (7%)	409	46	164	87



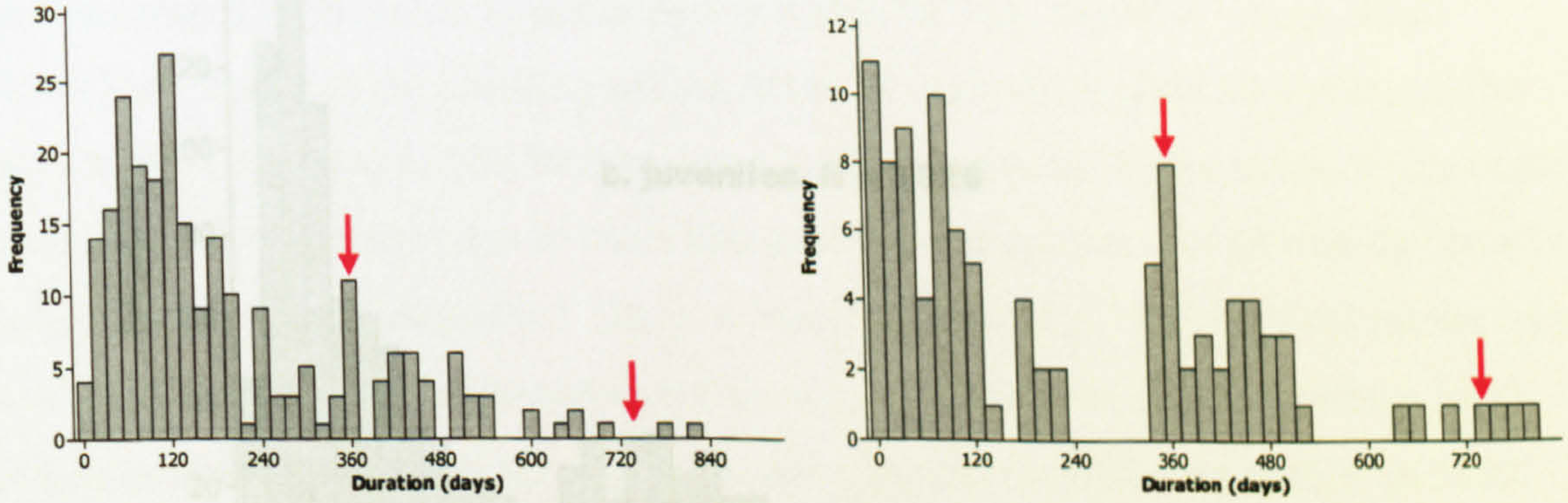
a. All species **b. Blue Tit, N = 858**



c. Blackbird, N = 129 **d. Dunnock, N = 131**



e. Greenfinch, N = 386 **f. Great Tit, N = 159**



g. House Sparrow, N = 246 **h. Robin, N = 104**

Figure 10.3. a – h. Frequency distributions of time in days (duration) between original ringing date and re-encounter date, repeat re-encounters of same individuals included. Anniversaries (durations 365, 730 and 1095 days post-ringing) shown by red arrows.

Considering the issue of variation in re-encounter patterns between age classes, from figures 10.4.a. and b., which include all re-encounters not just the longest duration per individual, birds ringed as juveniles generate many more short-duration re-encounters than birds ringed as adults, but birds ringed as adults persist for longer re-encounter duration times overall. However, when just the longest per-individual re-encounter durations are compared between the two age classes, among the nine most-re-encountered species only those for adult-ringed and juvenile-ringed Blue Tits differed significantly (table 10.2)

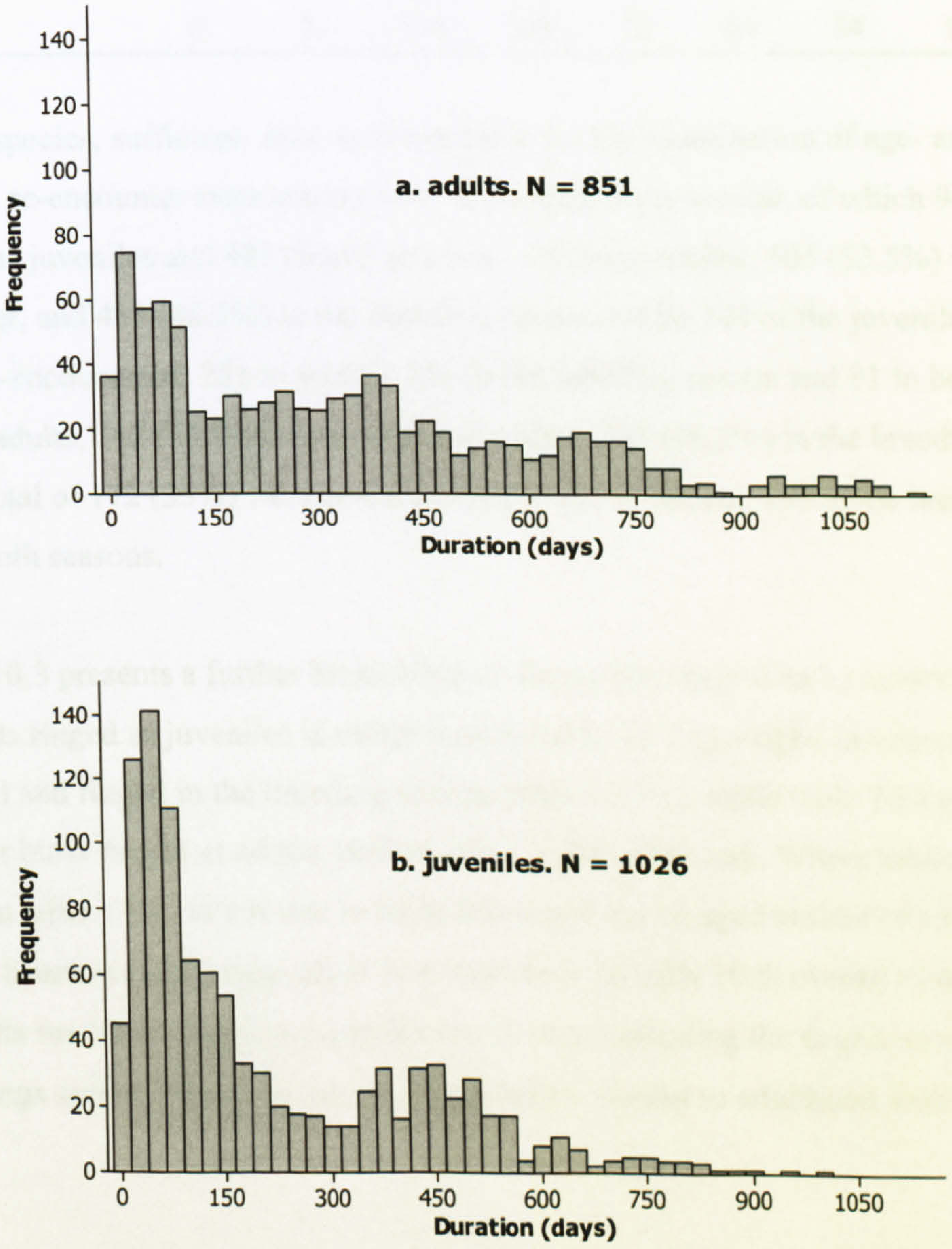


Figure 10.4. a. and b. Frequency distribution of time in days since date bird was originally ringed (duration) for all re-encounters, all species. Adults (**a.**) are birds ringed in the calendar year post-hatching or subsequently. Juveniles (**b.**) are birds ringed during their calendar year of hatching.

Table 10.2. Results of Wilcoxon two-sample test for differences between longest re-encounter durations of birds ringed as adults and birds ringed as juveniles. N = number of re-encounters, Mean = mean re-encounter duration (days) SE = standard error of mean duration. Median = median re-encounter duration (days) *P* = two-sided $P_r>|Z|$ from Wilcoxon two-sample test. juvs = juveniles, see 10.2. for derivation of age classes.

Species	**N**		**Mean**		**SE**		**Median**		***P***
	adults	**juvs**	**adults**	**juvs**	**adults**	**juvs**	**adults**	**juvs**	
Blackbird	16	4	477	136	80	28	399	124	0.065
Blue Tit	68	216	359	205	32	15	348	111	**<0.0001**
Coal Tit	4	10	155	128	51	52	177	66	0.479
Dunnock	15	12	296	312	63	75	266	163	0.826
Great Tit	9	35	235	177	40	27	236	121	0.172
Greenfinch	29	34	316	333	56	44	196	341	0.60
House Sparrow	15	25	246	285	48	44	179	244	0.716
Robin	8	10	230	148	81	75	150	66	0.182
Wren	5	2	154	130	72	64	54	130	0.85

For 11 species, sufficient data were available for the examination of age- and season-specific re-encounter rates among 1431 individual birds in total, of which 944 were ringed as juveniles and 487 ringed as adults. Of the juveniles, 505 (53.5%) were ringed in winter, and 439 (46.5%) in the breeding season, while 344 of the juveniles (36%) were re-encountered, 281 in winter, 154 in the breeding season and 91 in both seasons. Of the adults, 262 (53.8%) were ringed in winter, 225 (46.2%) in the breeding season and a total of 172 (35%) were re-encountered, 121 in winter, 107 in the breeding season, 56 in both seasons.

Table 10.3 presents a further breakdown of the re-encounter data by season and species for birds ringed as juveniles in either season (table 10.3 a), ringed in winter (table 10.3.b.) and ringed in the breeding season (table 10.3 c), while table 10.4 presents the data for birds ringed as adults, broken down in the same way. Where totals do not match those in table 10.1., this is due to birds that could not be aged at time of ringing (mostly House Sparrows and Long-tailed Tits in winter). In table 10.5, overall re-encounter rates as adults for birds ringed as juveniles are shown, indicating the degree to which local fledglings and/or dispersing juvenile immigrants persist to adulthood within SK3388.

Table 10.3. a – c Within age class re-encounter rates: birds ringed as juveniles. RE = overall re-encounter rate (proportion of birds ringed that were subsequently re-trapped, re-sighted or recovered). RE_b = birds re-encountered in breeding season. RE_w = birds re-encountered in winter. RE_{both} = birds re-encountered in both seasons.

a. Birds ringed as juveniles in either season

Species	Ringed	RE	RE_b	RE_w	RE_{both}
All 11 species	944	344 (36%)	154 (16%)	281 (30%)	91 (10%)
Blackbird	29	4 (14%)	4 (14%)	2 (7%)	2 (7%)
Blue Tit	491	214 (44%)	74 (15%)	188 (38%)	48 (10%)
Coal Tit	51	10 (20%)	5 (10%)	6 (12%)	1 (2%)
Dunnock	33	12 (36%)	8 (24%)	9 (27%)	5 (15%)
Great Tit	100	33 (33%)	19 (19%)	24 (24%)	10 (10%
Greenfinch	71	34 948%)	23 (33%)	28 (39%)	17 (24%)
House Sparrow	67	23 (34%)	16 (24%)	14 (21%)	7 (10%)
Long-tailed Tit	4	0	0	0	0
Robin	26	10 (38%)	4 (15%)	7 (27%)	1 (4%)
Siskin	49	3 (6%)	0	3 (6%)	0
Wren	23	1 (4%)	1 (4%)	0	0

b. Birds ringed as juveniles in winter

Species	Ringed	RE	RE_b	RE_w	RE_{both}
All 11 species	505	209 (41%)	76 (15%)	188 (37%)	55 (11%)
Blackbird	22	4 (18%)	4 (18%)	2 (9%)	2 (9%)
Blue Tit	247	131 (53%)	32 (13%)	127 (51%)	28 (11%)
Coal Tit	38	8 (21%)	4 (11%)	5 (13%	1 (3%)
Dunnock	19	8 (42%)	6 (32%)	6 (32%)	4 (21%)
Great Tit	38	17 (45%)	8 (21%)	14 (37%)	5 (13%)
Greenfinch	58	31 (53%)	21 (36%)	25 (43%)	15 (26%)
House Sparrow	1	0	0	0	0
Long-tailed Tit	0	0	0	0	0
Robin	15	6 (40%)	0	6 (40%)	0
Siskin	49	3 (6%)	0	3 (6%)	0
Wren	18	1 (6%)	1 (6%)	0-	0

c. Birds ringed as juveniles in breeding season

Species	Ringed	RE	RE_b	RE_w	RE_{both}
All 11 species	439	135 (31%)	78 (18%)	93 (21%)	36 (8%)
Blackbird	7	0	0	0	0
Blue Tit	244	83 (34%)	42 (17%)	61 (25%)	20 (8%)
Coal Tit	13	2 (15%)	1 (8%)	1 (7%)	0
Dunnock	14	4 (29%)	2 (14%)	3 (21%)	1 (7%)
Great Tit	62	16 (26%)	11 (18%)	10 (16%)	5 (8%)
Greenfinch	13	3 (23%)	2 (15%)	3 (23%)	2 (15%)
House Sparrow	66	23 (35%)	16 (24%)	14 (21%)	7 (10%)
Long-tailed Tit	4	0	0	0	0
Robin	11	4 (36%)	4 (36%)	1 (9%)	1 (9%)
Siskin	0	0	0	0	0
Wren	5	0	0	0	0

Table 10.4. a – c Within age class re-encounter rates: birds ringed as adults. Notation as table 10.3.

a. Birds ringed as adults in either season

Species	Ringed	RE	RE$_b$	RE$_w$	RE$_{both}$
All 11 species	487	172 (35%)	107 (22%)	121 (25%)	56 (12%)
Blackbird	47	15 (32%)	11 (23%	9 (19%)	5 (11%)
Blue Tit	123	67 (54%)	37 (30%)	51 (42%)	21 (17%)
Coal Tit	6	4 (67%)	1 (17%)	3 (50%)	0
Dunnock	33	15 (45%)	13 (40%)	9 (27%)	7 (21%)
Great Tit	27	8 (30%)	5 (19%)	6 (22%)	3 (11%)
Greenfinch	58	27 (47%)	20 (34%)	18 (31%)	11 (19%)
House Sparrow	93	14 (15%)	10 (11%)	9 (10%)	5 (5%)
Long-tailed Tit	46	9 (20%)	4 (9%)	7 (15%)	2 (4%)
Robin	13	8 (62%)	3 (23%)	5 (38%)	0
Siskin	20	0	0	0	0
Wren	21	5 (24%)	3 (14%)	4 (19%)	2 (10%)

b. Birds ringed as adults in winter

Species	Ringed	RE	RE$_b$	RE$_w$	RE$_{both}$
All 11 species	262	97 (37%)	49 (19%)	76 (29%)	28 (11%)
Blackbird	17	5 (29%)	3 (18%)	4 (24%)	2 (12%)
Blue Tit	80	43 (54%)	21 (26%)	34 (43%)	12 (15%)
Coal Tit	4	2 (50%)	0	2 (50%)	0
Dunnock	12	6 (50%)	5 (42%)	6 (50%)	5 (42%)
Great Tit	16	6 (19%)	1 (6%)	2 (13%)	0
Greenfinch	23	13 (57%)	8 (35%)	8 (35%)	3 (13%)
House Sparrow	29	6 (21%)	3 (10%)	5 (17%)	2 (7%)
Long-tailed Tit	40	9 (23%)	4 (10%)	7 (18%)	2 (5%)
Robin	8	6 (75%)	2 (25%)	4 (50%)	0
Siskin	20	0	0	0	0
Wren	13	4 (31%)	2 (15%)	4 (31%)	2 (15%)

c. Birds ringed as adults in breeding season

Species	Ringed	RE	RE$_b$	RE$_w$	RE$_{both}$
All 11 species	225	75 (33%)	58 (26%)	45 (20%)	28 (12%)
Blackbird	30	10 (33%)	8 (27%)	5 (17%)	3 (10%)
Blue Tit	43	24 (56%)	16 (37%)	17 (40%)	9 (21%)
Coal Tit	2	2 (100%)	1 (50%)	1 (50%)	0
Dunnock	21	9 (43%)	8 (38%)	3 (14%)	2 (10%)
Great Tit	11	5 (45%)	4 (36%)	4 (36%)	3 (27%)
Greenfinch	35	14 (40%)	12 (34%)	10 (29%)	8 (23%)
House Sparrow	64	8 (13%)	7 (11%)	4 (6%)	3 (5%)
Long-tailed Tit	6	0	0	0	0
Robin	5	2 (40%)	1 (20%)	1 (20%)	0
Siskin	0	0	0	0	0
Wren	8	1 (13%)	1 (13%)	0	0

If the re-encounter rates as adults for birds ringed as juveniles were significantly different between species, this would show that dispersal and/or survival varied between species and hence that the avifauna was unlikely to remain stable in composition over time. For ringing and re-encounter records within the breeding season only, there was no significant difference between re-encounter rates for birds of five species ringed as juveniles (Blue Tit, Coal Tit, Dunnock, Great Tit and Greenfinch, $\chi^2 = 1.035$, DF = 4, P 0.904, data from table 10.3.c). However, for ringing and re-encounter records in winter only there was a highly significant difference among nine species (Blackbird, Blue Tit, Coal Tit, Dunnock, Great Tit, Greenfinch, Robin, Siskin and Wren) for birds ringed as juveniles ($\chi^2 = 70.23$, DF = 8, P <0.001, data from table 10.3.b).

If the re-encounter rates of birds ringed as adults did not differ between species, this would indicate that all species in the avifauna had similar overall dispersal and mortality rates, a further indication of stability in the avifauna. For ringing and re-encounter records within the breeding season only, there was no significant difference between re-encounter rates of the five species providing adequate data for birds ringed as adults (Blackbird, Blue Tit, Dunnock, Great Tit and Greenfinch, $\chi^2 = 1.09$, DF = 4, P 0.895, data from table 10.4.c) although if House Sparrow was included the difference became significant ($\chi^2 = 13.41$, DF = 5, P 0.0198) but this is probably influenced by the notorious trap-shyness of this species (Summers-Smith 1963). In contrast, for ringing and re-encounter records in winter only, there was highly significant variation among eight species (Blackbird, Blue Tit, Dunnock, Great Tit, Greenfinch, Long-tailed Tit, Siskin and Wren) in re-encounter rates for birds ringed as adults ($\chi^2 = 22.94$, DF = 7, P 0.002) and somewhat more variation if House Sparrow was included ($\chi^2 = 25.5$, DF = 8, P 0.0013, data from table 10.4.b).

This would suggest that the breeding avifauna is relatively stable in composition. In contrast, the winter population would appear to contain variable proportions of transients, but for the fact that if the winter analyses were restricted to data for only the same five species as were used for the breeding season comparisons, there was no longer significant inter-specific variation in winter re-encounter rate for birds ringed as adults in winter ($\chi^2 = 7.43$, DF = 4, P 0.115). However, for birds of these five species ringed as juveniles in winter the inter-specific variation in winter re-encounter rate retained significance ($\chi^2 = 22.15$, DF = 4, P <0.001), suggesting that interspecific variation in proportions of winter transients is mostly accounted for by juveniles.

Comparing re-encounter rates between age classes, sufficient data on the proportions of ringed juveniles re-encountered as adults were available for six of the species in table 10.5, Blue Tit, Coal Tit, Dunnock, Great Tit, Greenfinch and House Sparrow; the difference was highly significant ($\chi^2 = 37.6$, DF = 5, $P < 0.0001$). Juvenile Greenfinches had an exceptionally high probability (28%) of being re-encountered as adults; re-encounter probability for Dunnock at 15% was more than twice the mean re-encounter probability of the six next most re-encountered species (6.3%).

Table 10.5 Between age class re-encounter rates: proportions of birds ringed as juveniles that were subsequently re-encountered (at any time) as adults.

Species	Individuals ringed as juveniles	Individuals re-encountered as adults	Species	Individuals ringed as juveniles	Individuals re-encountered as adults
Blackbird	29	1 (3%)	**Great Tit**	100	9 (9%)
Blue Tit	491	31 (6%)	**Greenfinch**	71	20 (28%)
Bullfinch	5	1 (20%)	**House Sparrow**	67	5 (7%)
Chaffinch	6	0 (0%)	**Long-tailed Tit**	4	0 (0%)
Coal Tit	51	4 (8%)	**Robin**	26	1 (4%)
Dunnock	33	5 (15%)	**Siskin**	49	0 (0%)
Goldcrest	28	0 (0%)	**Starling**	12	0 (0%)
Goldfinch	41	0 (0%)	**Wren**	23	1 (4%)

Relatively few birds were recovered dead; four long-distance recoveries are discussed in section 10.3.2. Of the 17 birds recovered within or near SK3388, seven (42%) were killed by cats with another four found freshly dead, cause unknown. Two Blue Tits (almost certainly a nesting pair) were road casualties, two were pulli found dead near boxes post-fledging (one drowned) as was one Great Tit. One adult female Blackbird ringed in at least her second winter on 21/02/2002 was found headless and freshly killed on the pavement over two years later in breeding condition and 1.5 km away.

10.3.2. Movements

Figure 10.5 maps the nominal linear trajectories of bird movements between feeding sites at which regular observations were made (i.e. excluding 'one-off' casual records) as vectors of varying colours and thicknesses according to the relative frequency of the movement in the dataset (see figure 10.5 legend). Figure 10.6 repeats this mapping but for numbers of individual birds, i.e. counting only one record per individual per movement. Comparing figures 10.7 and 10.8 reveals several cases of 51 – 100 movements and one of > 100 movements that were accounted for by only 5 – 20 birds.

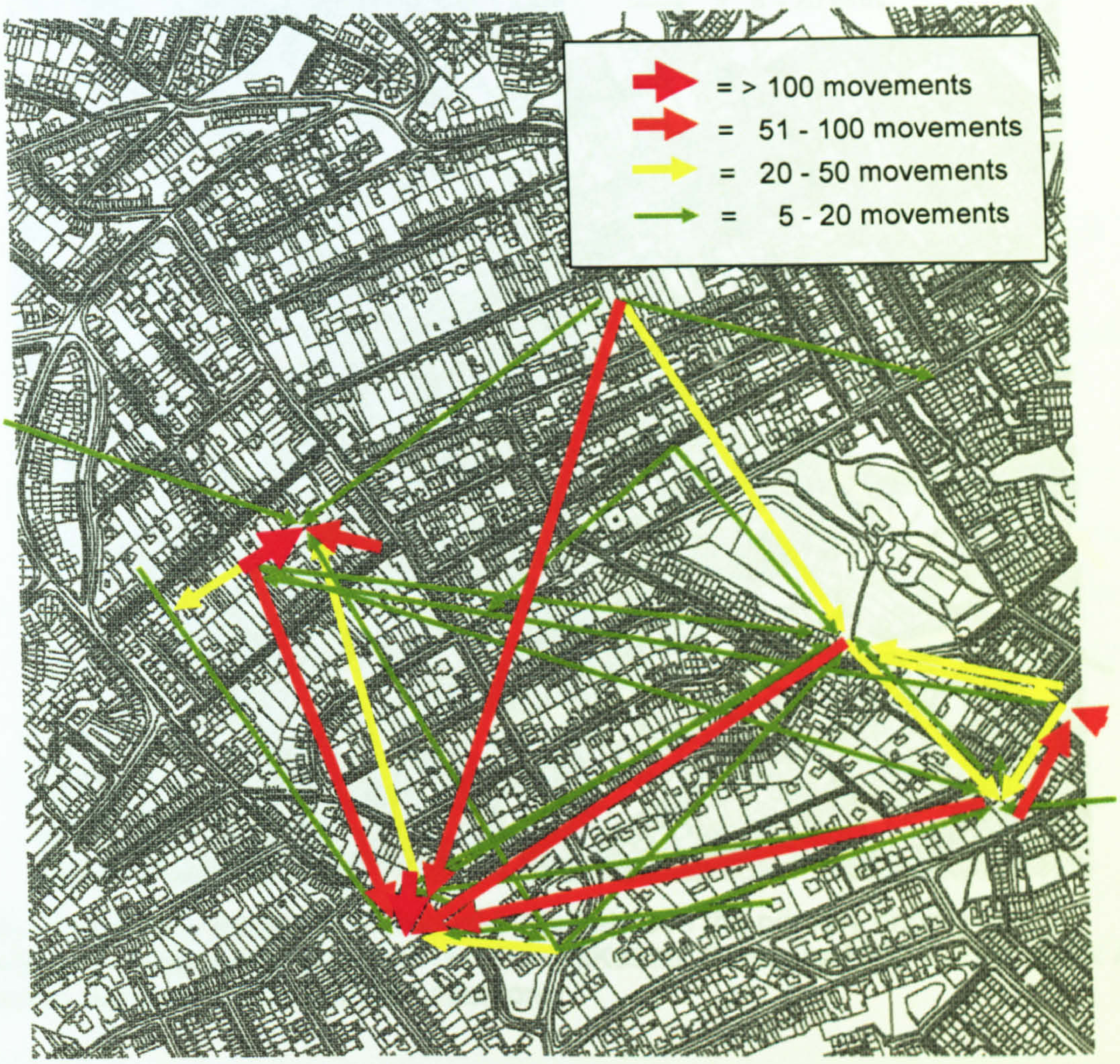


Figure 10.5. Bird movements between the primary ringing and observation sites within and near (< 500 m) SK3388, February 2002 – June 2005. All species, each repeat observation of same individual counted as one movement.

To map movements for all logged re-encounters including 'one-off' and casual records would have greatly cluttered figures 10.5 and 10.6 Instead, their frequency distributions were plotted as histograms, again both in terms of individual birds (figure 10.7 a) and total numbers of movements including repeated observations of the same individuals (figure 10.7 b). Close proximity of two productive ringing and re-sighting sites generated a bias in the distribution of movement distances (figure 10.7 b) towards short distance movements; when only one record per individual per movement was considered, the distribution of numbers of movements across distance classes was more even (figure 10.7 a).

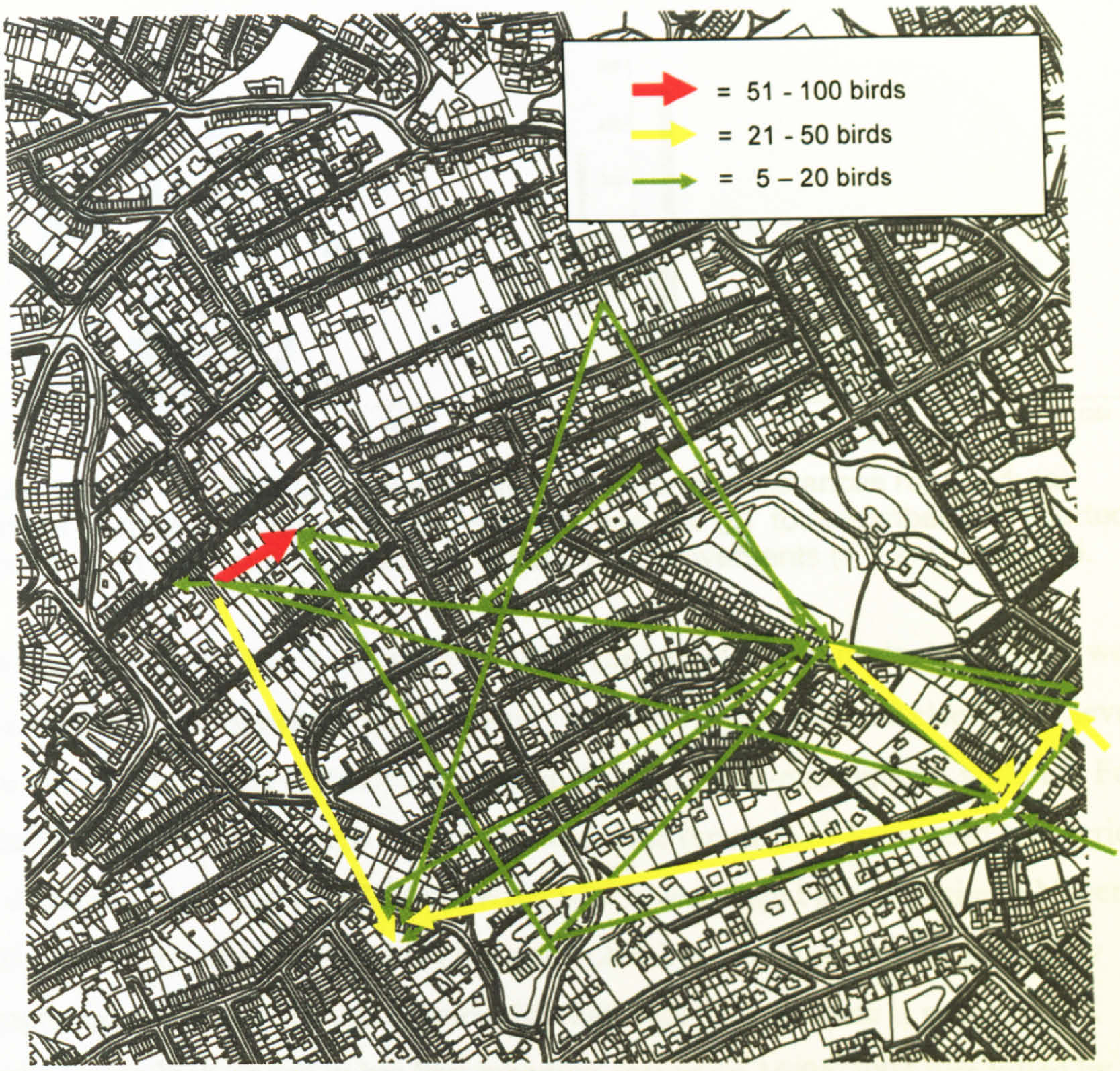


Figure 10.6. Movements of individual birds between the primary ringing and observation sites within and near (<500 m) SK3388, February 2002 – June 2005. All species, each individual counted once only.

Figure 10.8 shows the numbers of different sites at which individual birds of the nine most-re-encountered species were located. Of the most territorial species, Dunnock is the least mobile (figure 10.8 c) while Robin (figure 10.8 d) has a somewhat higher proportion of individuals found at two sites and Blackbird (figure 10.8 h) was more mobile with only slightly fewer single-site birds than Blue Tit (25% vs 27%) but again no birds using more than three sites, as was also the case for Long-tailed Tit (figure 10.8 e). A higher proportion of Blue Tits (figure 10.8 a) used only single sites than Great Tits (figure 10.8 b) although more of the former species were ringed. Both occurred at up to four sites, as did Coal Tit (figure 10.8 i) although far fewer of the latter were ringed. Among granivores, individual House Sparrows occurred at up to four different sites (figure 10.8 g) but Greenfinch was the most mobile of the nine species considered and the only one of which some individuals (3.2%) were re-encountered at five different sites during the study period (figure 10.8 f).

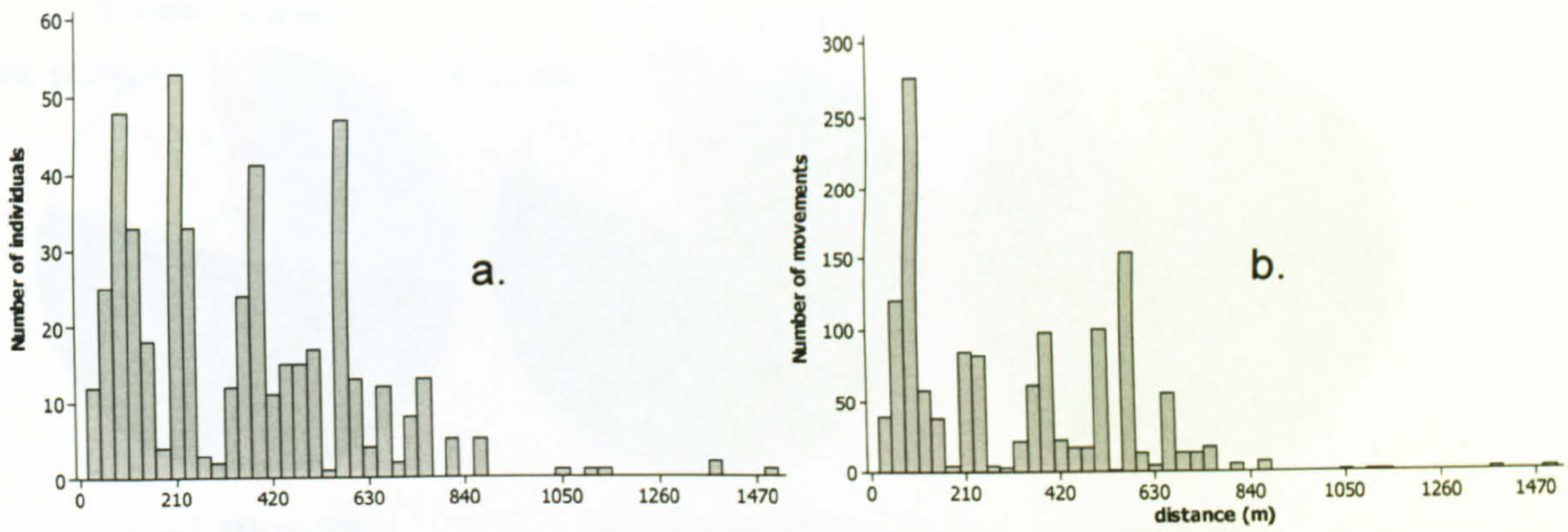


Figure 10.7.a. – b. Frequency distributions of movement distances reported: (a) numbers of individual birds in each distance class and (b) total numbers of reported movements in each distance class. Long distance movements (> 2 km) excluded.

Movements of more than 1 km were recorded for 18 individual birds, 11 of these were birds ringed within or nearby the core study area and re-encountered elsewhere, seven were birds ringed some distance from the study area but re-encountered within it. Four of these 18 mobile individuals were recovered dead (another 17 local dead recoveries are discussed in section 10.3.1). One Wren which was ringed as a juvenile in November 2003 was freshly dead in Berwick on Tweed (264 km) 193 days later, a nationally exceptional movement for this species although vehicle assistance is suspected. A female Greenfinch ringed in her first breeding season on 16/06/2004 was killed by a cat a few weeks later in a suburban Nottinghamshire garden 26 km away on 27/08/2004.

Two Siskins were recovered, both showing movements typical of birds ringed in the Sheffield area (Sorby Breck Ringing Group pers. comm). First winter male R606724 was ringed on 24/03/2004 and recovered 'long dead' a few weeks later on 09/05/2004 in Dumfries and Galloway (296 km), another bird ringed just south of Sheffield made an almost identical movement in the same spring. First winter male R088379 was ringed on 12/02/2003 and recovered just over one year later on 27/03/2004 27 km away in northeast Derbyshire. Even more regularity of movement in Siskins was demonstrated by first winter female R088383 which was ringed on 12/02/2003 and re-trapped at exactly the same SK3388 feeding station a year later on 21/01/2004.

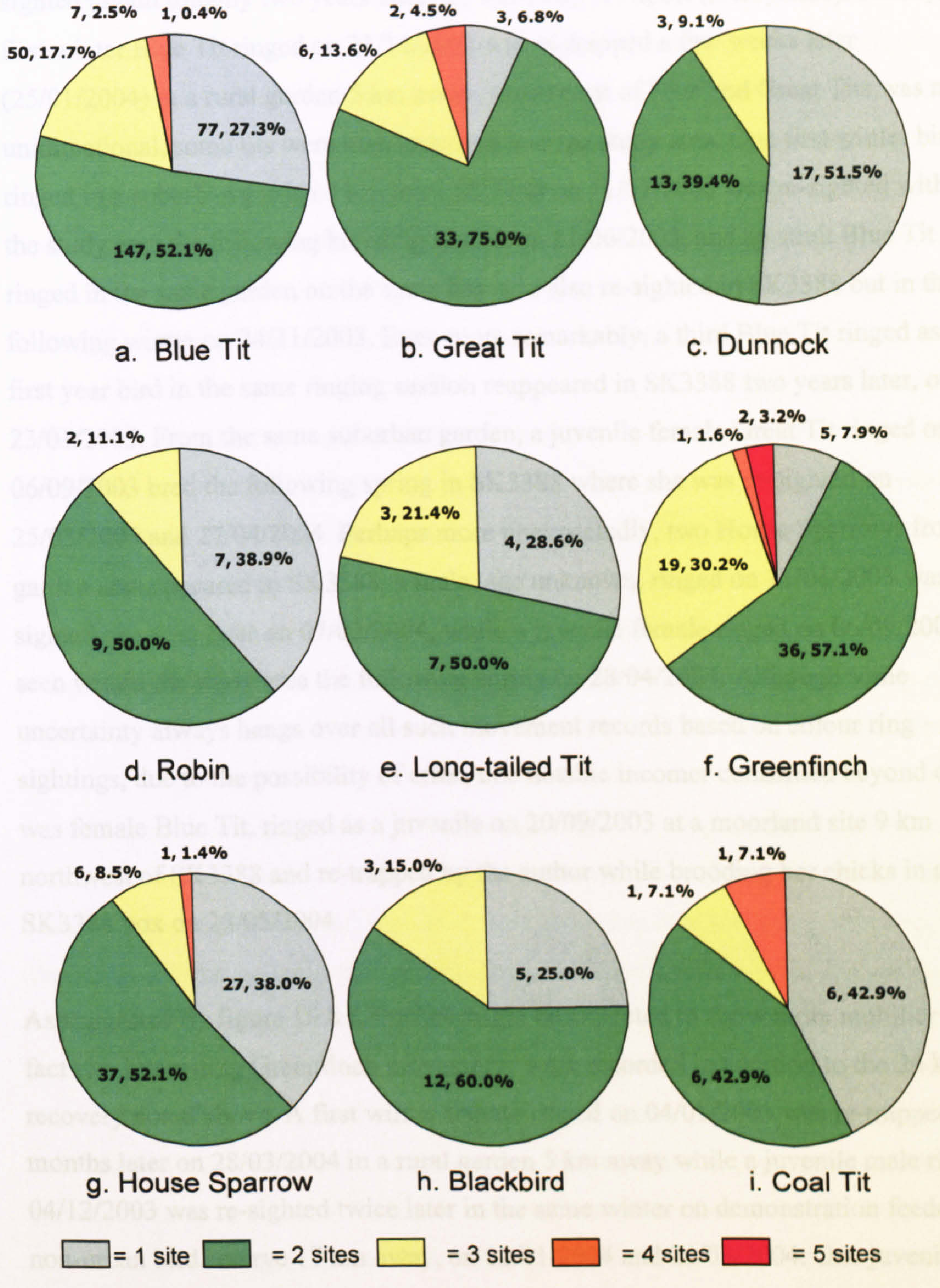


Figure 10.8. Relative mobility of re-encountered individuals of the nine most-ringed species, illustrated by the proportions of ringed birds encountered at varying numbers of different sites within the SK3388 study area. Birds re-encountered at least once only.

Fourteen long-distance colour-ring sightings were obtained. A Dunnock ringed as an adult male on 16/04/2002 just northwest of SK3388 was observed in January 2003 in a garden to the southeast, around 1.5 km away. A juvenile Blue Tit ringed on 21/06/2002 was observed two years later on 07/06/2004 in Sheffield Botanical Gardens some 2 km away; a longer-distance export was another juvenile Blue Tit, ringed on 04/09/2002 and sighted (again roughly two years later) 21 km away at Alport (Derbyshire). Finally, a first winter Blue Tit ringed on 21/11/2003 was re-trapped a few weeks later (25/01/2004) in a rural garden 5 km away. Movement of Blue and Great Tits was not unidirectional, some tits were also imported into the study area. One first winter bird ringed in a suburban garden 4 km from SK3388 on 11/01/2003 was re-sighted within the study area the following breeding season on 21/06/2003, and an adult Blue Tit ringed in the same garden on the same day was also re-sighted in SK3388 but in the following winter on 24/11/2003. Even more remarkably, a third Blue Tit ringed as a first year bird in the same ringing session reappeared in SK3388 two years later, on 23/01/2005. From the same suburban garden, a juvenile female Great Tit ringed on 06/09/2003 bred the following spring in SK3388 where she was re-sighted on 25/03/2004 and 27/04/2004. Perhaps more unexpectedly, two House Sparrows from this garden also appeared in SK3388, a male, age unknown, ringed on 11/01/2003 was sighted one year later on 07/02/2004, while a juvenile female ringed on 06/09/2003 was seen within the study area the following spring on 28/04/2004. Although some uncertainty always hangs over all such movement records based on colour ring sightings, due to the possibility of error, one notable incomer confirmed beyond doubt was female Blue Tit, ringed as a juvenile on 20/09/2003 at a moorland site 9 km northwest of SK3388 and re-trapped by the author while brooding her chicks in an SK3388 box on 28/05/2004.

As suggested by figure 10.8 f, finches might be expected to show more mobility and in fact two interesting Greenfinch movements were recorded in addition to the 26 km recovery noted above. A first winter female ringed on 04/01/2003 was re-trapped 14 months later on 28/03/2004 in a rural garden 5 km away while a juvenile male ringed on 04/12/2003 was re-sighted twice later in the same winter on demonstration feeders at a non-urban bird reserve 17 km away, on 02/01/2004 and 20/03/2004. One juvenile female Goldfinch ringed on 11/11/2002 was re-trapped in a rural garden 5 km away two winters later on 04/01/2004.

10.4. Discussion

Colour-ringing doubled the productivity of the study; approximately the same number of re-sightings was logged (1833) as birds were mist-netted (1785). However, sightings were heavily biased towards a few regular observers at fixed sites, the four most regular observers contributing 85% of the sightings received from the public, furthermore a few individual territorial birds contributed large numbers of repeat sightings at these sites and the true frequency of their numerous visits to the sighting locations was unknown. These regularly-sighted birds were generally present year-round and would have generated many more records had their territories been observed daily. In practice, regular observers tended to log birds roughly fortnightly and no systematic protocol could be imposed given variation in volunteers' lifestyles and availability.

Once re-sightings had gathered pace around month 13 (the keenest observers were also recruited around this time), the re-encounter rate started to converge with and eventually overtook the new bird trapping rate. In fact, the time series plot of cumulative re-encounters (figure 10.1.) shows the form that would be expected if survival of ringed birds over the three year study period exceeded mortality. This is encouraging in terms of the feasibility of acquiring data via colour ring sightings; however it actually means little in quantitative terms as the re-sighting rate data are not controlled for observer effort and are not adjusted for repeat re-sightings of the same birds in the same month or for differing recording protocols between observers. The original objective of studying spatial distribution and movement through the acquisition of large numbers of sightings over a wide area was not realised due to the acquisition of a small number of regular observers at fixed locations rather than a larger number of more widely-distributed and perhaps more mobile observers as was envisaged (despite considerable efforts to publicise the project). Furthermore, many 'one-off' records received from casual observers proved to be inaccurate; the difficulty of accurately re-sighting identifiable individuals for amateurs was under-estimated at the outset, in practice, only a few keen birdwatchers were able and willing to correctly resolve colour ring combinations on fast-moving birds and practice was evidently required before acceptable accuracy could be obtained.

Error rates in colour ring sightings decline with observer experience (Milligan et al. 2003) but even with motivated observers, error rates can be high. Milligan et al. (2003) found mean error rates of 16% ± 10.7% for untrained observers but still 5% ± 0.9% post- training and noted that one of their observers retained error rates of around 60% even after training; furthermore these were conservative estimates based on experiments in ideal laboratory conditions. In the present study only one of the regular observers produced records in a format that made error estimation straightforward, her proportion of invalid combinations (30 out of 534 records, including same-day repeat sightings which were not formally logged as re-encounters) was 5.6% overall with a mean error rate per data submission of 7.5% ± 2% (SE), which suggests that out of the 504 apparently valid records, another 38 could be erroneous giving a maximum total error rate of around 13%. In a colour-ringing study the error rate can only be measured by invalid combinations reported, however as Milligan et al (2003) also observe, the true error rate increases as more birds are ringed because increasing numbers of combinations reported incorrectly are nonetheless accepted because they have been fitted to other birds of the same species and are hence not recognised as invalid. In both the present study and the experiments of Milligan et al. (2003) apparent error rates also increased as more birds were marked and less distinctive colours had to be used. Errors are also much higher in studies that mark both legs than in studies that mark a single leg; Milligan et al. (2003) found that 57% of their errors were right/left leg switches.

Colour-ringing is generally considered not to significantly impact bird behaviour (Milligan et al. 2003; Redfern & Clark 2001; Weiss & Cristol 1999); the only documented effects concern sexual selection, particularly with regard to symmetry (Johnsen et al. 2000; Ligon 1999). Accordingly, although it increases handling time and so needs to be managed carefully in cold weather, it does not require additional licensing or welfare assessment, nor should it bias re-encounter probability with respect to birds wearing only metal rings. Nonetheless, some birds are clearly aware of their colour rings and in the present study, Greenfinches in particular appeared keen to remove them, as was also observed by Kosinski (2004), hence the need for heat-sealing. One territorial female Blue Tit was observed to ignore her rings for most of the year but during a period of around two weeks at the start of the breeding season, to make strenuous attempts to remove her orange ring only, neglecting the others. One possible explanation is that she perceived her visibility to predators at the nest might be increased (Kosinksi (2004) reported that female Greenfinches were also keener to remove colour rings than males) but the true cause of this behaviour remains unknown, particularly as birds' colour vision and hence their perception of their own colouring differs markedly from that of humans (e.g. Eaton 2005).

In terms of generating data for formal mark-recapture modelling of survival rates, focusing observation effort at a few key sites proved over time to be a more sustainable, productive, and probably more reliable approach to colour ring re-sighting in this study than soliciting casual observations over a wide area. Had this been realised at the outset, more formal sampling protocols at such key sites might have enabled the formal estimation of survival rates for the few birds using them, although over a timescale of just three years they would probably still have failed to contribute the volume of data required for adequate goodness of fit in formal models. As Anderson & Burnham (2004) have observed, with respect to formal modelling "relatively little can be learned from only 3-4 years of ringing".

Re-encounter rates of the 11 frequently re-encountered species were virtually identical for birds ringed as adults (35%) and as juveniles (36%). The similarity of re-encounter rates among the major species ringed and re-encountered in the breeding season suggests that the composition of the breeding avifauna is fairly stable. The variability of re-encounter rates among species for winter-ringed birds suggests that, in contrast, there is inter-specific variation in the dynamics of the winter assemblage, notably among juveniles. This difference in the degree of inter-specific variation in dynamics between the winter and breeding assemblages might be largely accounted for by differential emigration and immigration rates of juveniles, among resident species, and perhaps also influenced by the annually-varying dynamics of species that are predominantly winter visitors to SK3388 and hence were not caught in adequate numbers for the breeding season analyses, notably Long-tailed Tit and Siskin. Life history differences, for example between hole- and open-nesting species, may confound these comparisons.

Patterns in re-encounter data are also highly likely to be affected by behavioural differences between species, as suggested by figure 10.3. For example, highly territorial Robins are often re-encountered immediately after ringing (figure 10.3 h), whereas all the other species considered show a short post-ringing refractory period in which nets and/or observers may be avoided. The difference in the patterns of re-encounter durations between Robin and other resident territorial species such as Dunnock (figure 10.3 d) and Blackbird (figure 10.3 c) that lack anniversary peaks is striking, although winter use of 'sunflower heart' feeders by Robins was regularly observed (pers.obs.) Dunnocks and Blackbirds are less directly interested in the seed and peanut feeders that form the dominant winter resource in SK3388 for more granivorous species. Detectability of the behavioural difference between Robin and Dunnock may be biased by the larger numbers of Dunnocks ringed and the dominance of one individual Robin in the re-encounter data for that species. Nonetheless, these data (and anecdotal support) suggest that some Robins use the same feeders annually in winter but do not seek their assistance (or are less conspicuous) during the breeding season. In contrast, Dunnocks and Blackbirds are visible around feeding stations throughout the year. Another different behaviour pattern is that of the mobile and non-territorial Greenfinch which also shows a striking peak in re-encounter frequency around the second anniversary of ringing (figure 10.3 e). Greenfinches were only scarce breeders in SK3388 yet nonetheless numerous at feeders, the anniversary peak is probably due to the re-appearance of non-resident winter visitors the winter following ringing. The presence of an anniversary peak in Blue Tit (figure 10.3 b) but not in Great Tit (figure 10.3 f) is similarly of interest but Great Tits were relatively scarce and appeared to be newly in the process of colonising the study area; typical non-urban winter tit flocks were not observed in SK3388 during the study period. Figure 10.3 underlines the importance of interspecific behavioural differences in evaluating ringing re-encounter rates.

Insufficient data from recoveries were available to assess either relative mortality or its causes either generally or by age class or species. Of eight known cat kills (including one long-distance recovery), four were birds ringed as juveniles and killed within one year of ringing, four were either birds ringed as adults or killed more than one year after ringing i.e. individuals killed despite at least a year of life experience. The general re-encounter rates of 8 – 18% for tits are not atypical; juvenile survival rates in Great Tits vary between 3% and 21% (Gosler 1993).

The numbers of movements logged between pairs of observation sites appears to vary negatively with distance and are confounded by observer effort (figure 10.5), nonetheless, figure 10.6 suggests that in general individual birds move fairly freely within the plot, certainly within a range of around 500m and in some cases further. The general negative association with relative mobility and territoriality seen in figure 10.8 also suggests that the normal territorial and seasonal behaviours of the major species are not over-ridden in major or unexpected ways by abnormal habitat characteristics, although the absence of mobile winter tit flocks from SK3388 is striking. Long-tailed Tits are a frequent component of such flocks in other habitats, their apparent relative immobility is probably confounded by the very small numbers of this species breeding in SK3388; 75 out of 85 birds ringed were caught in winter and were therefore, in fact, probably relatively mobile individuals. In further evidence of winter mobility in this species, one breeding Long-tailed Tit caught in May in an urban garden 1 km from the main study site was a re-trap originally ringed in March of the same year in a rural garden some 3 km away. Furthermore, breeding individuals colour-ringed in another study approximately 7 km away started to appear in SK3388 during the winter of 2004-05, confirming that Long-tailed Tits exploiting the study area in winter may originate from a wide surrounding area. A similar inference can be drawn for Coal Tit from the fact that 43 out of the 58 birds ringed were caught in winter and SK3388 breeding numbers were very low, although notably increasing over the survey period. This increase, plus the colonisation of Great Tit, and the new arrival of Nuthatch in 2004 underscores an important caveat in the assessment of mobility and population dynamics in SK3388. It appears that though this is avifauna is generally stable, it was nonetheless undergoing some important changes in composition during the study period; unfortunately only three years' data are insufficient to evaluate their significance.

Relatively few records of bird movements beyond the immediate area of the study site were acquired but those few that were forthcoming tell some interesting stories. The winter-visiting Siskin provides one of the few examples of a species clearly using the study area as a single-season resource in appreciable numbers; the small numbers of recoveries and re-traps available hint at a rather regular seasonal pattern of movement between the Sheffield area and a breeding area elsewhere, although some Siskins do breed in the Peak District so considerably more records would be required to evaluate this. From the perspective of the present study what the Siskin records do suggest is that SK3388 is not a last-resort, emergency-only, refuge for occasional, transient Siskins but a regularly-used winter habitat that forms part of a normal seasonal movement pattern for this species. In 2003 they were accompanied in SK3388 by Lesser Redpolls, generally not considered an urban species, which did not merely pass through but remained in the study area for several weeks, clearly finding useful food resources among the small Birch and Alder street trees (pers.obs.). In fact, the general stability of the avifauna suggested by the re-encounter data and the general site-fidelity of the common species suggested by figure 10.8 leads to a conclusion that it is not just the winter visitors using SK3388 in a predictable, regular way. Despite scoring very highly on most conventional metrics of relative urbanisation, the study area shows every sign of supporting a sustainable breeding avifauna of stable composition, augmented by variable numbers of winter transient conspecifics in exactly the same manner as suburban and rural garden habitats.

11 Biometrics and condition of wild birds in SK3388

Abstract

Body weights and measurements of wild birds ringed in the SK3388 study area were analysed for evidence of ecological opportunities or constraints. Breeding season Blue Tits and juvenile Robins were heavier in SK3388 than at adjacent non-urban sites; urban Dunnocks and Long-tailed Tits were lighter, as were urban winter House Sparrows, while Blackbird, Greenfinch and Great Tit showed no inter-habitat variation. Resident juvenile Blue Tits had lower fat scores in winter than transients, suggesting they can optimise their body condition; a conclusion supported by generally negative associations between winter temperature and Blue Tit fat score. The bills of urban Great Tits appear to lengthen through the winter, suggesting that birds with access to feeders may not have to work as hard for their winter diet as woodland conspecifics.

11.1. Introduction

In this chapter, biometric data for birds caught by mist-netting in SK3388 during the study period are examined with specific reference to the question of whether this habitat provides ecological opportunities or imposes ecological constraints. Resource availability in urban ecosystems is likely to be very different from that of the natural habitats of their wild birds, both generally and in terms of seasonal variation. Perhaps the most apparent difference is that of food availability which is highly modified, primarily through anthropogenic supplementation. Consequently, the physiological and/or nutritional status of urban birds might differ with respect to non-urban conspecifics, may vary according to whether individuals are resident or transient users of the urban habitat and may change with time in ways that reflect the opportunities or constraints applicable to the bird species exploiting it.

Variations in weight and fat deposition are particularly valuable indicators of ecological status in small birds. The weights of small passerines show very significant diel variations that are linked to food availability and can be adjusted strategically by the bird according to environmental conditions, including perceived predation risk (Cresswell 1998; Gosler 2002; Gosler et al. 1995b; Macleod et al. 2005; Thomas 2000). If birds of the same species differ between urban and non-urban habitats in their weights, this would indicate the balance of food availability and perceived predation risk differed between the two habitats. Birds can be lighter, i.e. carry less fat, if food supplies are reliable; equally, if there is a very low perceived risk of predation and food is abundant, they may be generally heavier. Also, with *ad lib* food available, birds in SK3388 might need to vary their weights less with time of day than non-urban conspecifics, and this might be detectable as an interaction between habitat and time of weighing as predictors of weight /wing length ratio.

Four analyses are presented. Firstly, body weights of the ten most-ringed species caught within the SK3388 study area are compared with weights of conspecifics caught locally but outside the city of Sheffield over the same time period. Secondly, relationships between biometrics and re-encounter probability are examined for seven species. A third analysis examines the relationship between body fat deposition and temperature in SK3388 Blue Tits for evidence of ecological constraint in body condition regulation.

A fourth analysis considers a different issue, that of variation in winter diet between urban and non-urban birds. Seasonal variation in the bill shape of Great Tits reflects seasonal changes in their diet. The pattern of variation over the winter of 2003 – 2004 is examined for any differences with respect to the generally accepted pattern in woodland birds which might indicate that the winter diet of SK3388 birds differs from that in more natural habitat.

11.2. Methods

Birds were caught in mist nets, in SK3388 as described in chapter nine, in the case of the urban sample. The non-urban birds were mist-netted and ringed at a wide range of exurban sites within a 50 km radius of Sheffield during the study period, by volunteers of the Sorby Breck Ringing Group (R.D.R.Williams 2005, unpublished data). Mist-netted birds were weighed with Pesola spring balances (or electronic balances in the case of some non-urban birds) and measured with standard BTO wing rules and/or digital callipers as appropriate, wing lengths were maximum chord, bill length to skull, bill depth to distal edge of nostril. Fat scores representing the relative quantity of subcutaneous fat deposited within the furcular depression and upon the lower abdomen and visible upon parting feathers by blowing were recorded using the ESF scoring system (0 – 8, resolution of 0.5). Pectoral muscle condition was recorded on a four point scale (0 – 3) (see Redfern & Clark 2001; Svensson 1992 for measurement methods).

Weight and wing length were the only biometrics available for the non-urban sample, the ratio of weight to wing length was therefore used in the urban / non-urban comparison. Wing length effectively calibrates body weight to give a more accurate reflection of condition (Gosler et al. 1995a) and the use of a ratio avoids some of the interpretation issues applicable to univariate metrics of avian body size (Freeman & Jackson 1990). For the comparison of urban and non-urban weights, ANCOVA models were used of weight / wing length ratio against four categorical factors, (age and sex of birds and the season and habitat in which they were trapped), together with time of weighing (seconds after midnight) as a covariate. Data for 3024 non-urban individuals of the ten species most ringed in SK3388 during 2002 – 2004 were available for comparison.

All bird records, both SK3388 and non-urban, were classified into one of three age classes, *adult*, *juvenile* or *unknown*, and two classes of *habitat*, *urban* (i.e. SK3388) and *rural*. All captures were also designated as either *breeding* season (April – September) or *winter* season (October – March). For some species, factors such as *sex* or *ageclass* could not be used as adequate data were not available. Main effect *sex* was not used in species for which most individuals are unsexed, such as Blue Tit. Generally, only birds that were aged as either adult or juvenile at time of capture were included in the analyses, except where this caused severe loss of data as in, for example, House Sparrow and Long-tailed Tit which cannot be aged in autumn and spring, and Dunnock for which ageing is often difficult; birds of ageclass *unknown* were included only when overall model fit was inadequate without these data. To avoid pseudoreplication, only newly-ringed birds were included in the analyses, data from re-traps were discarded.

As the data were unbalanced, SAS procedure GLM was used rather than PROC ANOVA (SAS Institute Inc. 2004). Maximal models with weight / wing length ratio (*wtwing*) as the dependent biometric variable, *ageclass*, *habitat* class, *season* and *sex* as factors, *time* of weighing as covariate and all interaction terms were refined to minimal adequate models (MAM) by the successive removal of least-significant terms (backward selection) rather than forward or stepwise term selection methods which are not appropriate to unbalanced data (Crawley 2002). This initial backward model selection was performed automatically using experimental SAS procedure PROC GLMSELECT which selects terms based on the Schwarz Bayesian Information Criterion (SBC), an information-based parameter which overcomes some of the problems of model term selection using F- and P- based hypothesis testing (for discussion see e.g. Anderson & Burnham 2004; Der & Everitt 2002). The option HIERARCHY was set to 'single' such that model terms were removed in the conventional sequence, i.e. all the interactions of a higher order before any of the next lower order. To examine the directions and significances of variations in weight / wing length between factor levels, a further unbalanced multiway ANCOVA was then performed using PROC GLM in SAS following Der & Everitt (2002) for each of the MAMs. Plots of residuals against predicted values were checked for excessive heteroscedasticity and Tukey-Kramer studentised range tests for unbalanced groups were applied to the means of *wtwing* within levels of the main effects to determine significance and direction of any pairwise variance, and further applied to the least-squares means of all significant effects in the MAMs (main and interactions) to examine directionality and significance of interaction effects on the means of *wtwing* (SAS Institute Inc. 2004).

To examine the possibility of predictive relationships between biometrics and persistence of individual birds within the study area, logistic regression of the log-odds of the binary response variable *reenc* (set to one for each individual if bird re-encountered at any time subsequent to ringing, otherwise zero) against three biometric predictors (weight/wing length ratio, fat score and muscle score) was performed using PROC GENMOD in SAS (e.g. Der & Everitt 2002). Regressions were performed separately for birds ringed as adults and birds ringed as juveniles. With the exception of Blue Tit, for which winter ringed and breeding season ringed juveniles were modelled separately, insifficient data were available to segment this analysis any further.

To determine the direction of any relationship between Blue Tit fat score and temperature, 359 records of Blue Tit captures between October and March in the two complete winters 2002 –03 (winter1) and 2003 – 04 (winter2) were examined. Hourly meteorological data were available from the University of Sheffield weather station located 1.2 km from the centre of the SK3388 study area. For each one hour period the median of the minimum and maximum temperatures *medtemp* was used as the primary covariate. Fat scores had values of between zero and 45 in increments of 5, they were not normally distributed (Kolmogorov-Smirnov test $P < 0.01$) and so were transformed using a Box–Cox transformation with $\lambda = 0.64$ and 0.5 added to each fat score value, to achieve a normal distribution (Kolmogorov-Smirnov test $P > 0.15$). The value of λ was determined automatically using MINITAB v14.

After exploratory simple linear regression analysis of the likely form of the relationship, the transformed fat scores (*transfat*), were analysed by using PROC GLM in SAS to construct an ANCOVA model with *ageclass* (adult or juvenile) and *winter* (winter1 or winter2) as factors and time of day (seconds after midnight, designated *GMT*) as an additional covariate as this is known to be a strong predictor of observed fat scores (Gosler 2002). Wing length and weight were also available as additional covariates and pectoral muscle condition score (0– 3) as a factor. However, due to the large number of such possible predictors of *transfat*, SAS experimental procedure GLMSELECT was used to automatically select significant model terms, as previously described, with backward selection from maximal models and the hierarchy option set to 'single' (SAS Institute Inc. 2005b).

In the analysis of Great Tit bill shape, the ratio of bill depth to length was calculated, following Gosler (1987a), as an index of relative bill shape for Great Tits caught in SK3388 and measured after June 2002; measurements prior to that were anomalous due to issues of familiarisation and standardisation of the procedure. Values of this index were plotted against date of capture and simple linear regression used to examine trends.

11.3. Results

11.3.1. Inter-habitat variation in weight per wing length

Results of the minimum adequate ANCOVA models comparing the urban and non-urban weight/wing ratios (*wtwing*) are presented in the following tables, 11.1 – 11.9.

For Blackbird, table 11.1 shows that there was no significant effect of *habitat* on weight / wing length ratio. Across both habitats, females were generally heavier for their size than males and adults were heavier in winter than in the breeding season; winter juveniles were also significantly lighter than breeding adults. Weight per wing length in Blackbirds generally increased with time of day (parameter estimate = $1.41\times 10^{-6} \pm 0.7 \times 10^{-6}$ $P = 0.0449$) although significantly less so in adults in the breeding season.

Table 11.1. ANCOVA model results for Blackbird. DF = degrees of freedom, SS = sums of squares. Observations used: 227. $F_{8,218} = 10.55$, $P < 0.0001$. $r^2 = 0.279$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.070917	0.070917	20.55	**<.0001**
ageclass	1	6.34E-05	6.34E-05	0.02	0.8923
sex	1	0.027035	0.027035	7.83	**0.0056**
season	1	0.000408	0.000408	0.12	0.7313
time*ageclass	1	7.71E-05	7.71E-05	0.02	0.8813
time*season	1	0.000966	0.000966	0.28	0.5973
ageclass*season	1	0.023207	0.023207	6.72	**0.0102**
time*ageclass*season	1	0.031157	0.031157	9.03	**0.003**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
ageclass	adult	0.767	juvenile	0.7678	0.936 NS
season	breeding	0.749	winter	0.7858	**0.0002*****
sex	female	0.7788	male	0.7562	**0.0056****
	adult breeding	0.7385	adult winter	0.7957	**<0.0001*****
	adult breeding	0.7385	juvenile winter	0.776	**0.0009****

All other pairwise comparisons $P \geq 0.05$, NS

For Blue Tit, table 11.2 shows a highly significant effect of *habitat* that was interactive with *season*. Weight per wing length generally increased with time of day (parameter estimate = $3.3 \times 10^{-7} \pm 0.3 \times 10^{-7}$ $P < 0.0001$).

Table 11.2. ANCOVA model results for Blue Tit. DF = degrees of freedom, SS = sums of squares. Observations used: 1063. $F_{4,1058} = 40.2$, $P < 0.0001$. $r^2 = 0.132$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.007694	0.007694	103.49	**<.0001**
season	1	0.001741	0.001741	23.42	**<.0001**
habitat	1	0.003086	0.003086	41.51	**<.0001**
season*habitat	1	0.003218	0.003218	43.28	**<.0001**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
season	breeding	0.1713	winter	0.1685	**<0.0001*****
habitat	rural	0.1681	urban	0.1716	**<0.0001*****
	breeding rural	0.1677	breeding urban	0.1748	**<0.0001*****
	breeding urban	0.1748	winter rural	0.1686	**<0.0001*****
	breeding urban	0.1748	winter urban	0.1685	**<0.0001*****

All other pairwise comparisons $P \geq 0.05$, NS

Generally, breeding Blue Tits are heavier than winter birds, and urban Blue Tits are heavier than rural. Urban Blue Tits in the breeding season were significantly heavier for their size than rural birds in the breeding season but in winter, the weight / wing length ratios for urban and rural birds were virtually identical ($P \approx 1$). Incorporation of the effect *sex* reduced the sample size from 1063 to 97 observations and effectively limited it to breeding season adults; no effects incorporating *sex* were significant.

For Coal Tit, table 11.3 shows that *habitat* is significant in its interaction with *time* and *season.* Weights of rural breeding birds respond more positively to time of day than those of urban and winter birds (*time * season*habitat* parameter estimates: breeding rural $1.78 \times 10^{-6} \pm 0.6 \times 10^{-6}$, others 0). All pairwise comparisons between levels of 2nd order interactions had adjusted P values ≥ 0.05 (although the comparison between winter rural and winter urban was only marginally non-significant, $P = 0.0541$).

Table 11.3. ANCOVA model results for Coal Tit. DF = degrees of freedom, SS = sums of squares. Observations used: 122. $F_{10,111} = 3.75$, $P = 0.0002$. $r^2 = 0.252$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.000179	0.000179	3.32	0.0713
ageclass	1	0.000199	0.000199	3.69	0.0574
season	1	0.000299	0.000299	5.53	**0.0204**
habitat	1	0.000215	0.000215	3.97	**0.0487**
time*ageclass	1	0.000273	0.000273	5.05	**0.0266**
time*season	1	0.000262	0.000262	4.84	**0.0298**
season*ageclass	1	0.000243	0.000243	4.5	**0.0361**
time*habitat	1	0.000176	0.000176	3.25	0.0742
season*habitat	1	0.000431	0.000431	7.97	**0.0056**
time*season*habitat	1	0.000486	0.000486	8.99	**0.0033**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
ageclass	adult	0.1471	juvenile	0.1439	0.1143 NS
season	breeding	0.1453	winter	0.1456	0.9022 NS
habitat	rural	0.1454	urban	0.1456	0.8837 NS

All other pairwise comparisons $P \geq 0.05$, NS

For Dunnock, table 11.4 shows that *habitat* has a significant effect on *wtwing*. Rural Dunnocks are significantly heavier than urban birds, in contrast to Blue Tits. Dunnocks increase their weight with time of day (*time* parameter estimate $1.22 \times 10^{-6} \pm 0.26 \times 10^{-6}$) but less positively in the breeding season than in winter (*time* parameter estimates: breeding $-9.3 \times 10^{-7} \pm 3.0 \times 10^{-7}$, winter 0), when they are also heavier in general.

Table 11.4. ANCOVA model results for Dunnock. DF = degrees of freedom, SS = sums of squares. Observations used: 246. $F_{4,241} = 11.76$, $P < 0.0001$. $r^2 = 0.163$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.009004	0.009004	25.82	**<.0001**
season	1	0.001579	0.001579	4.53	**0.0344**
habitat	1	0.001996	0.001996	5.72	**0.0175**
time*season	1	0.003462	0.003462	9.93	**0.0018**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
season	breeding	0. 2878	winter	0. 2964	**0. 0009****
habitat	rural	0. 2953	urban	0. 2890	**0. 0175***

All other pairwise comparisons $P \geq 0.05$, NS

For Greenfinch, table 11.5 shows that there is no significant effect of *habitat* on weight / wing length ratio. The effects of *ageclass*, *sex* and *season* are highly interactive and pairwise comparisons are not tabulated in detail in table 11.5 as they have no bearing on the question of variation between the two habitats. In summary, pairwise comparisons showed that for their wing length adults are heavier than juveniles ($P< 0.0001$), females are heavier than males ($P< 0.0001$) and winter birds are heavier than those caught in the breeding season ($P= 0.0015$). For example, adult females are heavier than juvenile females ($P< 0.0001$),but adult males are not heavier than juvenile males ($P= 0.8485$). Breeding season adult females are significantly heavier than winter adult females ($P< 0.0001$), but breeding season juvenile females are significantly lighter than winter juvenile females ($P< 0.0001$). Breeding season adult males are almost identical to winter adult males ($P =0.9449$), but breeding season juvenile males are lighter than winter juvenile males ($P< 0.0001$).

Table 11.5. ANCOVA model results for Greenfinch. DF = degrees of freedom, SS = sums of squares. Observations used: 879. $F_{8,870} = 48.86$, $P < 0.0001$. $r^2 = 0.309$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.006065	0.006065	23	**<.0001**
ageclass	1	0.021453	0.021453	81.37	**<.0001**
sex	1	0.035747	0.035747	135.59	**<.0001**
season	1	0.001873	0.001873	7.11	**0.0078**
sex*ageclass	1	0.01684	0.01684	63.87	**<.0001**
season*ageclass	1	0.02111	0.02111	80.07	**<.0001**
season*sex	1	0.002447	0.002447	9.28	**0.0024**
season*sex*ageclass	1	0.007617	0.007617	28.89	**<.0001**

For Great Tit, table 10.6 shows that there is no significant effect of *habitat* on the ratio of weight to wing length. In general, males are heavier for their size than females and breeding season birds heavier than in winter.

Table 10.6. ANCOVA model results for Great Tit. DF = degrees of freedom, SS = sums of squares Observations used: 221. $F_{3,217} = 18.28$, $P < 0.0001$. $r^2 = 0.201$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.002541	0.002541	21.47	**<.0001**
sex	1	0.002932	0.002932	24.77	**<.0001**
season	1	0.00114	0.00114	9.63	**0.0022**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
season	breeding	0. 2471	winter	0. 242	**0. 0022***
sex	female	0. 2409	male	0. 2890	**<0. 0001*****

All other pairwise comparisons $P \geq 0.05$, NS

For House Sparrow, table 11.7 shows the results of two different models. Analysis for this species is complicated by the fact that birds cannot be aged in autumn or winter and that most birds caught are juveniles which cannot be sexed.

Table 11.7. ANCOVA model results for House Sparrow.
DF = degrees of freedom, SS = sums of squares

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
i. including *ageclass* but not *sex*. Observations: 160. $F_{2,157} = 32.96$, $P < 0.0001$. $r^2 = 0.296$					
time	1	0.025989	0.025989	57.47	**<.0001**
habitat	1	0.004896	0.004896	10.83	**0.0012**
Least squares means of *wtwing* and *P* values adjusted for multiple comparisons					
effect	**level**	**LS mean**	**level**	**LS mean**	***P* value**
habitat	rural	0. 338	urban	0. 349	**0. 0012****
ii. including *sex* but not *ageclass*. Observations: 236. $F_{5,230} = 14.5$, $P < 0.0001$. $r^2 = 0.24$					
time	1	0.02296	0.02296	47.27	**<.0001**
sex	1	0.006538	0.006538	13.46	**0.0003**
season	1	0.000469	0.000469	0.97	0.3269
habitat	1	2.2E-07	2.2E-07	0	0.9829
season*habitat	1	0.004844	0.004844	9.97	**0.0018**
Least squares means of *wtwing* and *P* values adjusted for multiple comparisons					
effect	**level**	**LS mean**	**level**	**LS mean**	***P* value**
sex	female	0.3517	male	0.341	**0.0003*****
	breeding urban	0.1748	winter urban	0.1686	**0. 0008**,**
All other pairwise comparisons $P \geq 0.05$, NS					

Habitat was significant as a main effect in the initial model with *ageclass* specified but birds unsexed. However, when the requirement to specify *ageclass*, which was not a significant effect, was relaxed, increasing the sample size by almost 50%, *habitat* then only had a significant effect on weight per wing length in House Sparrows in its interaction with *season*. Breeding urban birds were heavier than winter urban birds but there were no significant pairwise differences between urban and rural birds. House Sparrows significantly increased their weight per wing length with time of day (*time* parameter estimates $8.8 \times 10^{-7} \pm 1.2 \times 10^{-7}$, model i, $9.3 \times 10^{-7} \pm 1.3 \times 10^{-7}$, model ii) and, in general, females are heavier for their size than males.

Most Long-tailed Tits are ringed in winter when they can be neither aged nor sexed, but despite the low number of observations (25) available for a fully parameterised model, table 11.8 shows that both *habitat* and *sex* were significant predictors of *wtwing*.

Table 11.8. ANCOVA model results for Long-tailed Tit. DF = degrees of freedom, SS = sums of squares Observations used: 25. $F_{4,20} = 4.0$, $P < 0.0152$. $r^2 = 0.445$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
sex	1	0.000134	0.000134	6.12	**0.0224**
season	1	7.24E-05	7.24E-05	3.32	0.0836
habitat	1	0.000162	0.000162	7.42	**0.0131**
season*sex	1	0.000128	0.000128	5.84	**0.0253**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
sex	female	0. 1252	male	0. 131	**0. 0224***
habitat	female	0. 1313	male	0. 1249	**0. 0131***
	breeding female	0. 1258	winter male	0. 1354	**0. 0177***
	breeding male	0. 1266	winter male	0.7761354	**0. 0451*,**

All other pairwise comparisons $P \geq 0.05$, NS

Males were generally heavier than females and rural birds generally heavier than urban. Winter males were heavier than breeding season birds of both sexes although the samples were very small (10 winter, 15 breeding) and the fact that these birds were sexed means they were in breeding condition. When a simplified model with only *season* and *habitat* was run ($F_{2,300} = 16.51$, $P < 0.0001$, $r^2 = 0.099$), only *season* was a significant predictor of weight per wing length ($P < 0.0001$). Breeding season birds were heavier for their size (adjusted mean 0.1325) than winter birds (0.1268, $P < 0.0001$).

For Robin, table 11.9 shows that there was no significant effect of *habitat*, except in its interaction with *ageclass*. Adults are heavier than juveniles in rural habitat but in urban birds there was no significant difference between the age classes.

Table 11.9. ANCOVA model results for Robin. DF = degrees of freedom, SS = sums of squares Observations used: 171. $F_{6,164} = 8.84$, $P < 0.0001$. $r^2 = 0.244$

Source	DF	Type 3 SS	Mean Square	F value	$P_r > F$
time	1	0.008208	0.008208	18.3	**<.0001**
ageclass	1	0.000865	0.000865	1.93	0.1667
season	1	0.001628	0.001628	3.63	0.0585
habitat	1	0.00017	0.00017	0.38	0.5386
time*season	1	0.00425	0.00425	9.48	**0.0024**
ageclass*habitat	1	0.003021	0.003021	6.74	**0.0103**

Least squares means of *wtwing* and *P* values adjusted for multiple comparisons

effect	level	LS mean	level	LS mean	*P* value
ageclass	adult	0. 2628	juvenile	0. 2566	0. 1667 NS
season	breeding	0.2537	winter	0.2658	**< 0.0005****
habitat	rural	0. 2612	urban	0. 2583	0. 5386 NS
	adult rural	0. 2701	juvenile rural	0. 2522	**< 0.001**,**

All other pairwise comparisons $P \geq 0.05$, NS

Birds caught in winter increase their weight per wing length more positively with time of day than birds in the breeding season (*time* * *season* parameter estimates: breeding –

$1.04 \times 10^{-6} \pm 0.34 \times 10^{-6}$, winter 0); this *time*season* interaction accounts for the significant adjusted pairwise difference between winter birds and breeding season birds, the former are generally heavier for their size in the pairwise test despite the marginal non-significance of the *season* main effect. Again, most Robins are not sexed outside the breeding season; invoking *sex* in the models produced a sample of only 39 birds; a model could be fitted to this sub-sample ($F_{4,24} = 11.4$, $P < 0.0001$, $r^2 = 0.655$) but the distribution of residual variances was poor and neither *habitat* not any interaction with it were significant predictors of weight per wing length.

Wrens cannot be sexed outside the breeding season; when *sex* was included only 17 birds were available and no significant model terms were resolved. The fit of a model without *sex* was rather poor ($F_{1,169} = 5.97$, $P = 0.0156$, $r^2 = 0.034$) and the only significant predictor of weight per wing length was *ageclass* ($P = 0.0156$). Adult Wrens were significantly heavier per wing length (least squares mean 0.2052) than juveniles (0.1961, $P = 0.0156$). As this is a well-known result (Svensson 1992) and has no bearing on the question of inter-habitat variation, no ANCOVA table is presented.

11.3.2. Re-encounter probability in relation to biometrics

Logistic regression models of re-encounter probability against biometrics for adult-ringed and juvenile-ringed birds converged with reasonable data dispersion (0.5 < deviance/degrees of freedom < 1.7) for seven species, Dunnock, Blue Tit, Blackbird, Greenfinch, Great Tit, House Sparrow and Robin. Data for other species were inadequate for this type of model. Within the 14 models run, only two of the possible 42 predictive relationships were significant. In Dunnocks ringed as juveniles, muscle score was a significant negative predictor of overall re-encounter probability (logit parameter estimate = –2.477 ± SE 1.03, P (type 3) = 0.0046, deviance/DF = 1.07, N = 31). In Blue Tits ringed as juveniles, fat score was a significant negative predictor of overall re-encounter probability (logit parameter estimate = –0.0337 ± SE 0.135, P (type 3) = 0.0108, deviance/DF = 1.38, N = 360). This predictive relationship remained significant when only Blue Tits ringed as juveniles in winter were considered (logit parameter estimate = –0.05 ± SE 0.0178, P (type 3) = 0.0037, deviance/DF = 1.37, N = 228) but was not significant for Blue Tits ringed as juveniles in the breeding season (parameter estimate = –0.0334 ± SE 0.0276, P (type 3) = 0.2169, deviance/DF = 1.39, N = 132).

11.3.3. Relationship between fat score and temperature in Blue Tits

Transformed Blue Tit fat score (*transfat*) had a distribution approximating closely to normal and was significantly correlated with *wtwing* (Pearson $r = 0.302$, DF = 331, $P < 0.0001$) and pectoral muscle score (Spearman's rank correlation $r_s = 0.181$, N = 374, $P = 0.0004$), so these biometrics were not included in the model. Linear regression suggested an overall negative, significant but weak relationship between *transfat* and hourly median temperature (*transfat* = 8.84 – 0.189 *medtemp*, $F_{1,381} = 13.95$, $P < 0.001$, $r^2 = 0.035$) but also that when the two winters were considered separately the slope of the relationship varied between them (figure 11.1); this apparent difference is tested for significance in the ANCOVA model (see below). The regression relationship for winter2 catches only was more steeply negative (*transfat* = 11.1 – 0.327 *medtemp*, $F_{1,146} = 11.8$, $r^2 = 0.075$, $P = 0.001$) than that for winter1 catches only (*transfat* = 7.8 – 0.162 *medtemp*, $F_{1,209} = 9.76$, $r^2 = 0.045$, $P = 0.002$). Across all 26 weeks of each winter, hourly median temperatures did not differ significantly between winter 1 and winter 2 (winter1 mean 6.69° ± 0.057°, winter2 mean 6.82° ± 0.055°, t test, $t = -1.58$, DF = 8742, $P = 0.114$). Furthermore, the median temperatures of the hours in which Blue Tits were caught did not differ significantly between the two winters either (winter1 mean 6.89° ± 0.24°, winter2 mean 7.31° ± 0.28°, t test, $t = -1.13$, DF = 323, $P = 0.258$).

An ANCOVA model of *transfat* with *medtemp* and *GMT* as covariates and *ageclass*, and *winter* as factors, together with all their interactions, showed that a greater proportion of the variance in *transfat* than that explained by *medtemp* in isolation (r^2 = 0.043) was due to other predictors and their interactions with *medtemp* and with each other. Table 11.10. shows the terms from this model that were selected by PROC GLMSELECT for the MAM.

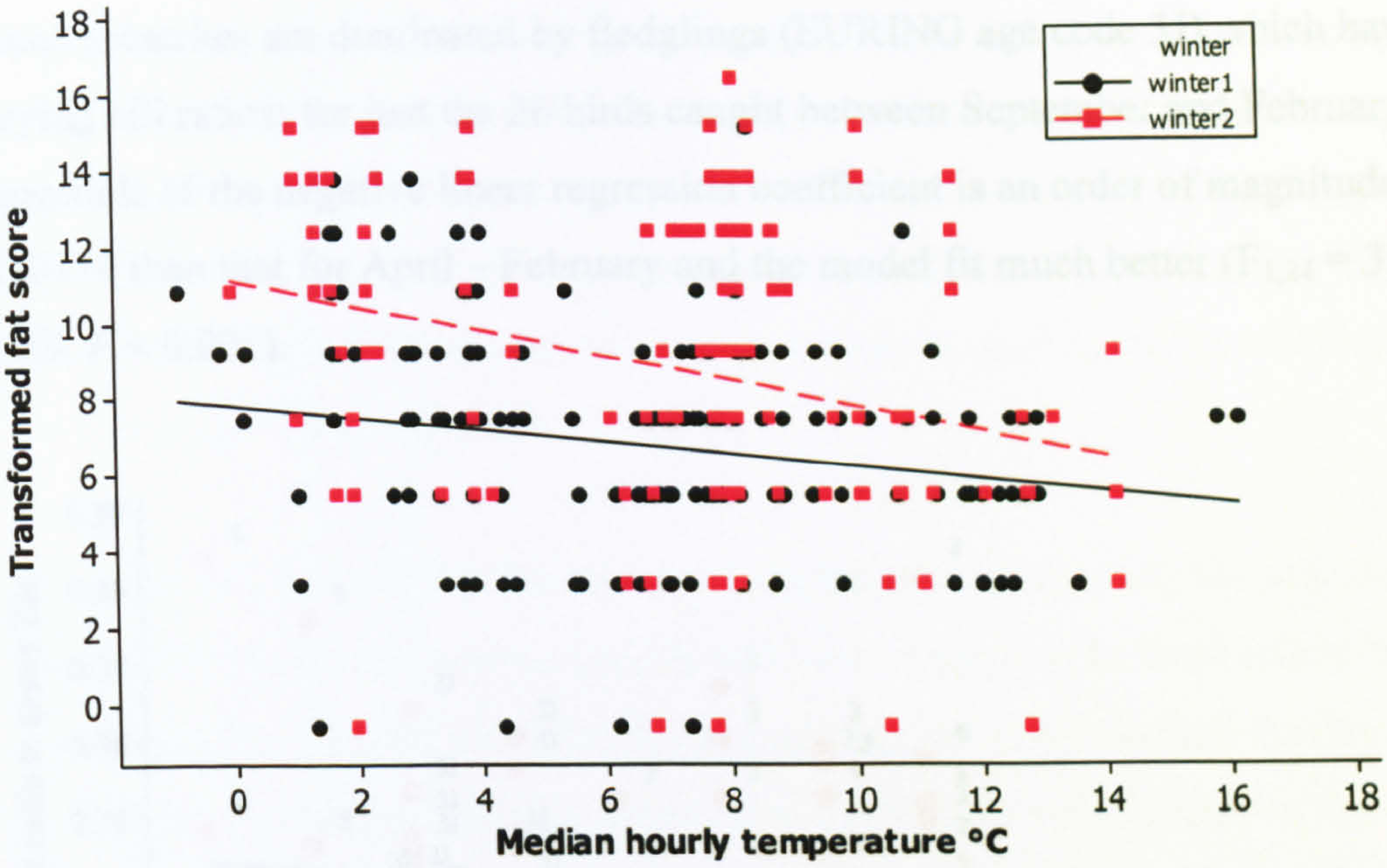


Figure 11.1. Scatterplot and OLS linear regression lines of transformed fat score in Blue Tits against hourly median temperature for winter1 (black) and winter2 (red)

Table 11.10. ANCOVA model results for transformed fat scores in Blue Tits (*transfat*). N= 359. $F_{5,353} = 48.33$, $P < 0.0001$. $r^2 = 0.406$

Parameter	DF	Estimate	Standard Error	t value	$P_r > \|t\|$
medtemp	1	48.88628	48.88628	6.67	**0.0102**
ageclass	1	64.32038	64.32038	8.78	**0.0033**
winter	1	98.4466	98.4466	13.43	**0.0003**
GMT	1	1081.243	1081.243	147.51	**<.0001**
GMT*winter	1	203.0096	203.0096	27.7	**<.0001**

Table 11.10 shows that generally there was a significant negative effect of *medtemp* on *transfat*. Fat scores were generally higher in adults than juveniles (least squares means of transformed scores adjusted for Tukey test 8.82 vs 7.81, $P = 0.0033$) and generally increased with time of day. A Tukey test also showed fat scores were generally higher in winter2 than in winter1 (9.97 vs 6.66, $P < 0.0001$) but they varied significantly more negatively with *GMT* in winter1 than in winter2.

11.3.4. Seasonal variation in bill shape in Great Tits

Bill index values for 63 Great Tits captured between September 2003 and October 2004 are plotted in figure 11.2. Only one bird was measured twice, all other points plotted are unique individuals. The negative linear regression coefficient for bill index against month number (April = 0, February = 10) is –0.00127 ($F_{1,61} = 2.12$, $r^2 = 0.034$, $P =$

0.0151). A quadratic regression was not significant ($F_{2,60} = 2.62$, $r^2 = 0.08$, $P = 0.081$). Summer catches are dominated by fledglings (EURING age code 3J) which have widely varying bill ratios; for just the 26 birds caught between September and February the magnitude of the negative linear regression coefficient is an order of magnitude larger at – 0.0114 than that for April – February and the model fit much better ($F_{1,24} = 33.51$, $r^2 = 0.583$, $P < 0.001$).

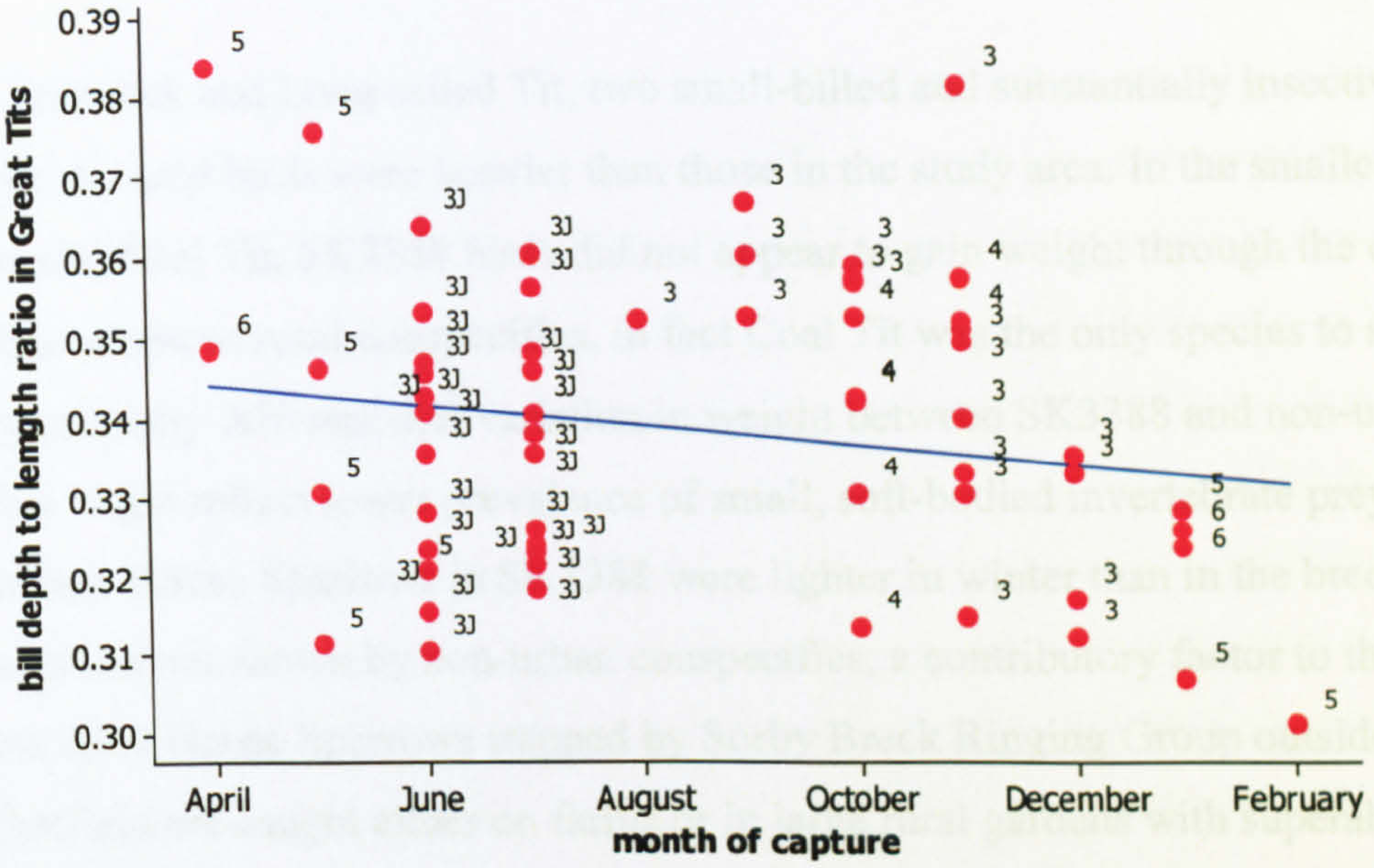


Figure 11.2. Bill depth to bill length ratio against month of capture for SK3388 Great Tits. Captures labelled with EURING age codes; 5 = hatched previous year, 6 = hatched year before previous, 3J = juvenile, 3 = hatched same year, 4 = hatched before current year.

11.4. Discussion

For three of the ten most-ringed species, Blackbird, Great Tit and Greenfinch, there was no significant difference in weight per wing length between SK3388 birds and birds from the surrounding non-urban area. This is perhaps unsurprising for the latter two given the relatively recent build-up of the SK3388 Great Tit population (Chapter 7), presumably from exurban immigrants, and the high relative mobility of the Greenfinch. It is possibly more surprising for Blackbird given the putative candidacy of this species for behavioural and/or genetic differentiation of its urban populations (Faivre et al. 2001). Also, it is one of the few species for which differences in body condition between urban and non-urban populations have been shown; urban Munich Blackbirds in spring had lower fat scores than non-urban conspecifics (although there was no inter-habitat difference in actual body mass within seasons) (Partecke et al. 2005). However there is substantial movement and population exchange of British garden Blackbirds, notably in a south-westerly direction between summer and winter (Chamberlain & Main 2002) and several of the birds caught in SK3388 in winter had plumage characteristics of Scandinavian winter immigrants which are typically larger than resident individuals and so would be likely to obscure any winter weight decline in the SK3388 birds, given the small sample of this species.

In Dunnock and Long-tailed Tit, two small-billed and substantially insectivorous species, rural birds were heavier than those in the study area. In the smallest-billed of the tits, Coal Tit, SK3388 birds did not appear to gain weight through the day to the same extent as rural conspecifics, in fact Coal Tit was the only species to show significantly different diel variation in weight between SK3388 and non-urban habitats. This might reflect lower prevalence of small, soft-bodied invertebrate prey in the urban habitat. House Sparrows in SK3388 were lighter in winter than in the breeding season, a variation not shown by non-urban conspecifics; a contributory factor to this could be that most House Sparrows trapped by Sorby Breck Ringing Group outside the city of Sheffield are caught either on farms or in large rural gardens with superabundant food. Winter food is also available *ad lib* in SK3388 but anecdotal reports suggest that House Sparrow populations in urban Sheffield have been under pressure and declining for several years; perhaps poor winter condition of urban birds has contributed to this.

In Blue Tit and Robin, arguably the two most confiding and regular garden-feeding species in SK3388, the urban habitat seems to confer a weight advantage. Juvenile Robins in SK3388 are as heavy as their parents, whereas in the non-urban sample juvenile birds are significantly lighter than adults suggesting they experience a nutritional disadvantage from which urban conspecifics may be protected. In the breeding season, the Blue Tits of SK3388 weigh more than non-urban conspecifics, possibly exploiting supplementary food to maintain their condition while provisioning generally smaller urban broods. In winter there is no difference in weight between urban and non-urban birds, understandable if winter Blue Tits are moving over a wider area in search of food and urban and non-urban populations are mingling at feeders. The winter increase in body mass seen in tits having access to supplementary food (Brittingham & Temple 1988b) does not differentially occur in SK3388 birds because all tits trapped in the Sheffield area, urban or exurban, probably have at least some access to feeders in winter. There can be issues with errors (compounded in ratios) and comparability between observers in volunteer ringers' biometric data (Morgan 2004) which may confound these analyses, nonetheless, the weighing and measuring procedures of Sorby Breck Ringing Group are performed conscientiously and supervised by highly experience ringers (pers. obs.) so are probably as reliable as any ringing data obtainable from national schemes.

The negative association of fat score with re-encounter probability among winter-ringed juvenile Blue Tits is consistent with the idea that fat is associated with higher predation risk and subordinate status (Gosler et al. 1995b). Winter juveniles with lower fat scores could be local birds that have recognised the availability of *ad lib* food and hence that they do not need to carry costly emergency fat reserves, possibly also individuals that have already become dominant and hence are likely to remain in the area. Birds with higher fat scores could be transient individuals unable to rely on *ad lib* food due to their higher mobility between habitat types, or sub-dominant local individuals, more likely to disperse out of the area than dominants. Hypothesis construction from the negative relationship between muscle score and re-encounter probability in juvenile-ringed Dunnocks should be more cautious, given the low numbers of birds, the low resolution of the ordinal 0 – 3 muscle scores and the complex behaviour of this species. Birds with low muscle scores may have been recent fledglings, or perhaps young residents expending energy on territory acquisition or in competitive polyandry (Davies 1992), whereas transient juveniles wintering near feeding stations might be expected to have good muscle condition but would be likely to disperse away from the area in spring.

The analysis of Blue Tit fat scores in winter clearly indicates a negative association with temperature, which suggests the birds of SK3388 are able to optimise their body fat, trading off food reserves against predation risk (Cresswell 1998; Gosler et al. 1995b; Macleod et al. 2005). According to Gosler (2002), a positive association, fat increasing as temperatures rise, would imply that the birds were severely nutritionally constrained, barely maintaining body weight at lower temperatures and only able to acquire fat as conditions improved. In contrast, these urban Blue Tits have sufficient resources to be able to 'plan ahead', maintaining higher fat reserves at lower temperatures and losing fat when they can afford to as temperatures rise. It would have been desirable to include sex as a factor in the ANCOVA of fat score against temperature but the majority of winter-caught Blue Tits cannot be sexed (except by specialists e.g. Harper 2000).

Comparing the difference between the two winters in the linear relationships between fat score and temperature (figure 10.3.4.) with the differences between the two winters in catch and re-trap rates (figure 9.3.3.) suggests some interesting hypotheses for further research. In February 2003 (winter1) catches were high but the re-trap ratio was low, while fat score varied less negatively with temperature, suggesting that abundant un-ringed birds, perhaps hungry winter immigrants, were more constrained in their energy budget management. In contrast, in February 2004 (winter 2), catches were low and re-trap ratios high, while the Blue Tit fat scores varied more negatively with temperature, suggesting there may have been fewer hungry transients and the assemblage was dominated by already-ringed residents, less constrained in their energy budget management.

Bill ratio in Great Tits caught in SK3388 shows a general decrease (bills lengthening) from spring through winter and a sharp and significant decrease from autumn to early spring. Summer fledglings probably obscure the overall pattern in this small sample but the autumn – winter lengthening trend is interesting as it occurs at a time of year in which the bills of woodland Great Tits become shorter and stouter in order to process their much harder winter food, primarily beech mast (Gosler 1987a). Seasonal variation in bill shape arises due to the continuous growth of the rhampotheca, the keratin sheath of the bill, which is affected by seasonal changes in hardness and pigmentation (Bonser & Witter 1993), can be manipulated by the bird through wiping and honing; variation in its growth/wear balance is most strongly associated with seasonal dietary variation (e.g. Davis 1954). If the autumn transition to hard foodstuffs in woodland Great Tits is reflected in a seasonal increase in rhampothecal growth rate, urban birds feeding on much softer foods such as sunflower hearts would not experience the same bill wear as woodland conspecifics and hence their adaptively growing bills might continue to lengthen through the winter, as in the SK3388 data, rather than being kept short by wear (A.G.Gosler 2005 pers. comm.). It remains a mystery why the birds' bills appear to suddenly shorten in late spring, unless they are used to enlarge nesting cavities. Clearly, it would be necessary to compare bill shapes of the same individuals repeatedly captured at different seasons in order to investigate this in any satisfactory depth, but the observations analysed suggest an intriguing possible difference in winter feeding ecology between urban and non-urban birds.

12. Specific opportunities and constraints affecting wild birds in SK3388

Abstract

Three investigations of factors affecting breeding and feeding birds in SK3388 are reported. The numbers and masses of caterpillars fed to their nestlings by Blue Tits and Great Tits in SK3388 was determined by counting lepidopteran mandibles in chick faecal sacs and comparing these data with samples from nearby but non-urban locations. Urban and rural birds provided similar numbers of caterpillars but those obtained by urban Great Tits were larger than in rural habitats. The daily energy expenditure of female Blue Tits and Great Tits provisioning broods was measured using doubly-labelled water; no clear differences were found between SK3388 birds and conspecifics in other habitats. Bird feeding stations in SK3388 were sampled during 2002 for contamination with pathogenic *Salmonella*; none was found.

General Introduction

A frequently-reported characteristic of urban avifaunas is lower breeding productivity than that observed in non-urban conspecifics (Chapter 1) and many experiments have confirmed that food supply influences the production of young in a wide range of species (Newton 1998). Given that supplementary food suitable for adult birds is available in many urban areas, including SK3388, year-round, it follows that quality and appropriateness of food available for chicks is likely to be a more limiting constraint on productivity than simple dietary energetics. Constraints on chick food quality might be manifest in two ways; firstly, through differences in the nature of the actual food provided compared to non-urban habitats, and secondly in the parent birds having to expend more energy than non-urban conspecifics in locating and providing adequate supplies. A third possible constraint on productivity may be bacterial contamination, which can cause high rates of egg failure in nestbox-using sparrows, for example (Kendeigh 1942; Kozlowski et al. 1988).

This chapter is presented in three sections, each reporting a field investigation into a specific ecological opportunity or constraint that may be applicable to birds breeding and feeding young within the SK3388 study area. Section 12.1 reports a field assessment of relative chick diet quality in Blue and Great Tits, based on numbers and sizes of lepidopteran mandibles in faecal samples. Section 12.2 reports the use of doubly-labelled water (DLW) in field measurement of the daily energy expenditure of provisioning females in the same species. Section 12.3 documents the prevalence of *Salmonella* spp. at SK3388 feeding stations as determined from field sampling during the breeding season.

12.1. Chick diet quality in urban and rural Blue and Great Tits

12.1.1. Introduction

Generally, tits breed earlier in gardens but with lower productivity (Cowie & Hinsley 1987), and although in Blue Tits supplementary food advances laying it has no effect on breeding performance unless of very high quality (Ramsay & Houston 1997). Studies of urban gulls and Jays found that anthropogenic supplementary food was of insufficient quality for chick rearing (Pierotti & Annett 1990; Schoech & Bowman 2001). There is no obvious reason why it might be any more appropriate for tits in SK3388, given the strong relationship between breeding success in tits and the numbers of caterpillars available for provisioning their young (Perrins 1991; Riddington & Gosler 1995) and that the survey of feeders (Chapter 8) did not detect any provision of live food in the study area. As urban and non-urban invertebrate faunas are known to differ (Chapter 1), a comparison of the availability of caterpillars to parent tits provisioning young in SK3388 with that in non-urban habitats was undertaken, as a further contribution to assessing the sustainability of the SK3388 breeding avifauna.

12.1.2. Methods

Altricial passerine chicks frequently defecate when handled for ringing. The droppings are drier than those of adults and surrounded by a slightly sticky gelatinous envelope, forming the characteristic faecal sacs that enable their removal from the nest by the parent birds and hence also easy removal of the complete intact faecal sample for laboratory examination by a human investigator. In total, 98 faecal sacks were collected during May and early June 2004, 38 from Great Tits and 60 from Blue Tits. Fifty-four 'urban' samples were obtained from the SK3388 study area, from eight Blue Tit and two Great Tit nests. 'Rural' samples from 13 Blue Tit and 19 Great Tit nests were collected by volunteer bird ringers as a by-product of normal chick ringing, 32 from woodland nestboxes in the Rivelin Valley approximately 3-5 km from the urban site (by Phil Lawson) and 12 from woodland nestboxes south of Dronfield, Derbyshire, aproximately 20 km from the urban site (by Ray Knock). Dates of sample collection are shown in figure 12.1.3. In the case of the urban broods, if no samples had been provided voluntarily by a particular brood, chicks were stimulated to defecate by the provision of a small food item, either a mealworm (larval *Tenebrio molitor*) or small earthworm (*Lumbricus terrestris*), upon which most defecated immediately. The number of samples per brood was variable, determined by constraints of safe chick handling (primarily temperature maintenance). Because of the need to handle broods speedily, samples were not acquired from chicks selected in any way but simply from those that chose to provide them during an acceptable handling time.

Samples were placed individually and immediately in colourless denatured ethanol (Industrial Methylated Spirit (IMS), 94% alcohols), in which they were then stored at normal room temperatures for variable time periods up to approximately one year, during which there were no visible changes nor obvious deterioration of arthropod exoskeletal or other chitinous material. Samples were dried in a fan-ventilated drying cupboard at 40°C for at least 48 hours, this having been found an adequate period to establish stable dry weights in pilot testing. After dry weighing, samples were re-wetted with tap water for at least 24 hours before being gently dissected into a mixture of water and IMS in a 36-segment inspection dish under a binocular dissecting microscope. Some samples had large caps of white uric acid, which clouds the re-wetting fluid and obscures mandibles; this was partially removed with a dissecting needle prior to re-wetting. Each lepidopteran mandible found was logged and digitally photographed with an accompanying photograph of a 0.01 mm resolution stage graticule slide also taken at the same magnification and camera zoom settings; mandible lengths at longest point were then measured by superimposition of these image pairs on a computer (using imageJ, http://rsb.info.nih.gov/ij/).

Most samples contained other arthropod remains, but time constraints prevented detailed investigation of these. However, three sets of simple subjective categorical data on basic sample composition were additionally recorded. It was observed in pilot examinations of samples that the quantity of minerals, primarily small quartz grains, varied greatly between them. One hypothetical explanation for this might be that urban birds, rather than foraging in the branches of large native trees, as in woodland, are forced to search for food among suboptimal substrates such as roadsides. To test whether this might be the case, negligible, moderate or high relative mineral content per sample was recorded. Another hypothetical constraint on urban birds foraging among a depauperate invertebrate community might be that in the absence of a wide range of prey taxa they are forced to disproportionately exploit particular types of prey, therefore it was also recorded if a sample was visibly dominated by any one particular taxon of natural prey remains, such as arachnid legs or coleopteran elytra. Thirdly, a binary variable was recorded representing the presence or absence in samples of unusual items clearly not typical of natural chick food, including anthropogenic items such as plastic, large or unusual plant material, identifiable artificial food such as sunflower seed, large stones, etc. Hypothetically, birds constrained by poor natural prey availability in urban habitats might be forced to resort to presenting these less suitable items to their chicks. To avoid investigator bias samples were examined 'blind', numbered anonymously then mixed and drawn quasi-randomly for dissection.

The biomass of each predated caterpillar was estimated using regression equation 12.1. which was obtained from three years of undergraduate project work on allometry in lepidopteran larvae at Cardiff University (P.Ferns 2005 pers. comm.).

$$\text{Log (caterpillar biomass (mg))} = 1.73 + 2.39 \log \text{(mandible length (mm))} \qquad (12.1.)$$
$$(r^2 = 0.4569, F_{1,94} = 79.09, P < 0.0001)$$

Biomass estimates for all the single mandibles extracted from all the samples (N = 202) were pooled and their means compared using *t*-tests with critical *P* values Bonferroni-corrected to $P \leq 0.01$ for five non-orthogonal comparisons (Sokal & Rohlf 1995). Caterpillars having two mandibles, caterpillar biomasses were calculated by dividing individual caterpillar estimates by two for the comparisons of means of individuals, and for the per-sample biomass models (below) by summing the biomasses estimated from single mandibles in each sample then dividing that sum by two. All means are quoted ± standard error. χ^2 tests were used to examine associations within categorical variables.

Caterpillar biomasses were plotted against dates of sampling to examine their degree of independence. Date is a potential confounding variable in this analysis as the samples were collected opportunistically as a by-product of other fieldwork rather than in a planned program with regard to date. The biomass of caterpillars available to breeding tits varies as the season progresses, caterpillars get larger with time and their availability rapidly decreases when certain abundant species pupate (Perrins 1991).

To test whether urban and rural birds differed in the numbers and/or masses of caterpillars per sample, PROC MIXED in SAS (SAS Institute Inc. 2004) was used to fit generalised linear models with nest as a random effect (Der & Everitt 2002), with species (Blue Tit or Great Tit) and habitat (urban or rural) and their interactions as factors and per sample mean individual caterpillar biomass, number of mandibles per sample, total caterpillar biomass per sample and total caterpillar biomass per weight of sample as dependent variables. Least-squares means were calculated for all model effects and their pairwise differences evaluated for significance using Tukey-Kramer corrected *P* values.

12.1.3. Results

There was a highly significant overall difference in the dry masses of the faecal samples from Blue Tits (0.03g ± 0.0021) and Great Tits (0.0522g ± 0.0052) (t-test, $t = -5.07$, $P < 0.001$, $N = 88$), as would be expected since Great Tits (mean adult weight 18.61g ± 2.78) are heavier than Blue Tits (10.88g ± 0.78) (Robinson 2005). Urban samples (both species) were significantly more highly mineralised (primarily with quartz grains) than rural ($\chi^2 = 12.4$, DF = 2, $P = 0.002$, figure 12.1.1). There was a significant association between species and relative mineralisation ($\chi^2 = 6.04$, DF = 2, $P = 0.049$), with more Blue Tit than Great Tit samples in higher mineralisation categories. Out of all 98 samples, 25 (26%) had one particular prey type obviously dominant (15 rural and 10 urban) but there was no significant difference between the frequency of dominance in urban and rural samples ($\chi^2 = 3.09$, DF = 1, $P = 0.079$). However, urban samples were significantly more likely than rural samples (24/54 compared to 11/44, $\chi^2 = 3.99$, DF = 1, $P = 0.046$) to contain items subjectively logged as 'unusual'. There were no significant differences between the species in frequencies of single taxon prey dominance or unusual items

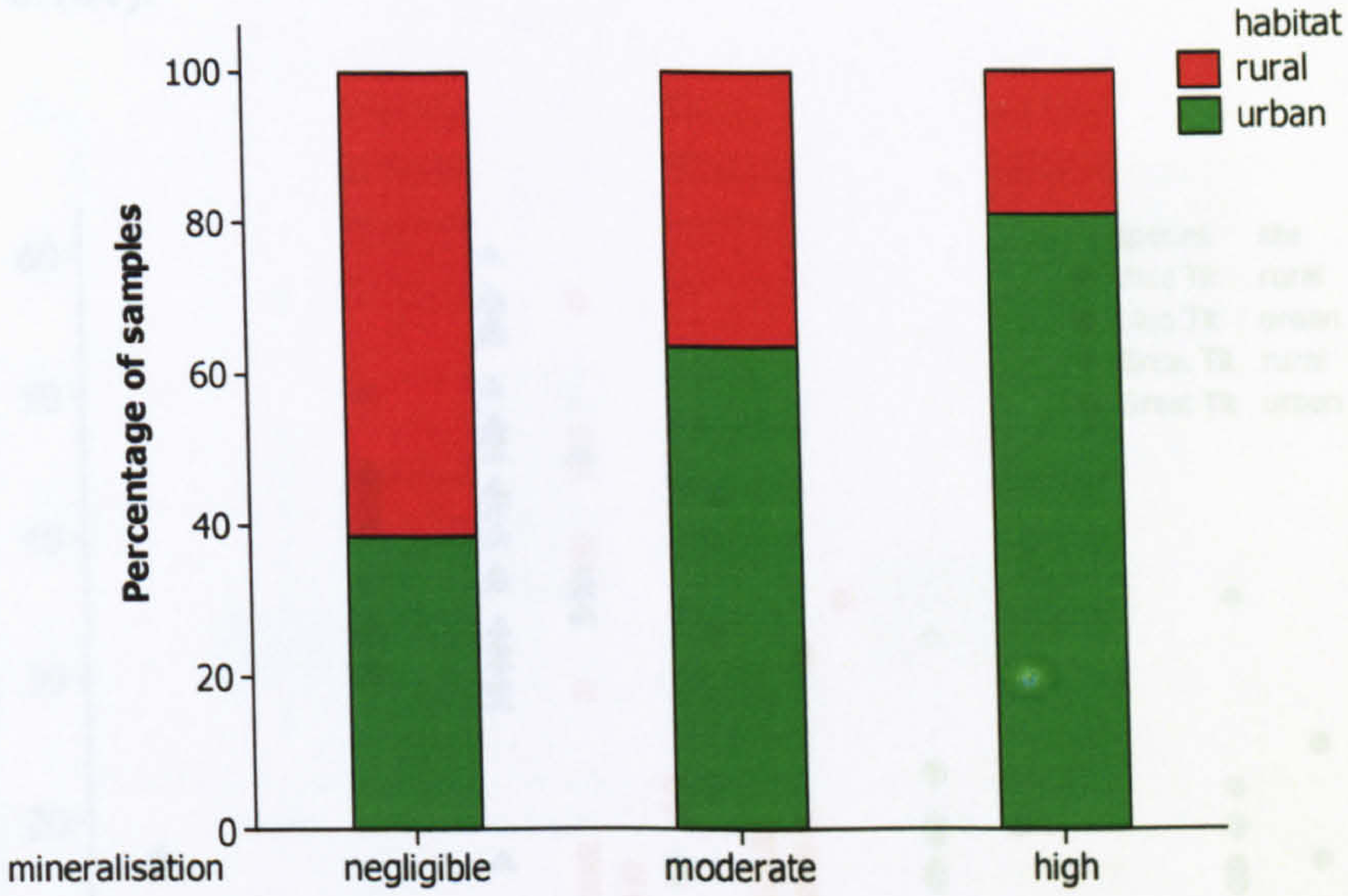


Figure 12.1.1. Proportions of faecal samples with negligible, moderate and high relative mineral content (subjective categories) obtained from urban and rural sites, both species.

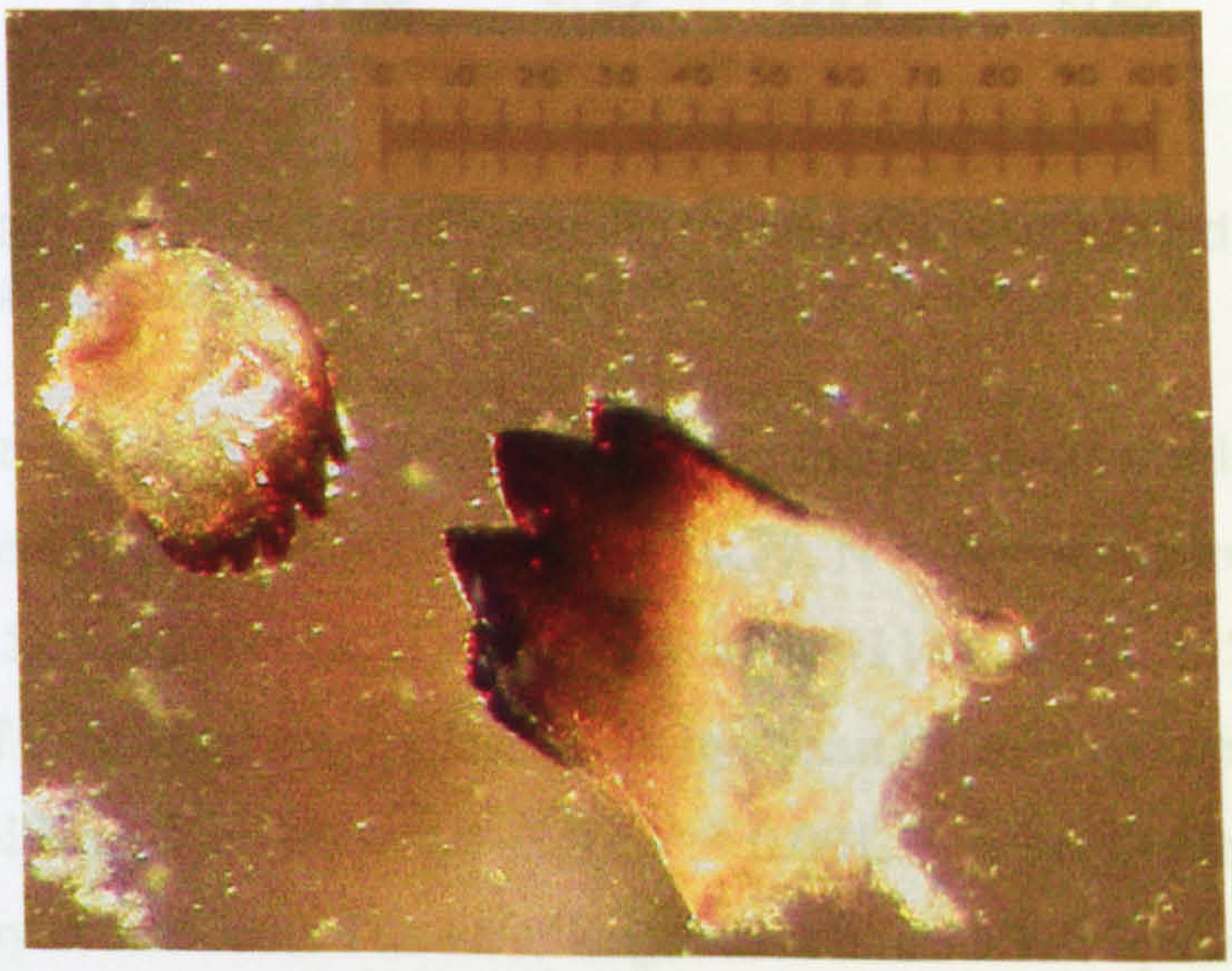


Figure 12.1.2. Lepidopteran larval mandibles from chick faeces. Scale: 0 – 100 = 1mm.

Figure 12.1.2 shows extreme examples of the sizes and shapes of mandibles that were present. Figure 12.1.3. shows that except for one very early rural Great Tit brood, urban samples were generally collected earlier than rural. Within each species/habitat class, there is no obvious confounding trend in available prey sizes; generally, urban caterpillars were both larger and earlier than non-urban. Altogether, 202 mandibles were found in 61 out of the 98 samples (62%), of which 94 were found in 31 out of 54 urban samples (57%) and 108 in 31 out of 44 rural samples (70%). The proportions of rural and urban samples containing mandibles were not significantly different ($\chi^2 = 1.792$, DF $= 1$, $P = 0.181$).

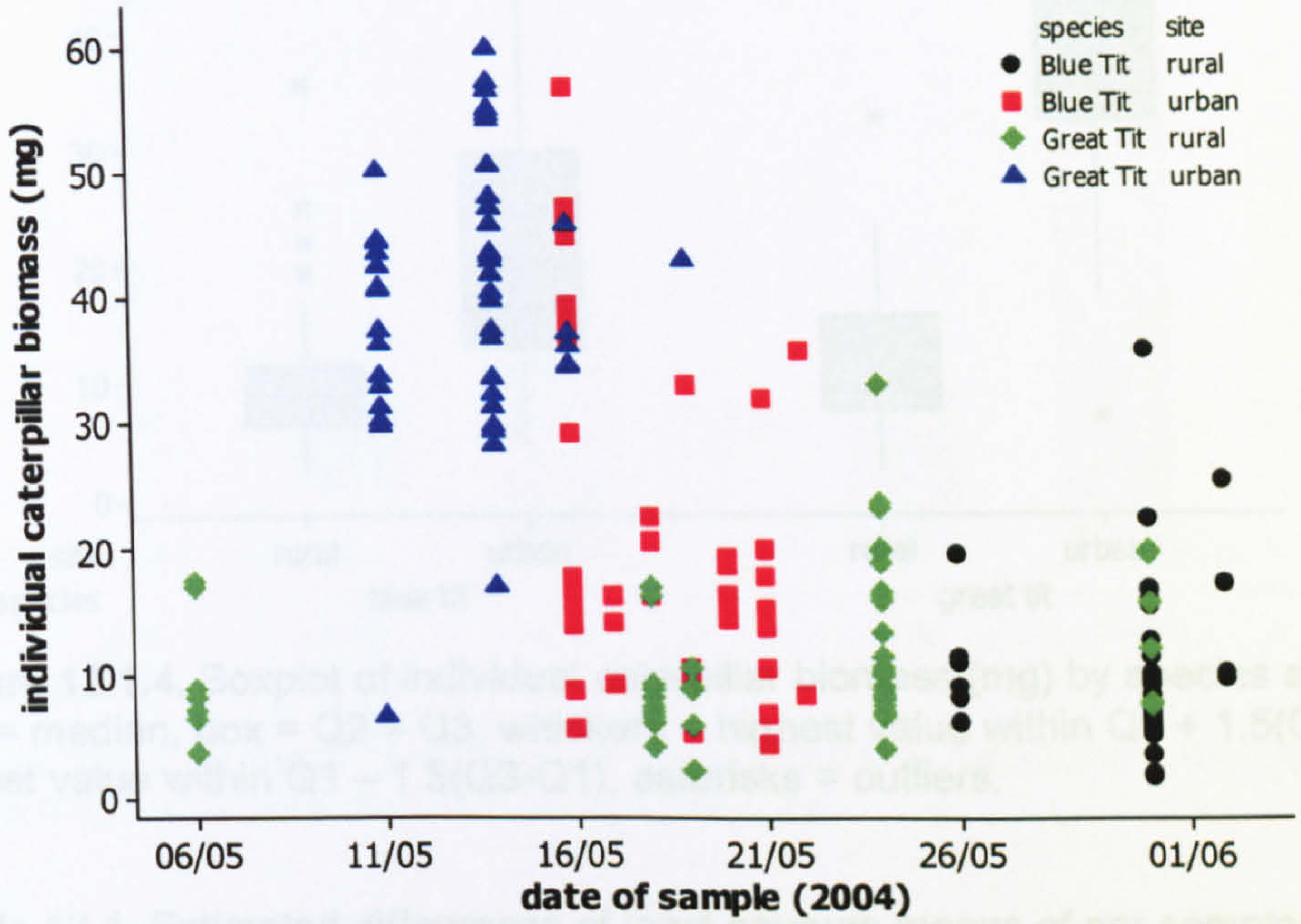


Figure 12.1.3. Scatterplot of individual caterpillar biomasses (calculated on single mandible basis) against date of faecal sample collection. N = 202.

As would be expected from figure 12.1.4, comparing individual caterpillar biomasses showed that urban caterpillars (mean 15.05 mg ± 0.77, N = 94) were generally larger than rural (mean = 5.35 mg ± 0.28, N = 108) (*t*-test, $t = -11.84$, $P < 0.001$, N = 202). Mean biomasses of individual caterpillars taken by urban Blue Tits were larger than of those taken by rural Blue Tits (*t*-test, $t = -5.07$, $P < 0.001$, N = 94) and individual caterpillars taken by urban Great Tits were larger than those taken by rural Great Tits (*t*-test, $t = -16.47$, $P < 0.001$, N = 108). Caterpillars taken by urban Great Tits were larger than those taken by urban Blue Tits (*t*-test, $t = -7.69$, $P < 0.001$, N = 94), but there was no difference between caterpillars taken by rural Great Tits and those taken by rural Blue Tits (*t*-test, $t = -0.92$, $P = 0.36$, N = 108). In the more conservative per sample models with nest as a random effect, species ($P = 0.0054$), habitat ($P = 0.0004$) and species * habitat ($P = 0.0051$) were all significant predictors of per sample mean individual caterpillar biomass (AIC = 724.0. DF = 57, all *P* values type 3). Table 12.1 shows the differences between the estimated least squares means for main effects and interactions and their *P* values, adjusted for pairwise comparison.

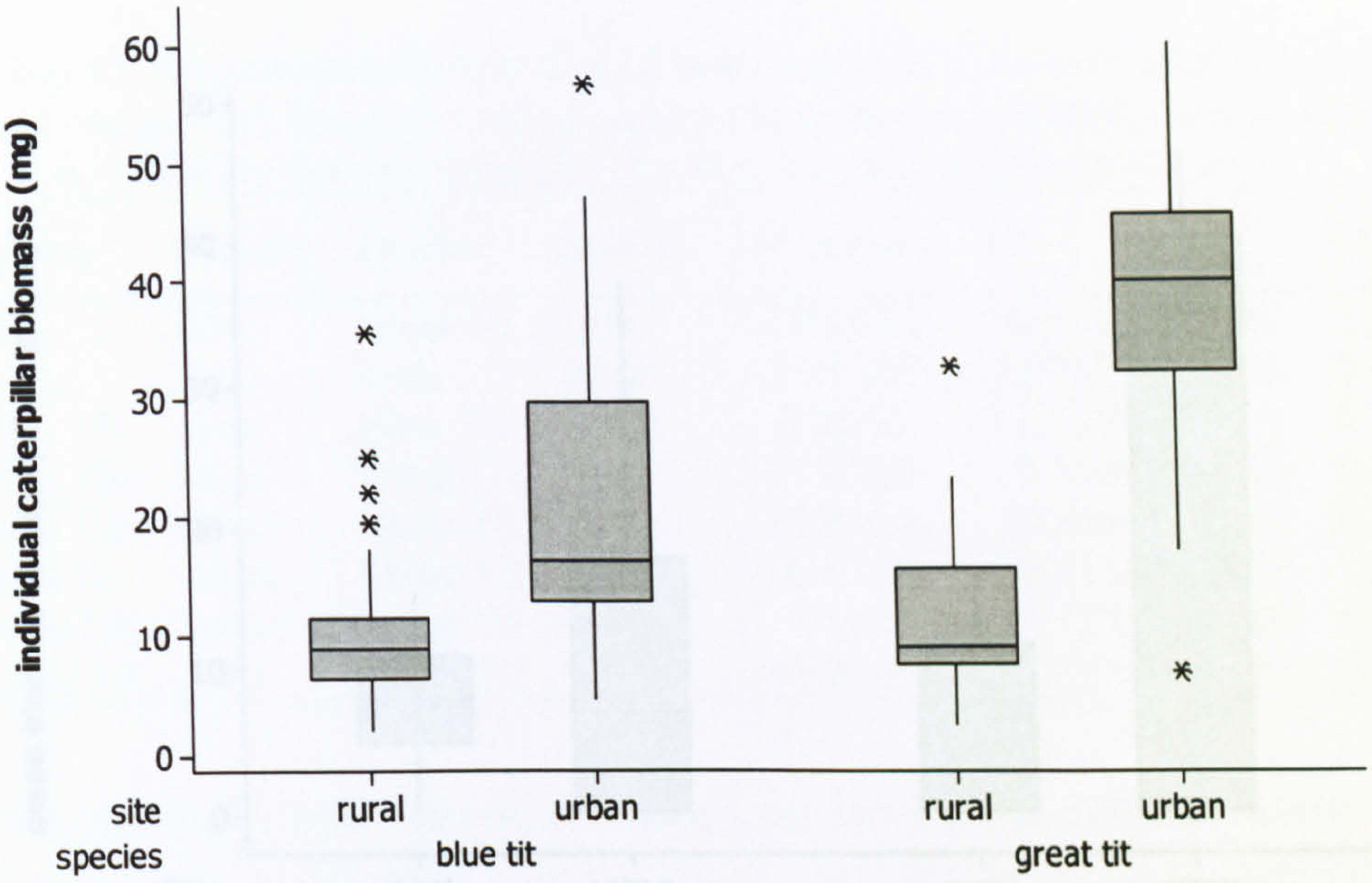


Figure 12.1.4. Boxplot of individual caterpillar biomass (mg) by species and site type. Bar = median, box = Q2 – Q3, whiskers = highest value within Q3 + 1.5(Q3 – Q1), lowest value within Q1 – 1.5(Q3-Q1), asterisks = outliers.

Table 12.1. Estimated differences of least squares means of per sample mean individual caterpillar biomass (mg) when modelled against species and habitat, nest as random effect. P (T-K) = Tukey-Kramer adjusted *P* value for pairwise comparison.

species	habitat	species	habitat	Difference	SE	t	Pr>|t|	P (T-K)
Blue Tit	both	Great Tit	both	-8.3674	2.8925	-2.89	0.0054	**0.0054**
both	rural	both	urban	-10.8962	2.8925	-3.77	0.0004	**0.0004**
Blue Tit	rural	Blue Tit	urban	-2.4749	3.3984	-0.73	0.4694	0.8854
Blue Tit	rural	Great Tit	rural	0.05399	3.4824	0.02	0.9877	1
Blue Tit	rural	Great Tit	urban	-19.2636	4.804	-4.01	0.0002	**0.001**
Blue Tit	urban	Great Tit	rural	2.5289	3.2229	0.78	0.4359	0.8611
Blue Tit	urban	Great Tit	urban	-16.7887	4.6194	-3.63	0.0006	**0.0033**
Great Tit	rural	Great Tit	urban	-19.3176	4.6815	-4.13	0.0001	**0.0007**

From table 12.1, pairwise tests show that overall rural caterpillars were smaller than urban caterpillars and that those taken by Blue Tits were generally smaller than those taken by Great Tits. In this model, the caterpillars taken by urban Blue Tits were not significantly different in mass from those taken by either rural Blue Tits or rural Great Tits, nor were those taken by rural Blue Tits and rural Great Tits significantly different. However, caterpillars taken by urban Great Tits were significantly larger than those taken by rural Blue Tits, rural Great Tits and urban Blue Tits. Figure 12.1.5 clearly shows from a boxplot of the per sample means how these results arise.

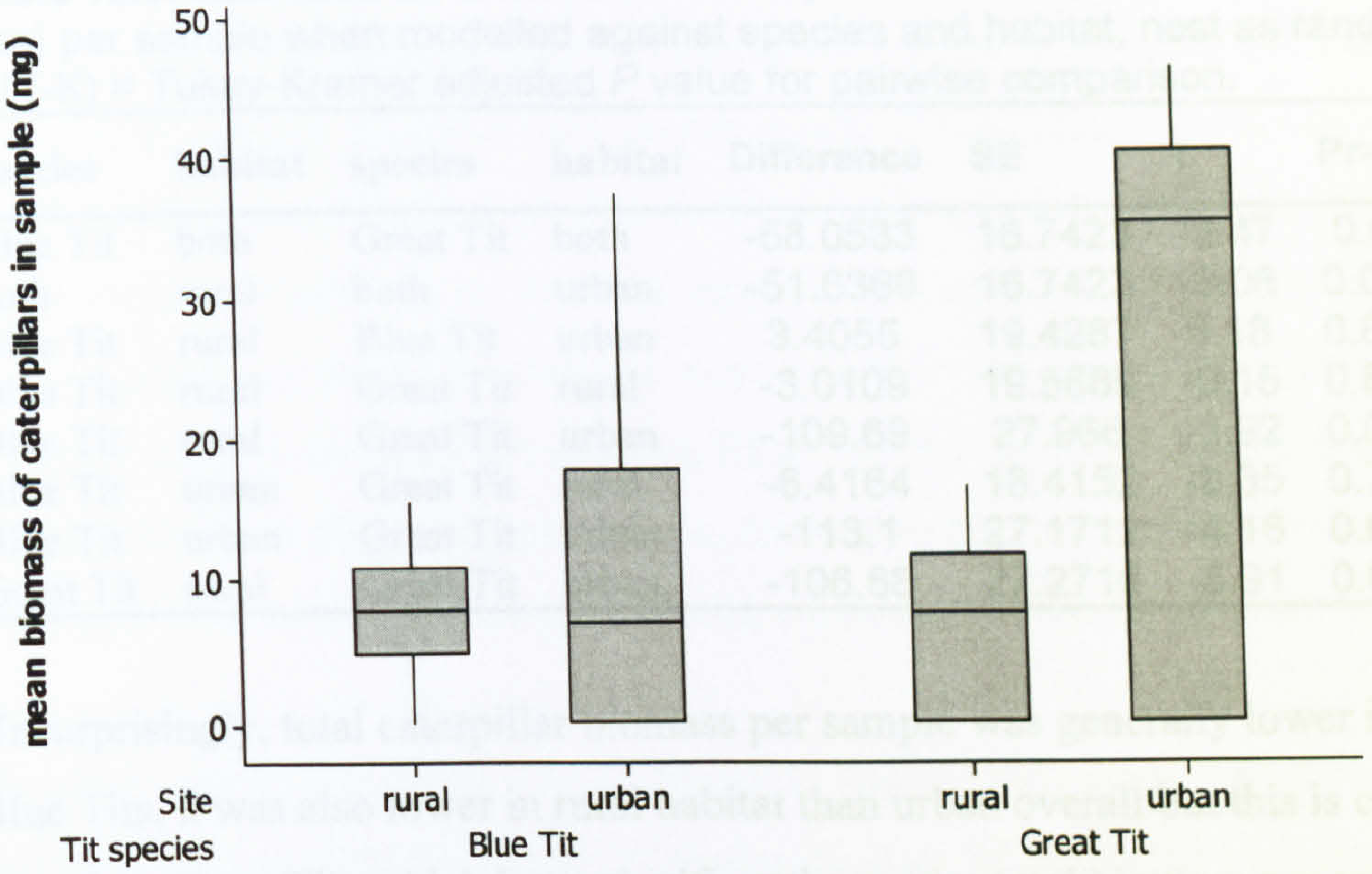


Figure 12.1.5. Boxplot of per sample mean individual caterpillar biomass (mg) by species and site type. Symbols as in figure 12.4.

Neither species ($P = 0.0648$), habitat ($P = 0.5003$) nor species * habitat ($P = 0.1364$) were significant predictors of mandibles per sample, modelled with nest as a random effect (AIC = 443.5. DF = 57). Table 12.2 shows the differences between the estimated least squares means and their P values, adjusted for pairwise comparison; none are significant.

Table 12.2. Estimated differences of least squares means of numbers of mandibles per sample when modelled against species and habitat, nest as random effect. P (T-K) = Tukey-Kramer adjusted *P* value for pairwise comparison.

species	habitat	species	habitat	Difference	SE	t	Pr>|t|	P (T-K)
Blue Tit	both	Great Tit	both	-1.1887	0.7427	-1.6	0.115	0.115
both	rural	both	urban	0.2951	0.7427	0.4	0.6926	0.6926
Blue Tit	rural	Blue Tit	urban	1.417	0.8493	1.67	0.1007	0.3497
Blue Tit	rural	Great Tit	rural	-0.06677	0.8376	-0.08	0.9367	0.9998
Blue Tit	rural	Great Tit	urban	-0.8935	1.2487	-0.72	0.4772	0.8905
Blue Tit	urban	Great Tit	rural	-1.4838	0.8046	-1.84	0.0704	0.2638
Blue Tit	urban	Great Tit	urban	-2.3105	1.2268	-1.88	0.0648	0.2466
Great Tit	rural	Great Tit	urban	-0.8267	1.2187	-0.68	0.5003	0.9049

Species ($P = 0.001$), habitat ($P = 0.0031$) and species * habitat ($P = 0.0017$) were all significant predictors of total caterpillar biomass per sample (AIC = 1048.0. DF = 57). Table 12.3 shows the differences between the estimated least squares means for main effects and interactions and their P values, adjusted for pairwise comparison.

Table 12.3. Estimated differences of least squares means of total caterpillar biomass (mg) per sample when modelled against species and habitat, nest as random effect. P (T-K) = Tukey-Kramer adjusted *P* value for pairwise comparison.

species	habitat	species	habitat	Difference	SE	t	Pr>|t|	P (T-K)
Blue Tit	both	Great Tit	both	-58.0533	16.7423	-3.47	0.001	**0.001**
both	rural	both	urban	-51.6369	16.7423	-3.08	0.0031	**0.0031**
Blue Tit	rural	Blue Tit	urban	3.4055	19.4287	0.18	0.8615	0.9981
Blue Tit	rural	Great Tit	rural	-3.0109	19.5689	-0.15	0.8783	0.9987
Blue Tit	rural	Great Tit	urban	-109.69	27.966	-3.92	0.0002	**0.0013**
Blue Tit	urban	Great Tit	rural	-6.4164	18.4152	-0.35	0.7288	0.9853
Blue Tit	urban	Great Tit	urban	-113.1	27.1712	-4.16	0.0001	**0.0006**
Great Tit	rural	Great Tit	urban	-106.68	27.2716	-3.91	0.0002	**0.0014**

Unsurprisingly, total caterpillar biomass per sample was generally lower in the smaller Blue Tits, it was also lower in rural habitat than urban overall but this is clearly due to the urban Great Tits which have significantly greater total biomass per sample than both rural Blue Tits and urban Blue Tits; perhaps more surprisingly, they also had greater total per sample biomass than rural Great Tits.

However, neither species (*P* = 0.4673), habitat (*P* = 0.0880) nor species * habitat (*P* = 0.0542) were significant predictors of total caterpillar biomass per mass of sample (AIC = 1355.4. DF = 50). Table 12.4 shows the differences between the estimated least squares means and their *P* values, adjusted for pairwise comparison; none are significant.

Table 12.4. Estimated differences of least squares means of total caterpillar biomass per mass of sample when modelled against species and habitat, nest as random effect. P (T-K) = Tukey-Kramer adjusted *P* value for pairwise comparison.

species	habitat	species	habitat	Difference	SE	t	Pr>|t|	P (T-K)
Blue Tit	both	Great Tit	both	-126.71	173	-0.73	0.4673	0.4673
both	rural	both	urban	-301.06	173	-1.74	0.088	0.088
Blue Tit	rural	Blue Tit	urban	40.0707	226.36	0.18	0.8602	0.998
Blue Tit	rural	Great Tit	rural	214.42	245.66	0.87	0.3869	0.8188
Blue Tit	rural	Great Tit	urban	-427.77	285.92	-1.5	0.1409	0.4474
Blue Tit	urban	Great Tit	rural	174.35	194.86	0.89	0.3752	0.8076
Blue Tit	urban	Great Tit	urban	-467.84	243.67	-1.92	0.0606	0.2329
Great Tit	rural	Great Tit	urban	-642.19	261.69	-2.45	0.0177	0.08

12.1.4. Discussion

These results show the importance of caterpillars as chick food for Blue and Great Tit. When these species urbanise, they do not appear to substitute other foods in their chicks' diets; caterpillars are present in the same proportions of the droppings of both urban and rural birds and in the same numbers per sample. The urban habitat enables them to provision chicks in a similar way to rural broods, rather than forcing them to radically adapt their diet. Furthermore, Blue Tits that colonise the urban habitats do not adjust their caterpillar size preference compared to the rural habitat, in which Blue Tits and Great Tits provision their chicks with small caterpillars of similar sizes.

However, urbanising Great Tits do switch to significantly larger caterpillars than rural conspecifics and actually provide a greater biomass of caterpillars per faecal sample, although caterpillar biomass as a proportion of sample dry mass is not significantly different after Tukey-Kramer adjustment of the *P* value (table 12.4). The fact that urban Great Tits do not differ from rural conspecifics in the numbers of caterpillars per sample provided to their young, despite their larger prey size, implies that the lepidopteran diet component in the chick diet of urban Great Tits may be significantly more important. This is perhaps surprising in view of the general view that a contributory factor to lower avian productivity in urban habitats might be lower availability of suitable invertebrate prey for feeding the young; it also differs from the results of Riddington & Gosler (1995) who found significantly fewer caterpillar remains in 'marginal' habitat faecal samples than in those from woodland (although they report that, unlike in SK3388, there was little supplementary food in their 'marginal' habitat). On the other hand, there is virtually no difference between the caterpillar component of chick diet in urban and rural Blue Tits, although the individual caterpillar *t*-tests (N = 202 both species) did show that urban Blue Tits were also taking significantly larger individual caterpillars than rural conspecifics, with a *P* value well within Bonferroni-corrected limits. However, this result was not sufficiently robust to be supported by the more conservative model of per sample data with nest as a random effect (N = 95 both species), which controls for the non-independence of samples from the same broods.

It is notable from figure 12.1.6 that rural Great Tits take caterpillars from a very similar range of sizes to those taken by rural Blue Tits, whereas urban Great Tits exploit a much larger range of prey sizes. It would be interesting to determine prey availability in both habitats, as the obvious issue arising from this is whether Great Tits prefer large caterpillars but they are not available in rural habitats, or whether conversely they prefer small caterpillars but these are not available in urban habitats. Lower urban productivity in Great Tits despite larger prey might be explained by it being energetically more efficient to glean numerous small caterpillars from a large native tree on which the nestbox is located, than to search a wider area of urban gardens for large caterpillars. Another contrasting possibility is that urban adults may be exploiting superabundant artificial foods and are hence able to provision their chicks with the large caterpillars that in rural habitats they would need to eat themselves, hence they do not need to collect the less efficient smaller caterpillars. In a Finnish study area where typically caterpillars made up more than 70% of Great Tit nestling diets was but were nonetheless scarce, Great Tits had poorer breeding success than in a more southerly site where caterpillars were more abundant (Rytkönen & Krams 2003) and the birds changed their foraging niche to widen the search. Northern Blue Tits foraging in the outer canopy had higher breeding success than the Great Tits, which were clearly dependent on caterpillars but were unable to emulate the Blue Tits in gleaning small prey from branch tips. In SK3388, they may make up for this inability by finding larger caterpillars in other kinds of habitat such as gardens. Native trees such as Oak which are a major foraging site for tits are scarce in the SK3388 study area; in contrast, large caterpillars might be scarce in rural woodland but easily found by a species able to shift its foraging niche among domestic garden plants such as *Brassica* spp.

The higher mineral content of Blue Tit chick faeces compared to those of Great Tits is perhaps surprisingly as the latter is generally considered to be more of a ground feeding species. The larger proportion of unusual items in urban faeces does suggest that some degree of flexibility in attempting to exploit foodstuffs not typical of woodland habitats is required of the urban birds. Figure 12.1. 3 suggests that any confounding effect of sampling date would tend to counterweigh the overall result; urban sampling was generally earlier than rural and so might be expected to record smaller prey, not larger as was observed. This may reflect not only relative phenological advancement in urban habitats but perhaps also that tits are taking different prey species in the two habitats.

In rural Great Tits in Oxfordshire, 3.62 mandibles were found per faecal sac in 1984 and 4.73 in 1985 (Gosler 1987b). These figures are comparable with those for urban Great Tits in this study (mean 3.71 per sac) but rather higher than those for rural birds (2.54

per sac). This may just reflect annual variation in prey availability; it is notable that the means between 1984 and 1985 in the Oxfordshire study vary by 23%. The present results are a 'snapshot' of a single breeding season and it may not be valid to generalise without replication over a number of years. One possible bias in the size distribution of caterpillar mandibles in faecal samples is that birds may remove the heads of some caterpillars before presentation to chicks, for example if the mandibles of larger caterpillars are perceived as a threat to the chicks' wellbeing. However, it is unlikely that rural birds should be doing this but not their urban conspecifics and in this study large caterpillar mandibles were more prevalent than small in the urban samples. Furthermore, Gosler (1987b) found strong correlation between numbers of caterpillar mandibles and spiracles in tit faecal samples, suggesting that no systematic bias of this nature is present, at least in Great Tits, which would be expected to be most affected as they take larger caterpillars.

Overall, these results suggest that urban Blue and Great Tits are not sufficiently constrained in their chick diets that they are forced to switch to novel prey or in the case of Blue Tits, to vary the lepidopteran component of chick diets significantly. Great Tits, however, are able to provide their chicks with significantly larger caterpillars in urban habitat; the costs and benefits of their doing so would be well worth further investigation particularly as other studies have shown this species has difficulty maintaining breeding performance in sub-optimal (Rytkönen & Krams 2003) and urban (Bezzel 1985) habitats.

12.2. Energy expenditure of female Blue & Great Tits provisioning young

12.2.1. Introduction

This section reports an investigation into the daily energy expenditure (DEE) of female Blue and Great Tits provisioning young in SK3388. There are a number of reasons why the DEE of these birds might differ from that of rural conspecifics. Generally in urban garden habitats anthropogenic supplementary food is abundant even in the breeding season; this is certainly the case in SK3388 but, nonetheless, urban clutch sizes are often smaller than non-urban (chapter 1). For hole-nesting species such as Blue Tit and Great

Tit low occupancy of newly-provided nest boxes suggests that nest sites are not a limiting resource. Only 10 out of 76 provided by this study were used in SK3388 but, nonetheless, urban breeding densities of these species are relatively low (chapter 1). Urban and rural birds maintain similar rates of caterpillar supply to their chicks (section 12.1), hence one possible explanation for smaller broods and low densities despite abundant food and nest sites might be that in urban habitats this natural invertebrate food for rearing chicks is less abundant, in which case, parent birds would have to expend more energy foraging.

Even though tits normally overcome the problem of variable food supply by adjusting their clutch sizes (certainly it is correlated with caterpillar numbers in Great Tits (Perrins 1991) and with habitat quality in Blue Tits (Stauss et al. 2005)), their perception of resource availability in an urban environment may be distorted by either the effects of artificial food, phenotype/habitat mismatch (the 'ecological trap' scenario) or both. It may seem surprising that clutch size in Blue Tits is unaffected by supplementary feeding (Ramsay & Houston 1997), given the adaptability of urban adults to a diet largely composed of anthropogenic supplements but, as suggested by Cowie and Hinsley (1988), it may be that parent tits prefer to rear their chicks on a more appropriate invertebrate diet and that, as Perrins (1991) points out, supplementary food might not be perceived as appropriate compensation for a shortage of natural food; birds may therefore discount its availability when assessing food abundance. If parent birds ignore artificial food completely when 'budgeting' but nonetheless, as is clearly the case, exploit it themselves while provisioning chicks, their energy expenditure per chick might be expected to be less than in non-urban habitats where the subsidy of artificial food was not available and hence the 'budget' calculation precise. Conversely, if adult birds do take the availability of an artificial subsidy into account when 'calculating' their overall brood provisioning 'budget' but feed their chicks selectively on the most appropriate food items within it, their energy expenditure per chick would be expected to be greater than in non-urban habitats, the subsidy fuelling the extra foraging effort to find the scarcer natural prey items. A further cause of variation in DEE in tits is that phenotypes mismatched to habitat have higher energy expenditure than habitat-matched phenotypes (Thomas et al. 2001).

It might be possible to study these effects experimentally by manipulating food availability, but in urban habitats the supplementary food supply is inherently uncontrollable. However, an alternative approach is to directly measure the daily energy expenditure (DEE) of actively provisioning adult birds in different types of habitat. In this section, the results of a doubly-labelled water (DLW) study of the energy usage rates of female Blue and Great Tits provisioning chicks in SK3388 are reported, and compared with results from similar studies in other habitats of varying relative urbanisation.

12.2.2. Methods

During autumn of 2002, 50 standard tit nestboxes with internal volume of aproximately 1.5 l and 32 mm diameter entrance holes were installed in the SK3388 study area, unfortunately none were used by Great Tits. For the 2003 breeding season 26 additional nestboxes were installed, of somewhat better quality (donated by CJ Wildbird Foods Ltd), and the project extended within SK3388 to include Blue Tits. Of the 76 boxes, seven were occupied by Blue Tits and three by Great Tits (in addition, one was occupied by Nuthatches, a new breeding species for the study area). Four additional nest sites (three Blue Tit boxes and one Great Tit wall nest) at which trapping appeared feasible were also identified, giving a total possible sample of ten Blue Tit and four Great Tit nests. Of these, eight Blue Tit and three Great Tit females were successfully sampled.

The DLW method is documented in Speakman (1997); it measures energy consumption of live animals indirectly by determining the CO_2 produced by an organism in a known time period, ideally a multiple of 24 hours in the case of DEE estimation. Essentially, both the oxygen and hydrogen in the blood are labelled with stable (i.e. not radioactive) isotopes (^2H and ^{18}O) and the difference between their turnovers indicates the quantity of CO_2 produced, which can be equated to DEE. In this case, birds were dosed by intraperitoneal injection with a known mass of water (around 0.08g, weighed to 0.0001 g accuracy) whose ^2H and ^{18}O isotope content had been artificially increased to adequate (known) levels that would enable their detection in a mass spectrometer. Initial blood samples were taken after the dose had equilibrated throughout the circulatory system for 30 minutes. From these, the initial isotope concentrations were subsequently measured. A second blood sample was taken after a period as near to 24 hours as possible (exact times were recorded) and the change in blood isotope concentration subsequently determined by comparing the two samples (samples were processed by J.R.Speakman et al. at the University of Aberdeen).

All nests were monitored during laying to establish hatch dates; blood samples for the DLW procedure were taken on days 10 and 11 post-hatch (hatch date = day 0). Blood samples were extracted from brachial veins pierced with a small hypodermic needle, using non-heparinised capillary tubes, the second sample from the wing that was not sampled the previous day. In Blue Tits approximately 40 μl was collected each day, generally as a single sample. In the larger Great Tits duplicate samples each of approximately 35 μl were taken on each day. An evaporation check syringe was carried with the dosing syringes and re-weighed after all fieldwork sessions, however because in the urban environment field sessions were fairly short, shade was available and return to base between birds was possible, no measurable evaporation occurred. The procedure was performed after training under UK Home Office licence PIL 80/8559 and English Nature licence 20040579, the birds were kept for an additional 30 minutes recovery period after sampling before being released upon confirmation that bleeding had ceased and they were apparently fit and well.

This method imposed the demanding requirement that the same individual bird be caught twice, as near to exactly 24 hours apart as practicable. Consequently, all nestboxes were fitted with permanently-installed traps to which birds would be habituated and hence repeatedly trapped. These consisted of aluminium trapdoors supported above the entrance hole by lengths of brazing rod (figure 12.2.1). In the case of boxes used for nesting, the retaining rod was removed prior to trapping and replaced with a shorter trigger pin that could be withdrawn from a distance via a length of nylon fishing line in order to trap the required bird. An elasticated cloth sleeve that fitted over arm and box was used to withdraw the trapped females from the boxes without risk of escape. After the first catch and blood sample, the females generally became very wary and even at the boxes with traps, a camouflaged hide was necessary to ensure re-trapping within a reasonable time.

All the broods of sampled females fledged either totally or with low levels of mortality typical for urban nestboxes. Females were identified by the presence of a brood patch and in most cases carried previously-fitted colour rings. At the first catch, any unringed females were colour-ringed and in addition females were marked with white correcting fluid on the tail to avoid catching the male in error the following day. Females and chicks were weighed to 0.01 g using a battery-powered laboratory balance (Adam equipment ACB 300).

Figure 12.2.1. Permanently-installed nestbox trap, from above. The wooden block on the left secures the retaining bar which prevents the aluminium trapdoor from dropping when the not in use. In use, this is replaced with a shorter trigger pin which is removed remotely via fishing line causing the door to drop, trapping the adult female bird inside the box.

12.2.4. Results.

One Blue Tit sample failed in processing, DEE values from a total of seven Blue Tits and three Great Tits are shown in table 12.5 and plotted against brood biomass in figure 12.2.2. For Great Tits, only three samples were obtained and one of these was a clearly atypical brood (very late, very sickly, only one chick remaining alive by second blood sample). Therefore, comparisons with other locations are rather weak. However, figure 12.2.3. shows that the values for SK3388 lie at the lower end of the general range, particularly if the atypical brood (which had the highest of the three DEE values obtained) is ignored.

Table 12.5. Summary of results of DLW procedure for measuring Daily Energy Expenditure in female Blue and Great Tits provisioning young

Species	adult mean weight (g)	brood size	mean chick weight (g)	chick biomass (g)	date (2004)	DEE kJ $24h^{-1}$
Blue Tit	9.53	8	8.70	69.6	18/5	58.64
Blue Tit	10.45	8	10.30	82.2	20/5	56.30
Blue Tit	10.91	8	8.91	67.1	20/5	70.47
Blue Tit	10.72	8	10.20	81.7	20/5	58.63
Blue Tit	10.52	8	9.70	77.7	22/5	56.07
Blue Tit	10.25	12	7.71	92.5	24/5	54.55
Blue Tit	10.5	6	10.00	60.0	28/5	39.39
Great Tit	16.38	9	17.50	157.1	13/5	75.50
Great Tit	16.94	5	14.60	73.0	18/5	59.82
Great Tit	18.35	1	15.10	15.1	4/6	86.03

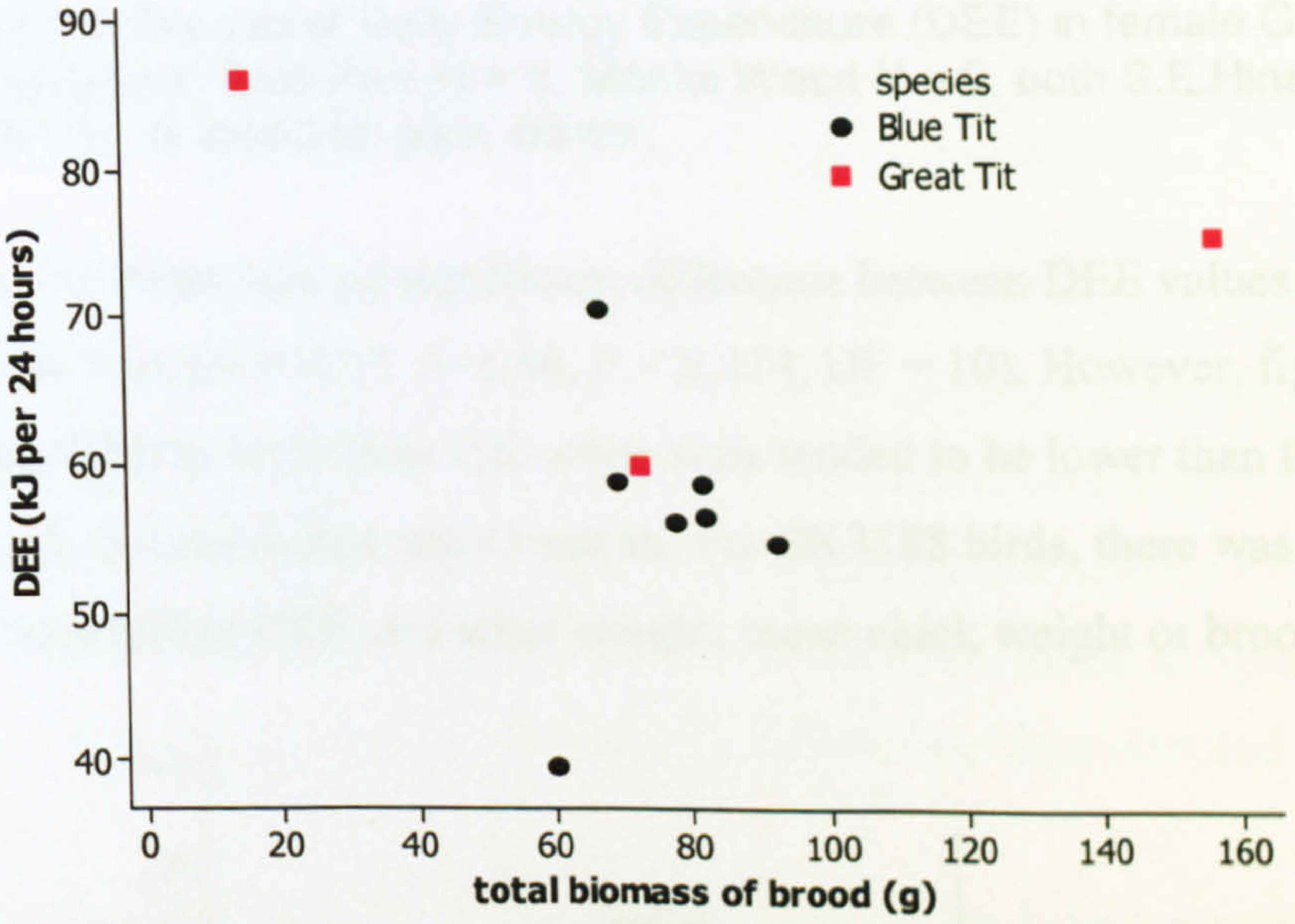


Figure 12.2.2. Relationship between daily energy expenditure (DEE) and brood biomass in SK3388, both species.

The difference between Monks Wood (rural woodland in Cambridgeshire) and Bute Park (urban park in Cardiff) is not significant ($t = 2.07$, $P = 0.093$, DF = 5). The values for the Vlieland site as reported in Verhulst and Tinbergen (1997), an area of continuous woodland in Holland (S.Verhulst pers.comm.) were significantly greater than those from woodland birds at Monks Wood ($t = 7.06$, $P < 0.001$, DF = 36), perhaps suggesting that habitat is not the primary factor affecting DEE in this species. There was no significant difference between Great Tit DEE values for Holland and Bute Park ($t = -1.25$, $P < 0.257$, DF = 6).

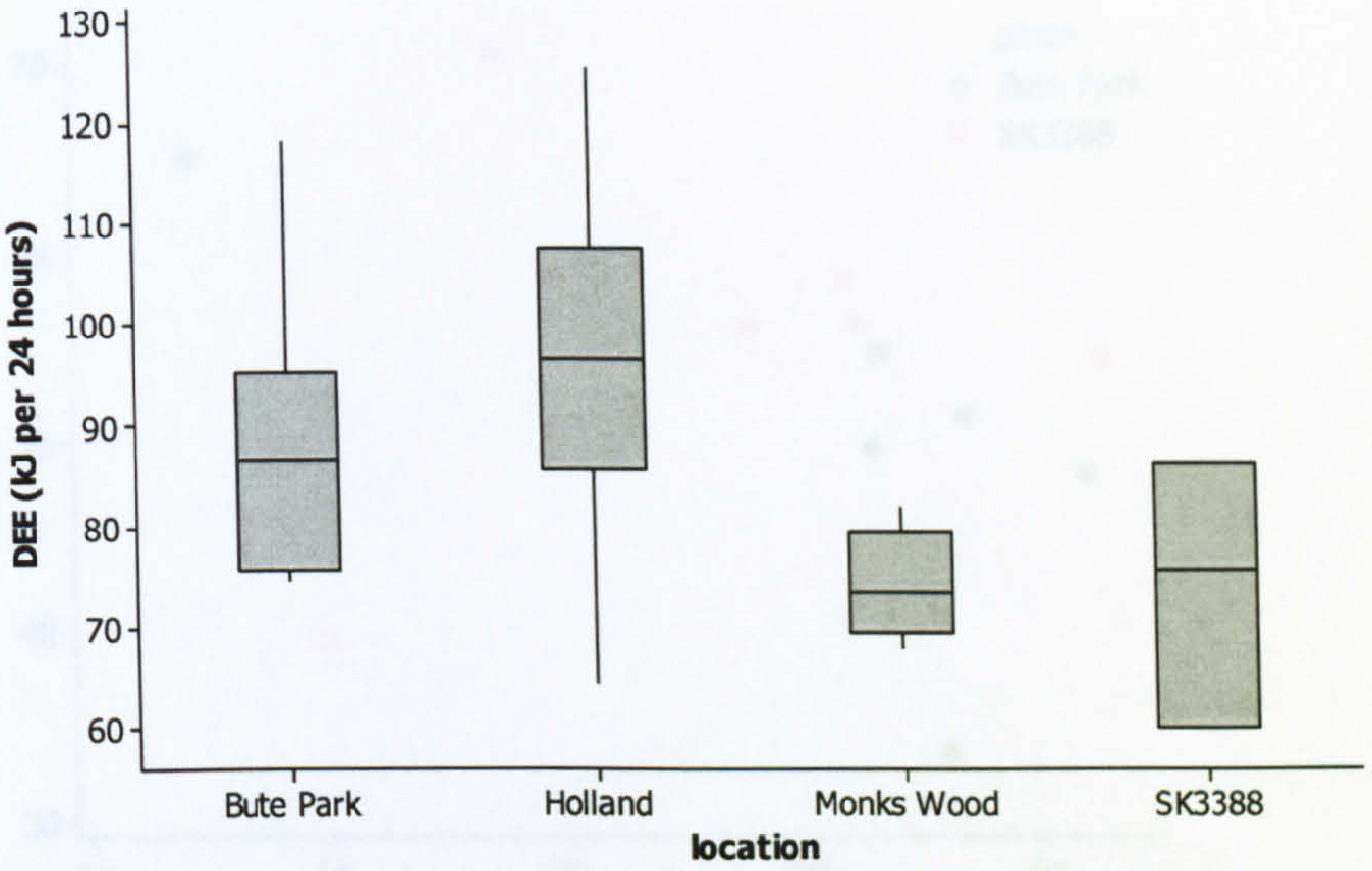


Figure 12.2.3. Boxplot of Daily Energy Expenditure (DEE) in female Great Tits at four different locations. Bute Park N = 6, Monks Wood N = 9, both S.E.Hinsley pers.comm. Holland N= 31, S.Verhulst, pers. comm.

For Blue Tits, there was no significant difference between DEE values for SK3388 (N = 7) and Bute Park (N = 6) (T = -1.06, *P* < 0.314, DF = 10). However, figure 12.2.4. shows that DEE in both these UK urban sites tended to be lower than that for French Blue Tits, both continental and Corsican. For SK3388 birds, there was no significant correlation between DEE and adult weight, mean chick weight or brood biomass.

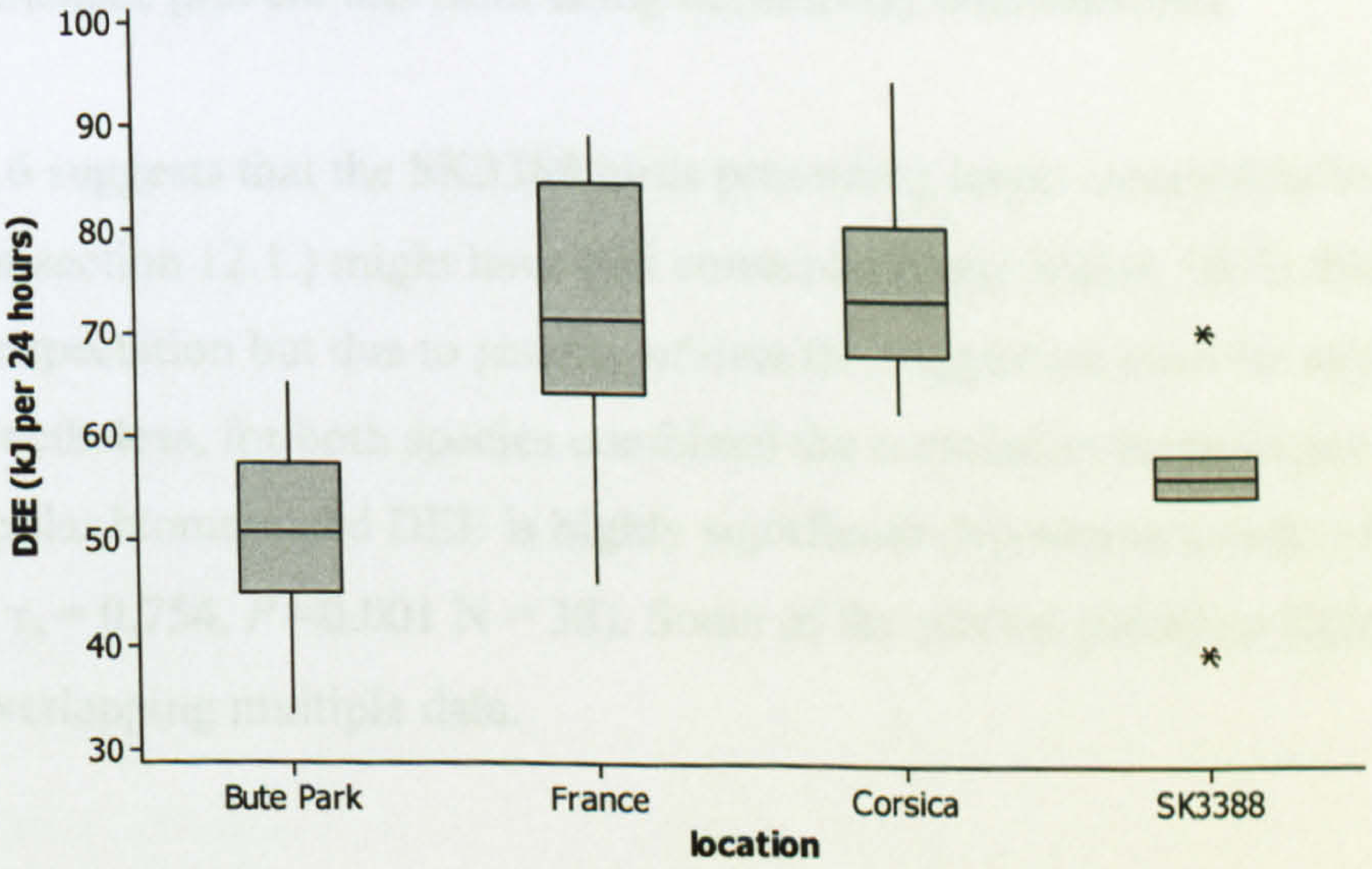


Figure 12.2.4. Boxplot of Daily Energy Expenditure (DEE) in female Blue Tits at four different locations. Figures for France (N = 13) and Corsica (N = 14) read from graph in Thomas, Blondel et al. (2001), Bute Park (N = 6) S.E.Hinsley pers. comm.

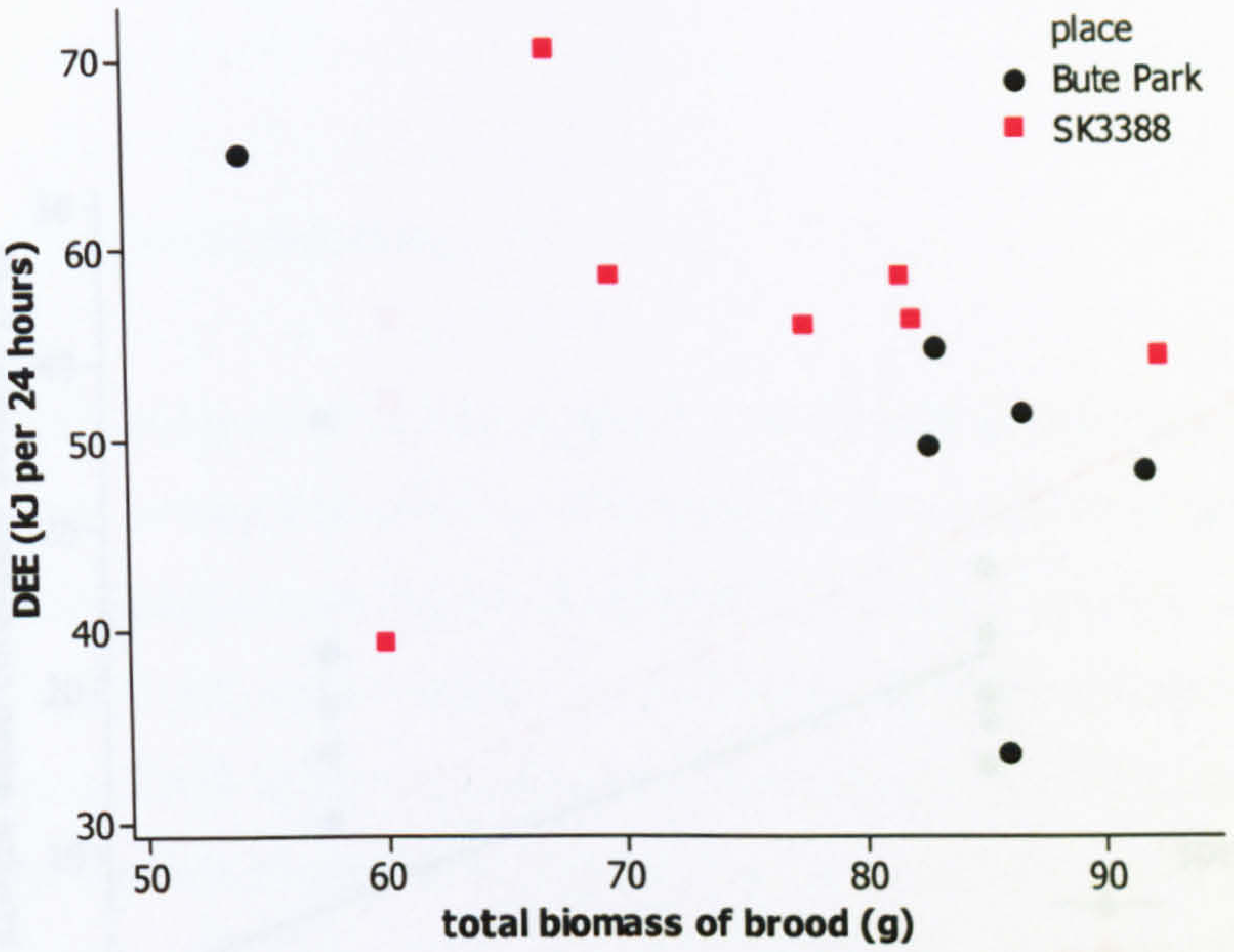


Figure 12.2.5. Relationship between daily energy expenditure (DEE) against total brood biomass in female Blue Tits at SK3388 and Bute Park sites.

There was a significant negative correlation between DEE and date ($r_s = -0.889$, $P = 0.007$, N = 7) but this is probably due to two outlying DEE values. Combining SK3388 and Bute Park data, there was still no significant correlation between DEE and brood biomass although figure 12.2.4 suggests that if outliers are ignored Bute Park birds had generally lower DEE and larger broods than in SK3388. Small samples and lack of formal significance prevent this from being definitively demonstrated.

Figure 12.2.6 suggests that the SK3388 birds presenting larger caterpillars to their chicks (from section 12.1.) might have had correspondingly higher DEE; this might be a reasonable expectation but due to paucity of data the suggestion must be treated with caution. Nonetheless, for both species combined the correlation between per-sample mean caterpillar biomass and DEE is highly significant (Spearman's rank-order correlation $r_s = 0.754$, $P < 0.001$ N = 38). Some of the plotted points on figure 12.2.6 represent overlapping multiple data.

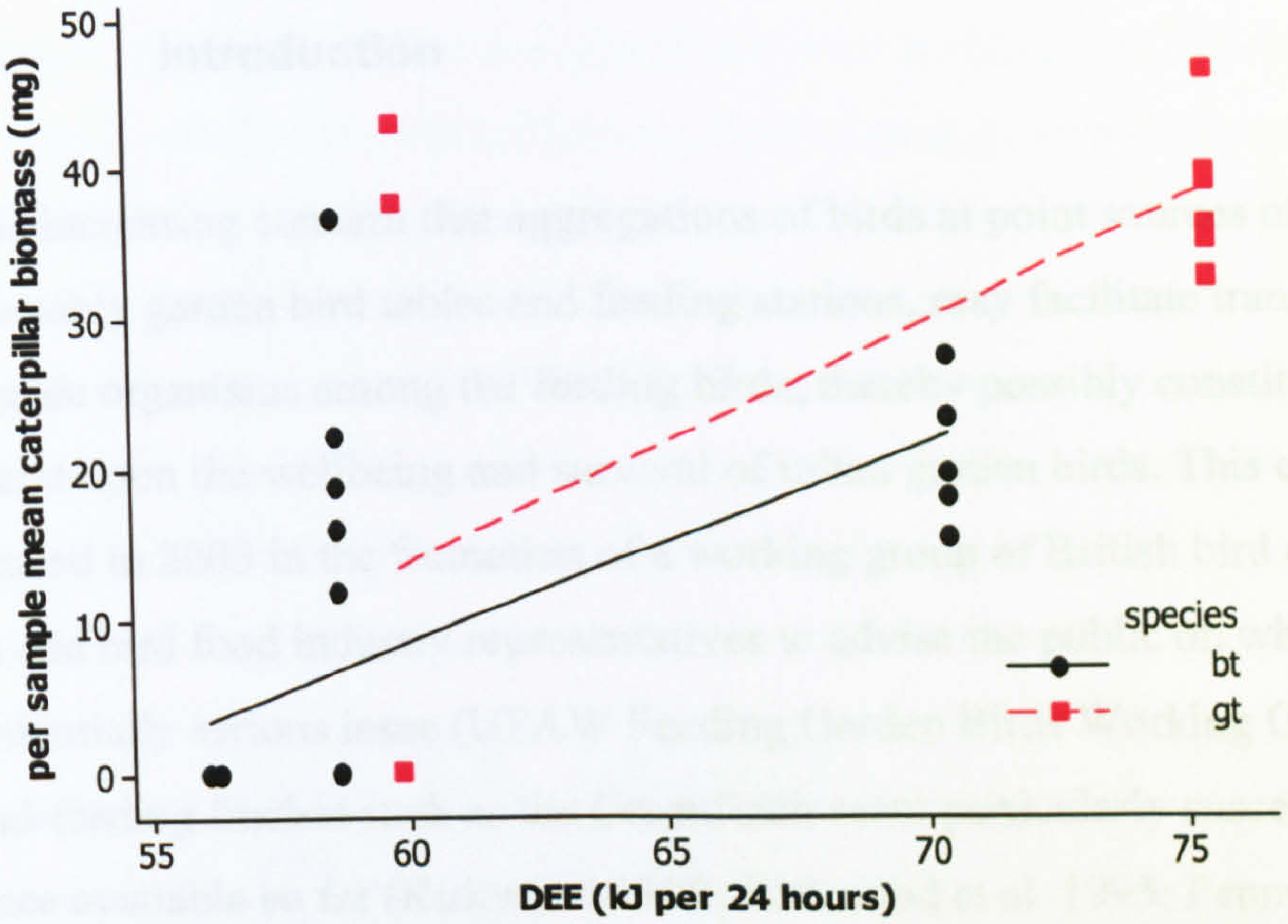


Figure 12.2.6. Relationship between mean per faecal sample biomass (mg) of caterpillars fed to young (section 12.1.) against DEE for female Blue Tits (5 birds, 24 samples) and Great Tits (2 birds, 14 samples) at SK3388 site. OLS regression lines shown, for Great Tit $F_{1,12} = 10.77$, $r^2 = 47{,}3\%$, $P = 0.007$. For Blue Tit $F_{1,22} = 14.31$, $r^2 = 39{,}4\%$, $P = 0.001$.

12.2.5. Conclusions

There is little in the DEE comparisons to suggest that the birds of SK3388 are struggling to provision their chicks, neither are they obviously energetically subsidised. For Great Tits in SK3388, which adapt the diets of their chicks to larger caterpillars (section 12.1), DEE is at the lower end of the observed range whereas for SK3388 Blue Tits which provide similar sized caterpillars to rural conspecifics, DEE is somewhat higher than in Bute Park; lack of formal significance means these observations must be treated with caution. Comparisons with birds from other countries should be treated as for interest only; Corsican Blue Tits, for example, are genetically distinct from north European conspecifics (Kvist et al. 2004).

12.3. Prevalence of infectious disease at bird feeding stations

12.3.1. Introduction

There is increasing concern that aggregations of birds at point sources of anthropogenic food, notably garden bird tables and feeding stations, may facilitate transmission of pathogenic organisms among the feeding birds, thereby possibly constituting a constraint upon the wellbeing and survival of urban garden birds. This concern culminated in 2003 in the formation of a working group of British bird conservation NGOs and bird food industry representatives to advise the public on what is now seen as a potentially serious issue (UFAW Feeding Garden Birds Working Group 2005). Ground-feeding finches such as the Greenfinch seem particularly susceptible and evidence available so far (Kirkwood 1998; Kirkwood et al. 1995; Pennycott et al. 1998) suggests that the main infection threats at British bird feeding stations are *Escherichia coli* (Migula 1895) Castellani and Chalmers, 1919 and *Salmonella* spp., particularly *Salmonella typhimurium* (Loeffler 1892) Castellani and Chalmers, 1919.

Salmonella shed by infected birds can remain viable in dry environments outside its host organisms for weeks or months (International Commission on Microbiological Specifications for Foods 1996) and is likely to be easily transmitted by ingestion or inhalation of fresh or dried faecal material, especially in crowded environments such as busy bird tables. Another transmission mode prevalent in poultry is via infected crop contents passed from adults to young. It can also be transmitted from adult birds to eggs, the embryo dying if levels become too high (Kozlowski et al. 1988). The persistence of *Salmonella* in the environment facilitates environmental sampling for this organism using relatively simple protocols. In this section the prevalence of *Salmonella* at feeding station in the SK3388 study area during the 2002 breeding season, as determined by field sampling, is reported.

12.3.2. Methods

During May and June 2002 twenty-five bird feeding stations in private gardens were sampled, one in each 200m square of the 1 km^2 SK3388 study area (figure 12.3.1) At each feeding station a sample of faecal material was obtained by rolling a sterile transport swab in fresh material and adding any adjacent dryer material to form wherever possible a composite sample of several grams following Pennycott, Cinderey et al (2002). Transport swabs were placed in Amies transport medium (with charcoal) and kept in a normal domestic refrigerator before being collected by staff of the Institute of Zoology, London (IOZ) where they were cultured and screened for *Salmonella* as part of a larger study. In addition, nine cloacal samples were collected during June 2002 from adult House Sparrows (6), Blue Tits (2) and Greenfinch (1) using small sterile transport swabs. again with Amies medium and similarly screened at the IOZ (by M.Pinches, S.K.MacGregor et al).

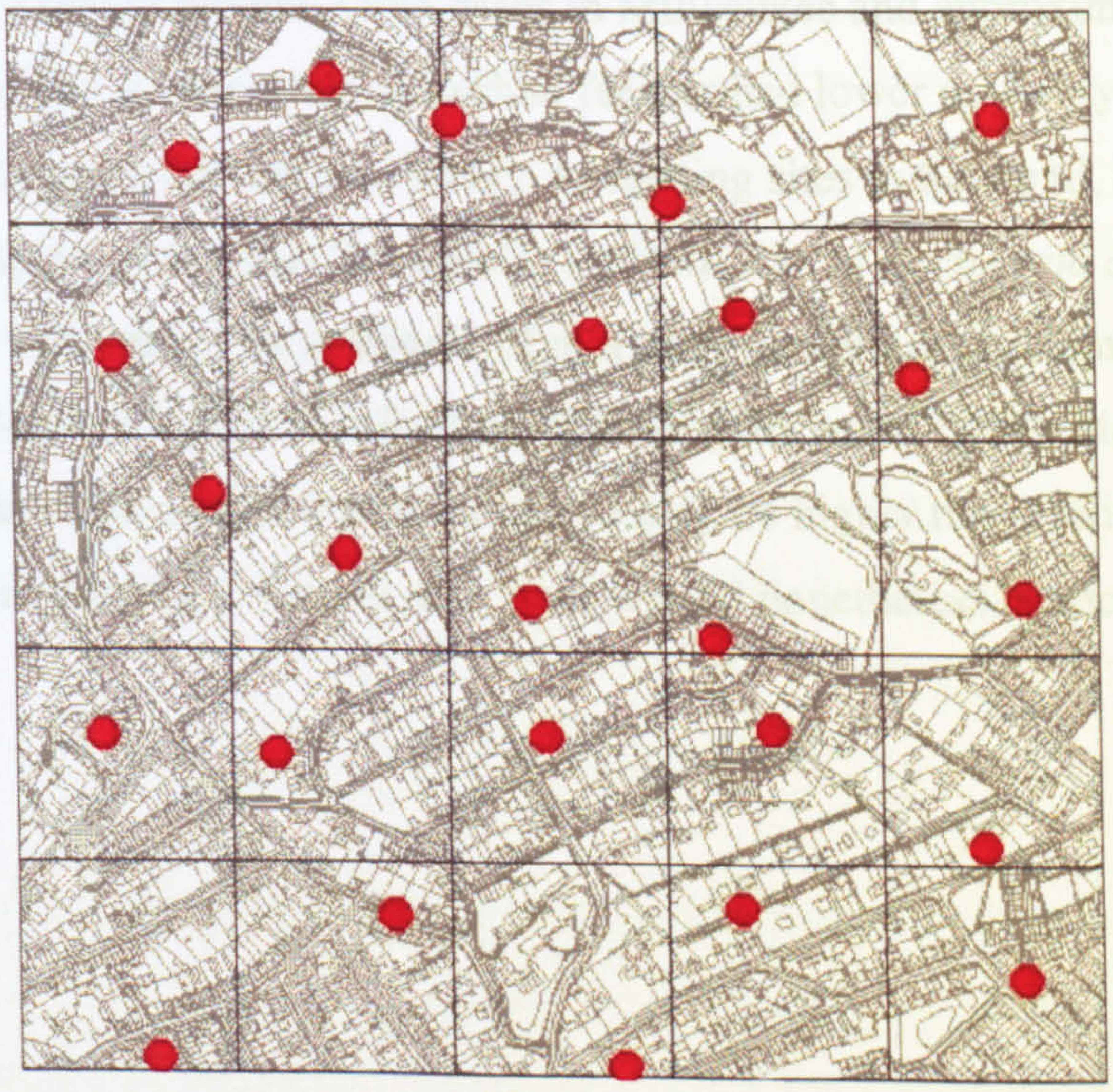


Figure 12.3.1. Locations of the 25 sampled bird feeding stations within the 1km^2 SK3388 study area. Grid squares are 200m × 200m.

12.3.3. Results

All samples submitted to the Institute of Zoology were negative for *Salmonella spp.* (M.Pinches 2002 *pers. comm.*).

12.3.4. Conclusion

This investigation suggests that the transmission of *Salmonella* at garden feeding stations was not a serious problem for birds in SK3388 during 2002. This is supported by the fact that no sickly birds with symptoms characteristic of *Salmonella* infection were observed, trapped or reported during three years of fieldwork in the study area. Nonetheless,, according to Friend et al. (2001) *Salmonella* spp. at feeding stations is a problem of international importance and urban feeding increases opportunities for zoonosis. In Wisconsin, 36% of feeding stations had recurring mortality incidents (Brittingham & Temple 1988a); although the mean death rate through disease and unknown causes was insignificant for a single bird feeder at 1 bird per 21.5 feeder years, the same rate would predict 3,995 cases in Milwaukee and approximately 35 cases in SK3388 in one winter, although urban feeders had lower mortality than busier rural feeders (Brittingham & Temple 1988a). At feeding sites in Scotland, 94 out of 103 deaths were associated with either *Salmonella typhimurium* or *Eschericia coli* (Pennycott et al. 1998) and of 60 incidents of mortality or welfare problems at British feeding stations, 50 were linked to infectious disease (Kirkwood 1998). Many wild bird mortalities go undetected and their true incidence may be higher than realised; despite a negative result in a 'snapshot' sample, this issue should nonetheless be monitored.

13. Synthesis & Conclusions

Abstract

This chapter briefly summarises and brings together the key messages arising from the investigations presented in this thesis, and proposes some future research themes that might build on them effectively. Primary discussions of methodology and conclusions are included within each of the separate analytical chapters.

There are no universal answers to the questions of whether urbanised habitats either presently or potentially support sustainable, representative avifaunas and whether they contribute meaningfully to bird populations and their conservation. This thesis adopted a multi-scale approach, examining on a national scale which birds urbanise and why, then focusing on a particular type of habitat, private gardens, that has been very little-studied, both generally and in an urban context. Fieldwork within this habitat in Sheffield then provided community- and individual-level insights into the ecological opportunities and constraints in operation. Several of the investigations reported are the first of their kind and, as such, point the way for future work.

Chapter two presents the first national scale analysis of relative avian urbanisation accounting formally for spatial autocorrelation. At first sight, the species which did not urbanise are unsurprising but some of the positive species associations seem counter-intuitive, until the marginal habitats associated with urbanisation at the landscape level are considered. Whitethroat is more urban than Feral Pigeon in this analysis but breeds among urban tramlines in Sheffield and in scrub and allotments on the edges of many small towns in which pigeons are scarce (pers obs). Mallard and Moorhen are ubiquitous in urban parks, while Little Ringed Plover breeds among urban mining flashes and gravel pits. This analysis shows that more species associate with urbanisation than previously realised. It also provided, for the first time, a systematic continuous measure of relative urbanisation, which enabled the first comparative analysis of relative urbanisation and brain size that both formally controlled for phylogeny and was not based on simple occurrence data, as reported in chapter three.

This showed that successful urbanisation is not restricted to a handful of the most overtly 'intelligent' species; on the contrary, birds of a wide range of capabilities and lifestyles exploit the opportunities provided by urban habitats. This interpretation is supported by the fact that further preliminary analyses (unpublished) have so far failed to relate the measure of relative urbanisation derived in chapter 2 to any particular ecological traits; this is an obvious avenue for future research.

Turning to private gardens as a particular resource available to birds among human habitation, chapter four shows how trends in their usage rates are related to national population variation for 15 species. For many birds, gardens are an extension of 'natural' habitat, although why a few species such as Greenfinch appear to use them in a different manner remains an open question. Considering urban gardens specifically, chapter five documents a general tendency for reporting rate trends to be more negative in urban gardens than elsewhere (figure 5.1), although urban Dunnocks are doing better; it would be fascinating to discover why. Perhaps even more important would be greater understanding of why the red-listed Song Thrush is apparently doing so poorly in urban gardens, certainly they struggle in SK3388. It may be that factors such as predation by Magpies, which are ubiquitous and still increasing in SK3388, are important issues within urban landscapes, despite the known absence of any significant association of their numbers with declines of their prey species nationally. Researching urban predation is challenging in many ways but is potentially a very important future line of enquiry. Among rural, suburban and urban landscapes, there is notable seasonality in the exploitation rates of gardens. This suggests that a proportion of the birds that use them do not do so all year round, their apparent use by both breeding residents and winter transients is supported by the results of the SK3388 ringing study (below).

Chapter seven presents one of the most detailed studies ever attempted of the breeding avifauna across a substantial area of highly-urbanised residential habitat. It is also one of very few studies that focus on a uniform plot of 'secondary urbanisation' (section 7.2.1), rather than park, city centre or a suburban garden habitats. In this study area, territorial species generally had higher densities than in more highly urbanised habitats but the overall bird density was lower, in particular there were very few pigeons and Starlings compared to city centre study sites. Rapid changes made some densities hard to assess; Magpies were increasing, in opposition to the national trend, Great Tits actively colonising and House Sparrows in rapid decline. Nonetheless, it is clear that

SK3388 supports a viable avifauna but is an intermediate habitat with an assemblage showing characteristic urban duality of stenotopic and eurytopic species; it supports more 'garden' birds but fewer 'urban' birds than core urban habitat.

In view of the rather low overall bird density, further investigation of the ecological constraints that may be limiting this would be extremely valuable. Low take-up of provided nestboxes suggests that holes for tits are not in short supply in SK3388. Negligible use of additional bird feeding stations, experimentally introduced into the study area, and observations during the field survey of numerous unused feeders suggest that energy-rich supplementary food for adults is superabundant. An estimate (unpublished) of daily energy expenditure based on body mass for the entire breeding avifauna of SK3388 (from table 7.18) indicated that all the study area's adult birds of all species could be sustained by just 7 kg of peanuts per day, the total theoretical maximum post-breeding population by 39 kg of peanuts per day. Casual observations suggest that far more than 7 kg of supplementary food is freely available in SK3388 on any one day of the year, but the true provisioning and consumption rates at garden feeding stations remain to be quantified.

The exhaustive mapping of the breeding avifauna undertaken for chapter seven enabled the first spatial analysis of breeding species richness against habitat variables across a large urban study area that controlled formally for spatial autocorrelation, as reported in chapter eight. Cats are often blamed for disrupting the lives of urban birds but their presence does not appear to affect choice of nesting location, although whether they affect subsequent productivity would be another fruitful line of enquiry. The role of supplementary food in the breeding season has also been hotly debated; this study presents, for the first time, clear evidence of a spatial relationship between the presence of year-round food and breeding species richness, controlling for other environmental variables. Even if the habitat is depauperate in, for example, invertebrate prey or nesting cover, introducing high-quality year-round food supplementation may well nonetheless have a substantial effect on bird distribution and perhaps density; a controlled experiment is badly needed.

The work presented in chapters nine to 11 represents an ambitious multi-species investigation into the use of an urban garden habitat by individual birds. Inter-species comparisons of catch rates show that in SK3388 the breeding avifauna is also the feeding avifauna and its composition is rather stable, but transient foragers boost feeder traffic in winter. In other words, birds exploit these gardens exactly as they do larger non-urban gardens, albeit at somewhat lower densities, with the same seasonal pattern; SK3388 is not simply a 'larder' for birds breeding elsewhere. It is also not a habitat in which birds, perhaps attracted by artificial food, simply disappear. Individuals were very persistent at feeders, some generating numerous repeat sightings and individuals of seven species persisting for more than two years. Nor did birds move around the site randomly, they appeared to operate normal territoriality with most re-encountered individuals faithful to particular feeders. At the same time, there clearly is some population exchange with other habitats; the avifauna of SK3388 is not isolated.

Finally, the investigations presented in chapter 12 show how Blue and Great Tits adapt well to urban garden habitats but perhaps in somewhat different ways; an intriguing difference between two species both scoring very highly on the relative brain size scale developed for chapter three (ranked 19/104 and 24/104 respectively), but nonetheless showing differing aspects of ecological versatility in SK3388. Great Tits, newly colonising the study area, seemed to be urbanising through flexibility. Compared to non-urban conspecifics they feed their chicks on caterpillars of very different sizes and their bill shape variation suggest the winter diet of this species in urban habitats may also differ from that in other habitats, the latter result requires confirmation via inter-season comparison of repeat-caught individuals, potentially a fascinating project for any garden ringer.

In contrast, Blue Tits seem to be well-adapted *a priori* to SK3388; their population in the study area is remarkably stable, they maintain higher weights than non-urban conspecifics in the breeding season and manage their weights optimally in winter. In addition, they feed their young with the same sizes and quantities of caterpillars as non-urban birds and do not seem to be struggling to provision their broods, according to DEE measurements. Their main mechanism of adaptation to urban garden habitats is probably regulation of density, which is much lower in SK3388 than the maximum they attain in other habitats. Chapter eight suggests that they and the other territorial species take feeders into account in their spatial distribution; feeders which, according to the last, smallest and simplest investigation reported in chapter 12, are not hotbeds of infectious disease as suggested in some reports, but in fact reasonably hygienic.

In conclusion, the work presented in this thesis further challenges the prevailing anthropomorphic characterisation of urban birds as 'poor little things', 'stuck' in an unfavourable habitat because they have nowhere better to go. Thousands of humans move to cities every day because they perceive better opportunities within them for themselves and their offspring. There is no reason to suppose that birds urbanise any less rationally than humans do, arguably more so, their rationality being ecological rather than sociological. Many cities support high densities of commensal birds and even high-density urban residential areas, if they contain private gardens, can support assemblages of non-urban species of low density but nonetheless similar seasonality, stability and sustainability to the avifaunas of non-urban garden habitats. Furthermore, attempts by human residents to assist these birds with food are apparently neither wasted nor disregarded by the birds in their resource assessments. They clearly influence breeding species' distributions, and the fact that primary feeder-using species such as Blue Tit breed successfully and sustainably in SK3388 casts doubt on suggestions that supplementary food amounts to an ecological trap in urban habitats.

This is not to say that urban birds can be taken for granted, as reported in chapter five a number of species have negative reporting rate trends in urban gardens and two core urban species are now red-listed in the UK, House Sparrow and Starling. Some of the more charismatic species that frequently use suburban gardens, such as Great Spotted Woodpecker and Sparrowhawk, do not breed in SK3388; there is clearly more that can be learnt, and more that can be done. Throughout Sheffield, it is apparent that the regeneration and enhancement of urban quality of life is a grand theme for city planners and residents in the 21st century, yet chapter 6 suggests that urban birds may not be directly benefiting from conservation successes that have improved their lot in other habitats. If urban enhancement can include resources such as good quality year-round food for birds, and regeneration does not cover areas like SK3388 with luxury flats, commanding higher prices than traditional terraced homes with their mosaic of small gardens, then sparse but sustainable avifaunas like that of SK3388 are safe. Not all the signs in Sheffield and other cities are encouraging, but if the garden bird enthusiasts who made the fieldwork reported in this thesis possible have their way, the density, diversity and sustainability of the avifauna of SK33388 are secure and likely to improve.

Appendices

A. Abbreviations and acronyms

ANOVA	Analysis of Variance
AUTOCAT	Program suite for autologistic regression (He et al. 2003)
BBS	BTO/JNCC/RSPB Breeding Bird Survey www.bto.org/bbs
BLABI	Blackbird *Turdus merula.*
BLUTI	Blue Tit *Parus caeruleus*
BTO	British Trust for Ornithology. www.bto.org
CAIC	Program suite: Comparative Analysis via Independent Contrasts www.bio.ic.ac.uk/evolve/software/caic/
CBC	Common Birds Census www.bto.org/survey/cbc
CEH	NERC Centre for Ecology & Hydrology www.ceh.ac.uk
COATI	Coal Tit *Parus ater*
DFA	Discriminant Function Analysis
EDINA	JISC National Data Centre at Edinburgh www.edina.ac.uk
ESF	European Science Foundation. (Bird fat scoring system, Redfern & Clark (2001))
GBW	BTO/CJ Wildbird Foods GardenBirdWatch. www.bto.org/gbw/
GEE	Generalised estimating equations (in regression analysis)
GIS	Geographic Information System
GOLDF	Goldfinch *Carduelis carduelis*
GRETI	Great Tit *Parus major*
HOUSP	House Sparrow *Passer domesticus*
IPMR	Integrated Population Monitoring Recorder. Database package used by bird ringers. www.bto.org/ringing/ringsoft/ipmr/index.htm
IWC	Irish Wildbird Conservancy (now BirdWatch Ireland www.birdwatchireland.ie)
JISC	Joint Information Systems Committee www.jisc.ac.uk
JNCC	Joint Nature Conservation Committee www.jncc.gov.uk
LCM2000	Land Cover Map 2000 www.cs2000.org.uk
LOTTI	Long-tailed Tit *Aegithalos caudatus*
MCL	Monte Carlo Likelihood (in regression analysis)
MCMC-SA	Markov Chain Monte Carlo Stochastic Approach (in regression analysis)
ML	Maximum Likelihood (estimation method in regression analysis)
MPL	Maximum pseudo-likelihood (estimation method in regression analysis)
NERC	Natural Environment Research Council www.nerc.ac.uk
OLS	Ordinary Least Squares (estimation method in regression analysis)
OS/OSGB	Ordnance Survey of Great Britain. www.ordnancesurvey.co.uk
RSPB	Royal Society for the Protection of Birds www.rspb.org.uk
SISKI	Siskin *Carduelis spinus*
SOC	Scottish Ornithologists' Club www.the-soc.zenwebhosting.com

B. Scientific names of organisms

Vernacular name	Scientific name
American Goldfinch	*Carduelis tristis* (L.)
Australian Magpie	*Gymnorhina tibicen* (Latham, 1802)
Barn Owl	*Tyto alba* (Scopoli, 1769)
Black Grouse	*Tetrao tetrix* L.
Black Guillemot	*Cepphus grylle* (L.)
Blackbird	*Turdus merula* L.
Blackcap	*Sylvia atricapilla* (L.)
Black-headed Gull	*Larus ridibundus* L.
Black Redstart	*Phoenicurus ochruros* (S.G.Gmelin, 1774)
Blue Tit	*Parus caeruleus* L., *Cyanistes caeruleus* (Sangster et al. 2005)
Brown Rat	*Rattus norvegicus* (Berkenhout, 1769)
Bullfinch	*Pyrrhula pyrrhula* (L.)
Buzzard	*Buteo buteo* (L.)
(Greater) Canada Goose	*Branta canadensis* (L.)
Carrion Crow & Hooded Crow	*Corvus corone* L. & *Corvus cornix* L.
Chaffinch	*Fringilla coelebs* L.

Chiffchaff	*Phylloscopus collybita* (Vieillot, 1817)
Coal Tit	*Parus ater* L., *Periparus ater* (Sangster et al. 2005)
Collared Dove	*Streptopelia decaocto* (Frivaldszky, 1838)
Common Gull	*Larus canus* L.
Common Sandpiper	*Actitis hypoleucos* L.
Common Tern	*Sterna hirundo* L.
Coot	*Fulica atra* L.
Corn Bunting	*Miliaria calandra* L.
Crossbill & Scottish Crossbill	*Loxia curvirostra* L. & *Loxia scotica* Hartert, 1904
Cuckoo	*Cuculus canorus* L.
Curlew	*Numenius arquata* L.
Dipper	*Cinclus cinclus* L.
Domestic Cat	*Felis silvestris* Schreber, 1775
Dunlin	*Calidris alpina* L.
Dunnock	*Prunella modularis* L.
Dusky Warbler	*Phylloscopus fuscatus* (Blyth, 1842)
Eastern Screech Owl	*Asio otus* (L.)
Eider	*Somateria mollissima* L.
Feral pigeon	*Columba livia* J. F. Gmelin, 1789
(Common) Fig (tree)	*Ficus carica* L.
Fulmar	*Fulmarus glacialis* L.
Garden Warbler	*Sylvia borin* (Boddaert, 1783)
Goldcrest	*Regulus regulus* L.
Golden-cheeked Warbler	*Dendroica chrysoparia* Sclater & Salvin, 1860
Golden Plover	*Pluvialis apricaria*
Goldfinch	*Carduelis carduelis* L.
Goosander	*Mergus merganser* L.
Grasshopper Warbler	*Locustella naevia* (Boddaert, 1783)
Great Black-backed Gull	*Larus marinus* L.
Great Crested Grebe	*Podiceps cristatus* L.
Great Spotted Woodpecker	*Dendrocopos major* L.
Great Tit	*Parus major* L.
Green Woodpecker	*Picus viridis* L.
Greenfinch	*Carduelis chloris* L.
Greenish Warbler	*Phylloscopus trochiloides* (Sundevall, 1837)
Grey Heron	*Ardea cinerea* L.
Grey Partridge	*Perdix perdix* L.
Grey Squirrel	*Sciurus carolinensis* Gmelin, 1788
Grey Wagtail	*Motacilla cinerea* Tunstall, 1771
Greylag Goose	*Anser anser* L.
Hen Harrier	*Circus cyaneus* L.
Herring Gull	*Larus argentatus* Pontoppidan, 1763
Holly Blue (butterfly)	*Celastrina argiolus* (L.)
House Crow	*Corvus splendens* Vieillot, 1817
House Finch	*Carpodacus mexicanus* (Muller, 1776)
House Martin	*Delichon urbica* L., *Delichon urbicum* (Sangster et al. 2005)
House Sparrow	*Passer domesticus* L.
House Wren	*Troglodytes aedon* Vieillot, 1809
Indigo Bunting	*Passerina cyanea* (L.)
Italian Sparrow	*Passer domesticus italiae*
Jackdaw	*Corvus monedula* L.
Jay	*Garrulus glandarius* L.
Kestrel	*Falco tinnunculus* L.
Kingfisher	*Alcedo atthis* L.
Lapwing	*Vanellus vanellus* L.
Large White (butterfly)	*Pieris brassicae* (L.)
Lesser Black-backed Gull	*Larus fuscus* L.
Lesser Redpoll	*Carduelis cabaret* L.
Lesser Spotted Woodpecker	*Dendrocopos minor* L.
Lesser Whitethroat	*Sylvia curruca* L.
Linnet	*Carduelis cannabina* L.
Little Grebe	*Tachybaptus ruficollis* (Pallas, 1764)
Little Owl	*Athene noctua* (Scopoli, 1769)
Little Ringed Plover	*Charadrius dubius* Scopoli, 1786
London Plane (tree)	*Platanus x acerifolia* (Aiton) Willd.
Long-eared Owl	*Asio otus* L.
Long-tailed Tit	*Aegithalos caudatus* L.

Magpie	*Pica pica* L.
Mallard	*Anas platyrhynchos* L.
Marsh Tit	*Parus palustris* L., *Poecile palustris* (Sangster et al. 2005)
Meadow Pipit	*Anthus pratensis* L.
Merlin	*Falco columbarius* L.
Mistle Thrush	*Turdus viscivorus* L.
Moorhen	*Gallinula chloropus* L.
Mourning Dove	*Zenaida macroura* (L.)
Mute Swan	*Cygnus olor* (J. F. Gmelin, 1789)
Nightingale	*Luscinia megarhynchos* (Brehm, 1831)
Nightjat	*Caprimulgus europaeus* L.
Noisy Miner	*Manorina melanocephala* (Latham, 1802)
Northern Cardinal	*Cardinalis cardinalis* (L.)
Nutcracker	*Nucifraga caryocatactes* (L.)
Nuthatch	*Sitta europaea* L.
Oriental Plane (tree)	*Platanus orientalis* L.
Oystercatcher	*Haematopus ostralegus* L.
Peregrine	*Falco peregrinus* Tunstall, 1771
Pheasant	*Phasianus colchicus* L.
Pied Flycatcher	*Ficedula hypoleuca* (Pallas, 1764)
Pied Wagtail	*Motacilla alba* L.
Raven	*Corvus corax* L.
Red-breasted Merganser	*Mergus serrator* L.
Red-legged Partridge	*Alectoris rufa* L.
Red-winged Blackbird	*Agelaius phoenicius* (L.)
Redshank	*Tringa totanus* L.
Redstart	*Phoenicurus phoenicurus* L.
Reed Bunting	*Emberiza schoeniclus* L.
Reed Warbler	*Acrocephalus scirpaceus* (Hermann, 1804)
Ring-billed Gull	*Larus delawarensis* Ord, 1815
Ring Ouzel	*Turdus torquatus* L.
Ringed Plover	*Charadrius hiaticula* L.
(Greater) Roadrunner	*Geococcyx californianus* (Lesson, 1829)
Robin	*Erithacus rubecula* L.
Rock Pipit	*Anthus petrosus* (Montagu, 1798)
Rook	*Corvus frugilegus* L.
Rufous collared Sparrow	*Zonotrichia capensis* (Muller 1776)
Sand Martin	*Riparia riparia* L.
Sedge Warbler	*Acrocephalus schoenobaenus* L.
Serin	*Serinus serinus* (L.)
Shag	*Phalacrocorax aristotelis* L.
Shelduck	*Tadorna tadorna* L.
Short-eared Owl	*Asio flammeus* (Pontoppidan, 1763)
Siskin	*Carduelis spinus* L.
Skylark	*Alauda arvensis* L.
Small White (butterfly)	*Pieris rapae* (L.)
Snipe	*Gallinago gallinago* L.
Song Sparrow	*Melospiza melodia* (Wilson, 1810)
Song Thrush	*Turdus philomelos* Brehm, 1831
Sparrowhawk	*Accipiter nisus* (L.)
Spotted Flycatcher	*Muscicapa striata* (Pallas, 1764)
Speckled Pigeon	*Columba guinea* L.
Starling	*Sturnus vulgaris* L.
Stickleback	*Gasterosteus aculeatus* L.
Stock Dove	*Columba oenas* L.
Stonechat	*Saxicola torquata* L.
Swainson's Hawk	*Buteo swainsoni* Bonaparte, 1838
Swallow	*Hirundo rustica* L.
Swift	*Apus apus* L.
Tawny Owl	*Strix aluco* L.
Teal	*Anas crecca* L.
Thrush Nightingale	*Luscinia luscinia* (L.)
Torresian Crow	*Corvus orru* Bonaparte, 1850
Tree Pipit	*Anthus trivialis* L.
Tree Sparrow	*Passer montanus* L.
Treecreeper	*Certhia familiaris* L.
Tufted Duck	*Aythya fuligula* L.

Turtle Dove	*Streptopelia turtur* L.
Twite	*Carduelis flavirostris* L.
Wheatear	*Oenanthe oenanthe* L.
Whinchat	*Saxicola rubetra* L.
White-collared Pigeon	*Columba albitorques* Ruppell, 1837
Whitethroat	*Sylvia communis* Latham, 1787
Willow Tit	*Parus montanus* L., *Poecile montanus* (Sangster et al. 2005)
Willow Warbler	*Phylloscopus trochilus* L.
Willow/Red Grouse	*Lagopus lagopus* L.
Wood Duck	*Aix* sponsa (L.)
Wood Mouse	*Apodemus sylvaticus* (L.)
Wood Warbler	*Phylloscopus sybillatrix* (Bechstein, 1793)
Woodcock	*Scolopax rusticola* L.
Woodpigeon	*Columba palumbus* L.
Wren	*Troglodytes troglodytes* L.
Yellow Wagtail	*Motacilla flava* L.
Yellowhammer	*Emberiza citrinella* L.

Appendix C.

Supplementary figures for chapter 4.

Figures S1.1 – S1.40. Weekly reporting rates calculated from original data ('noisy' plots) and probabilities of occurrence predicted by 'minimum adequate' GEE models ('smooth' plots). Week numbers 1 – 416 run from January 1995 to December 2002. Models using 'all sites' data (black) are plotted for all species. Raw data and model results using 'species positive' data (dotted) are additionally plotted for species in which there is either a gain or loss of formal significance in the year term or an improvement in data dispersion, or an interesting difference in the form of the two plots.

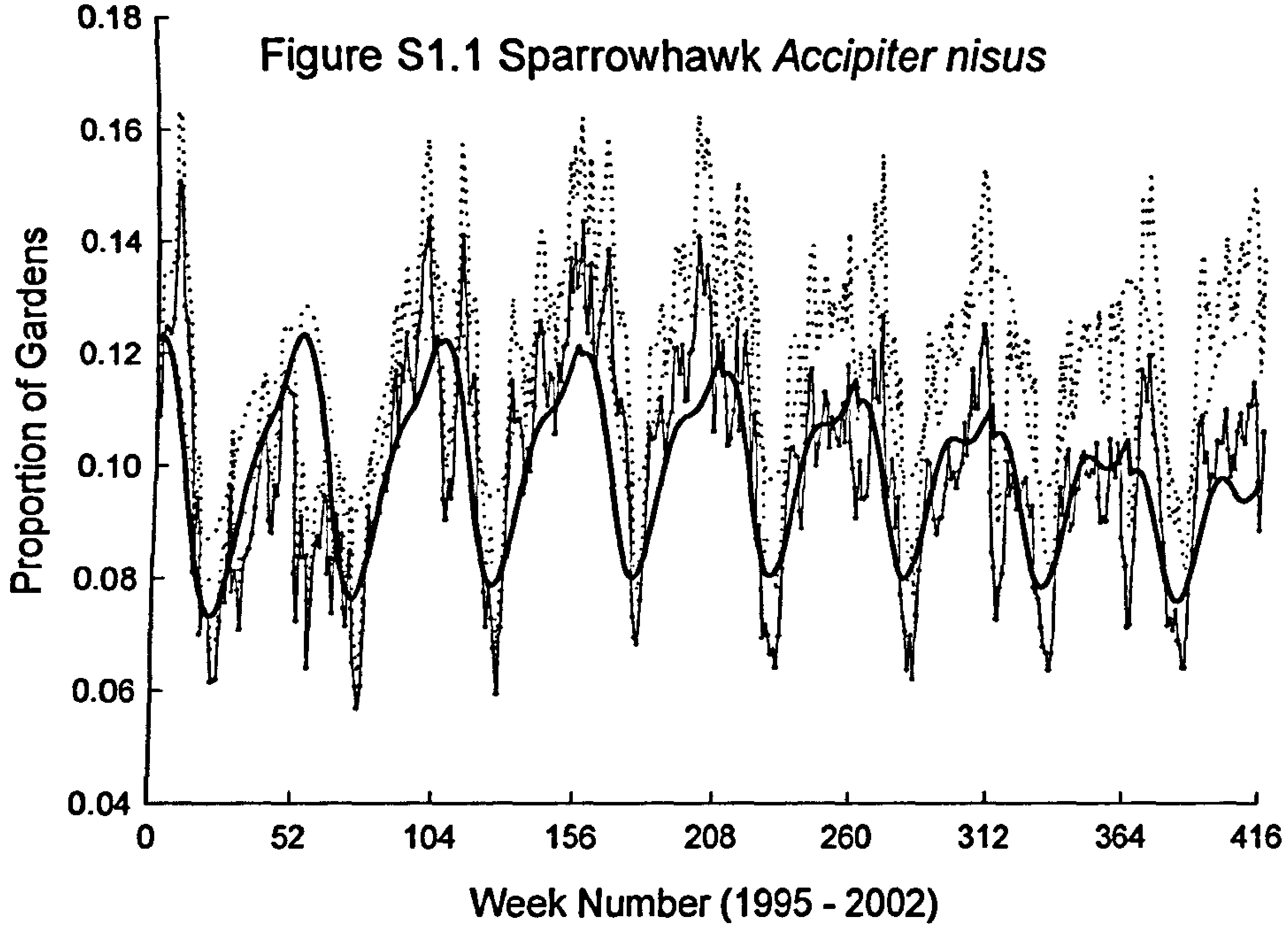


Figure S1.1 Sparrowhawk *Accipiter nisus*

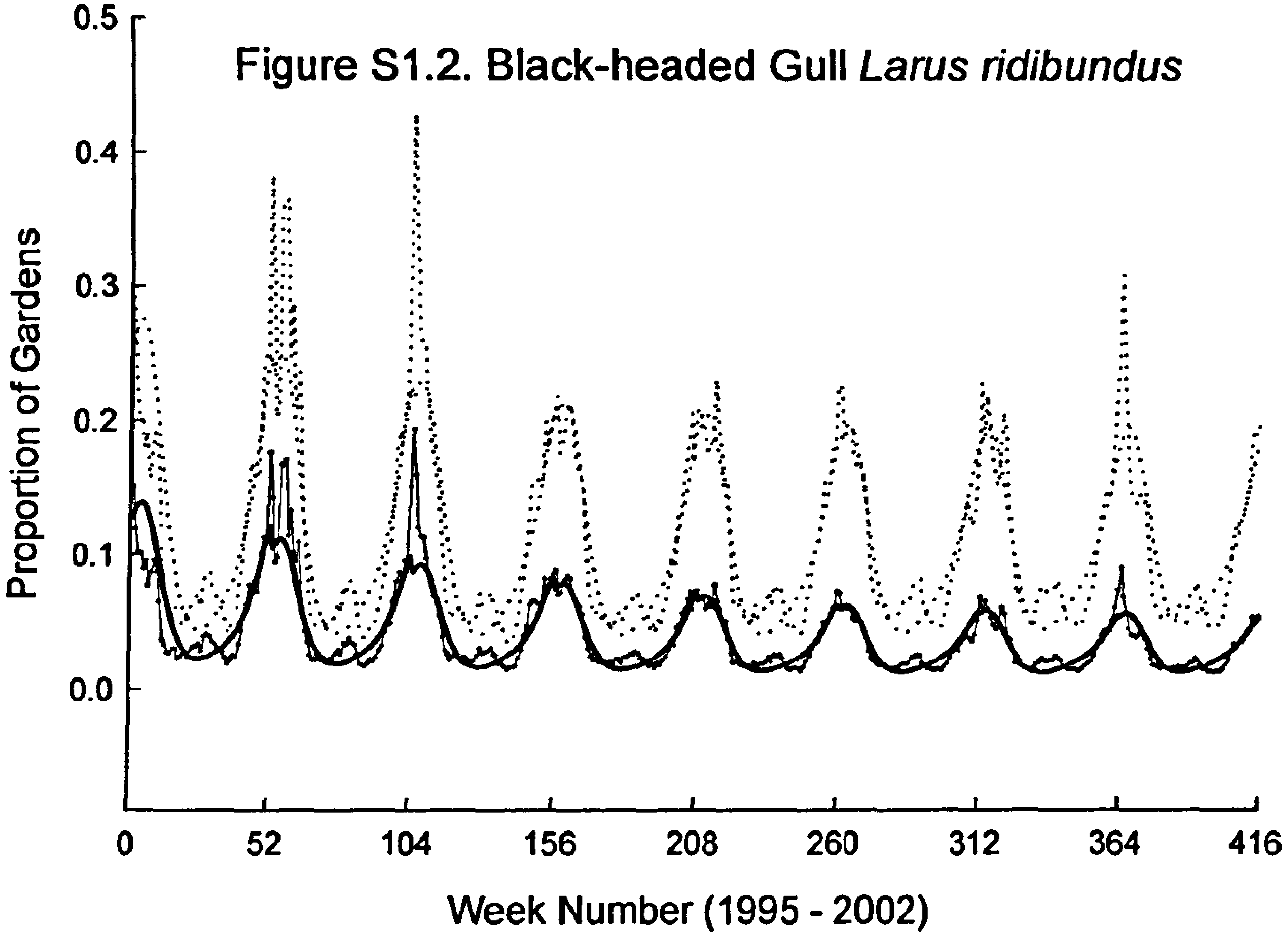


Figure S1.2. Black-headed Gull *Larus ridibundus*

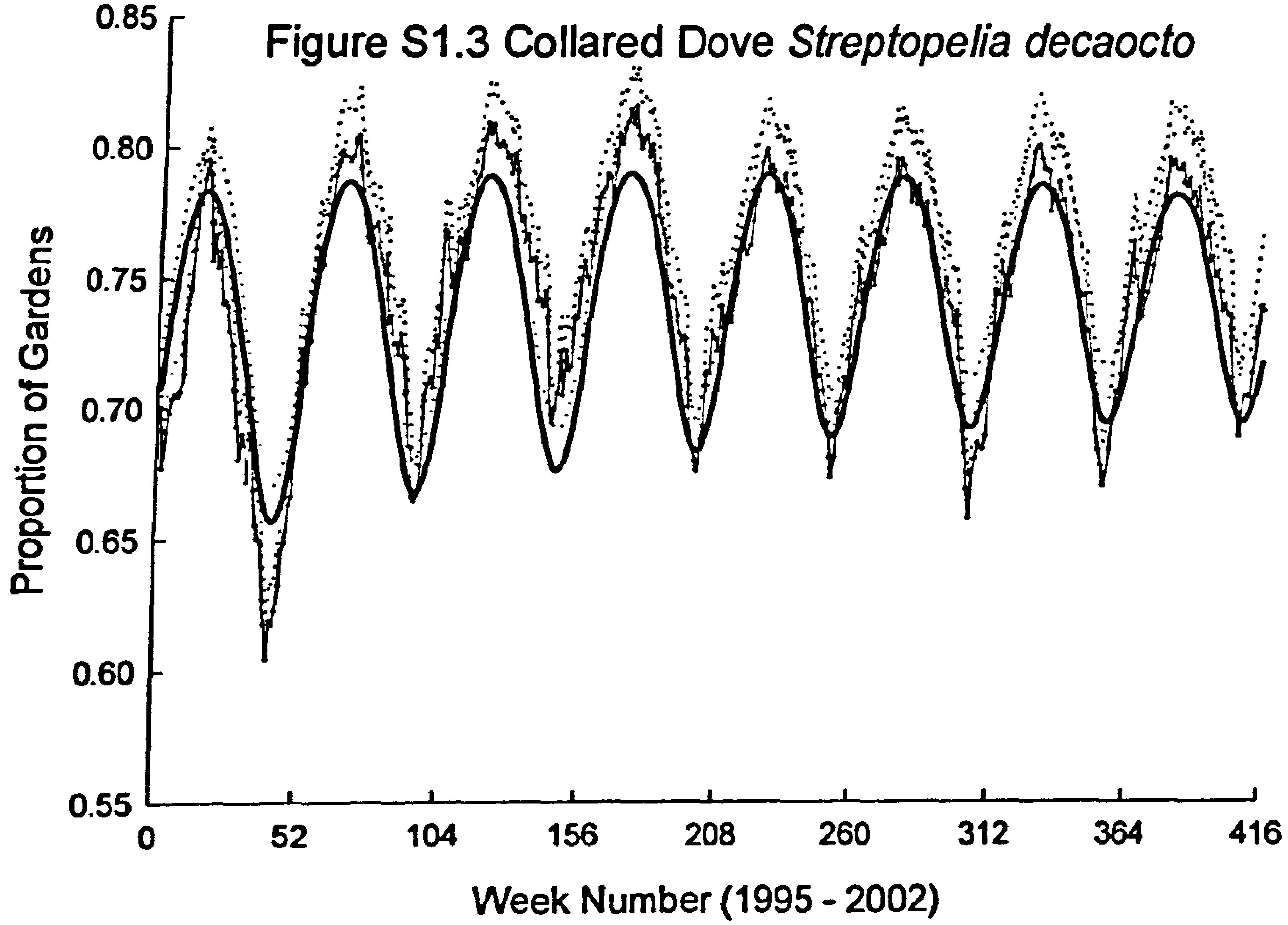


Figure S1.3 Collared Dove *Streptopelia decaocto*

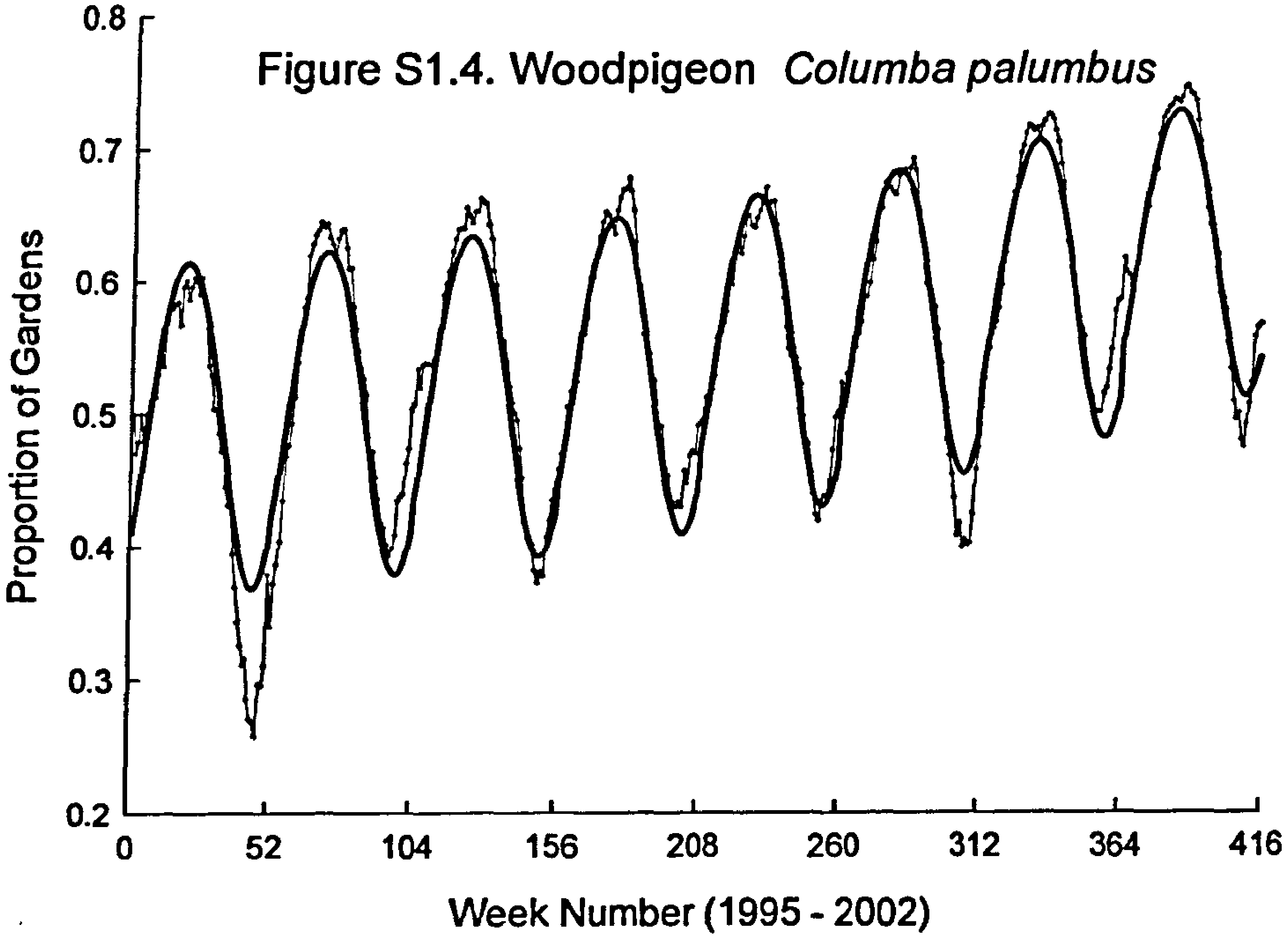


Figure S1.4. Woodpigeon *Columba palumbus*

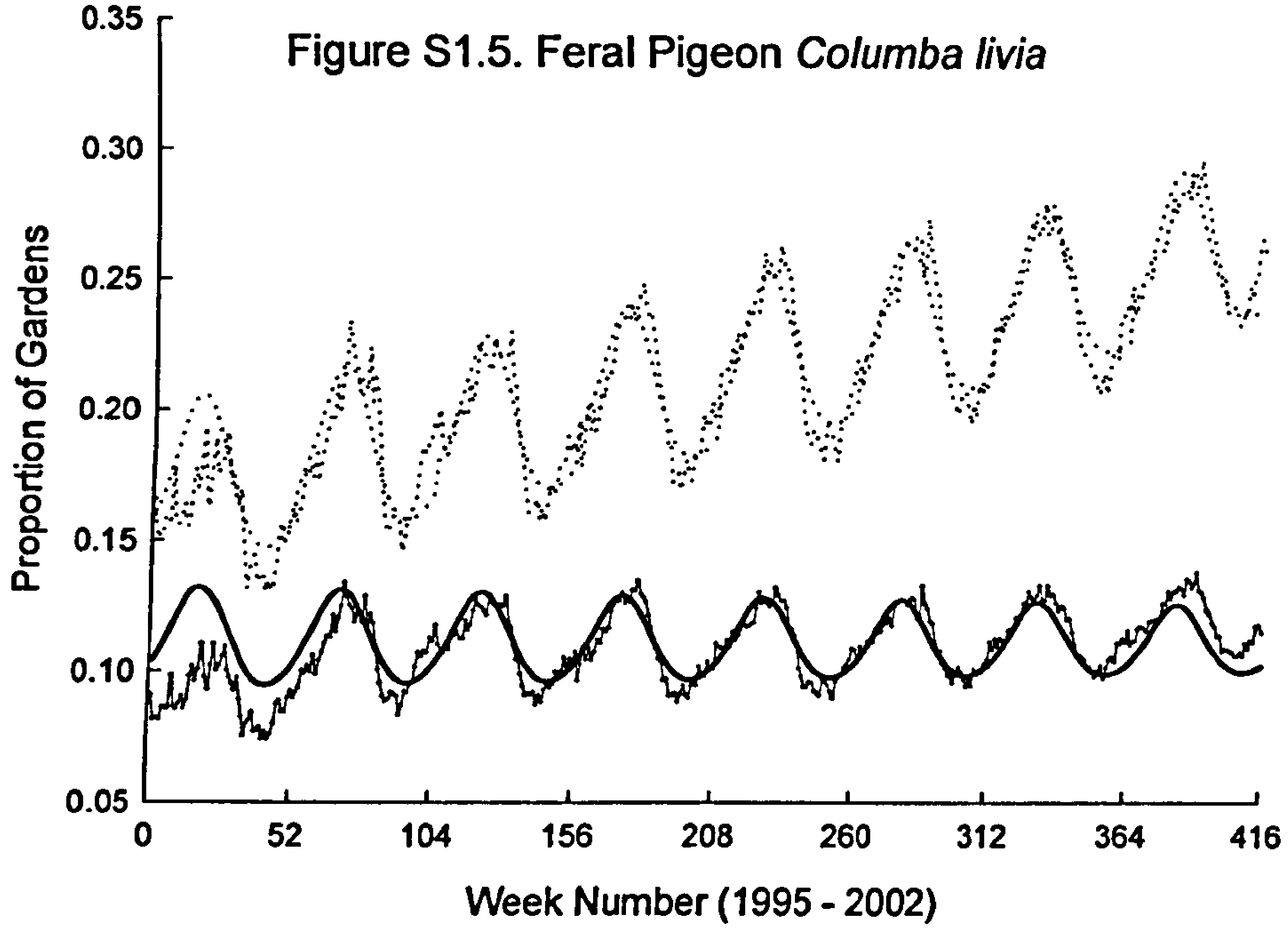


Figure S1.5. Feral Pigeon *Columba livia*

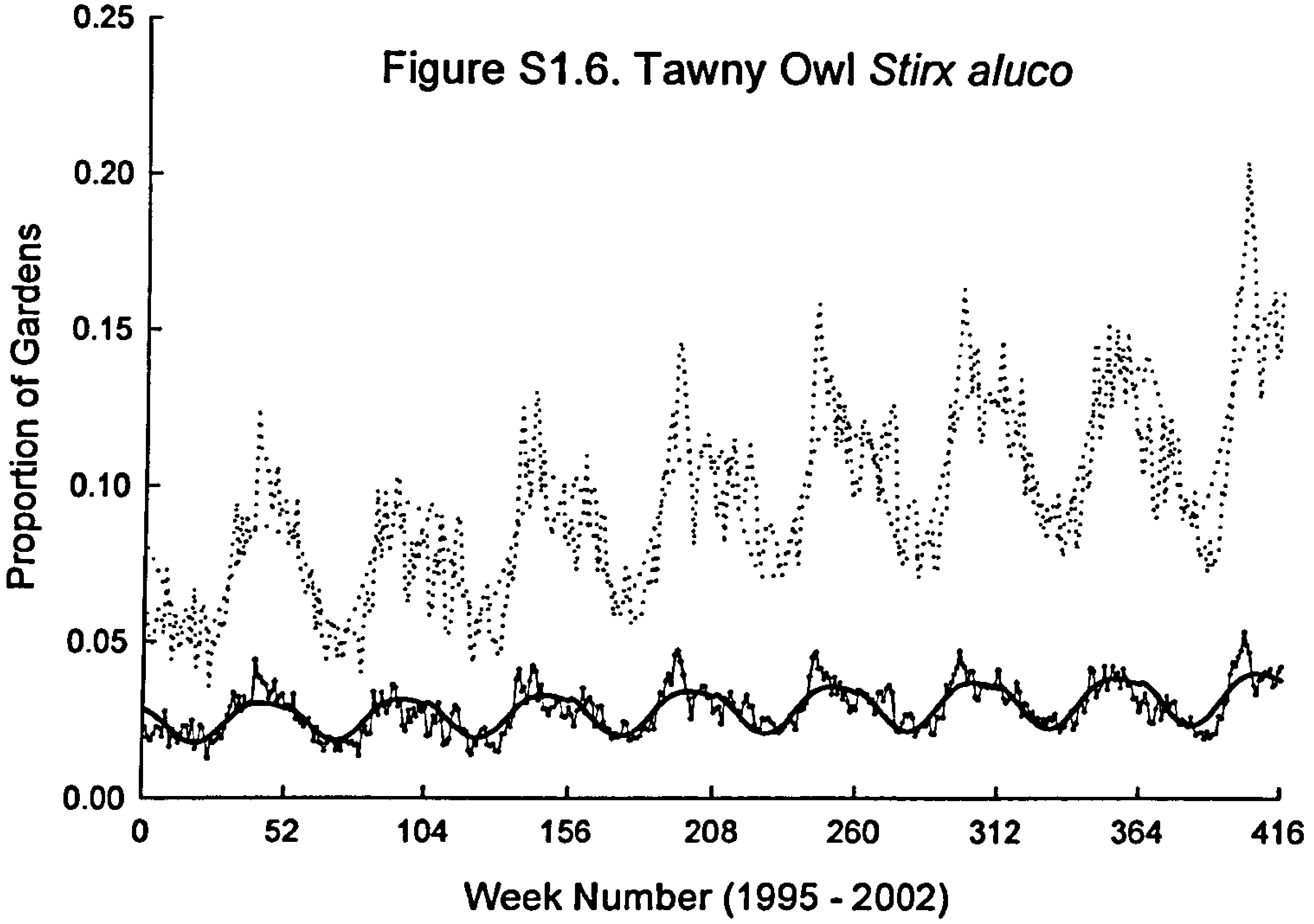


Figure S1.6. Tawny Owl *Stirx aluco*

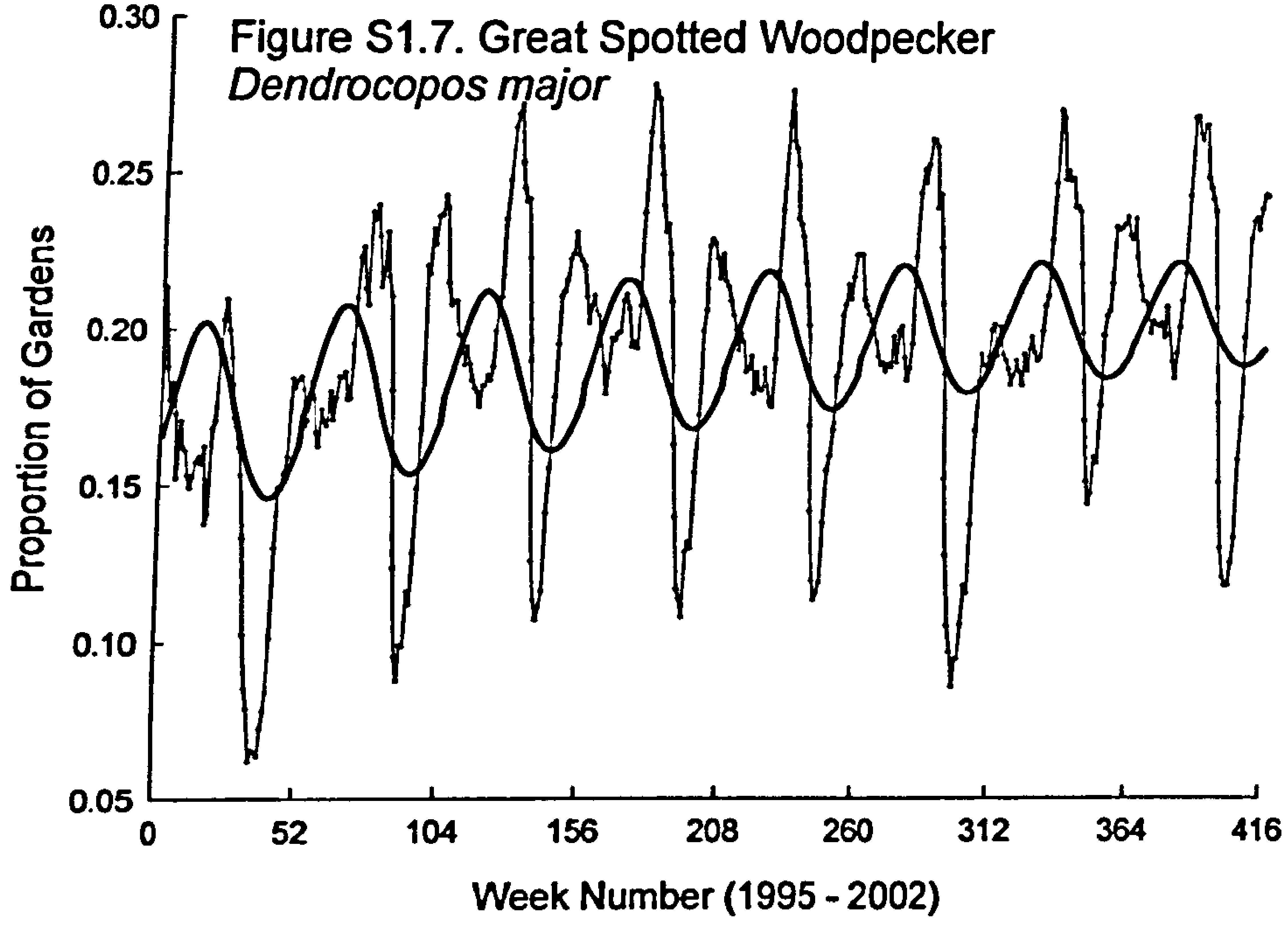


Figure S1.7. Great Spotted Woodpecker *Dendrocopos major*

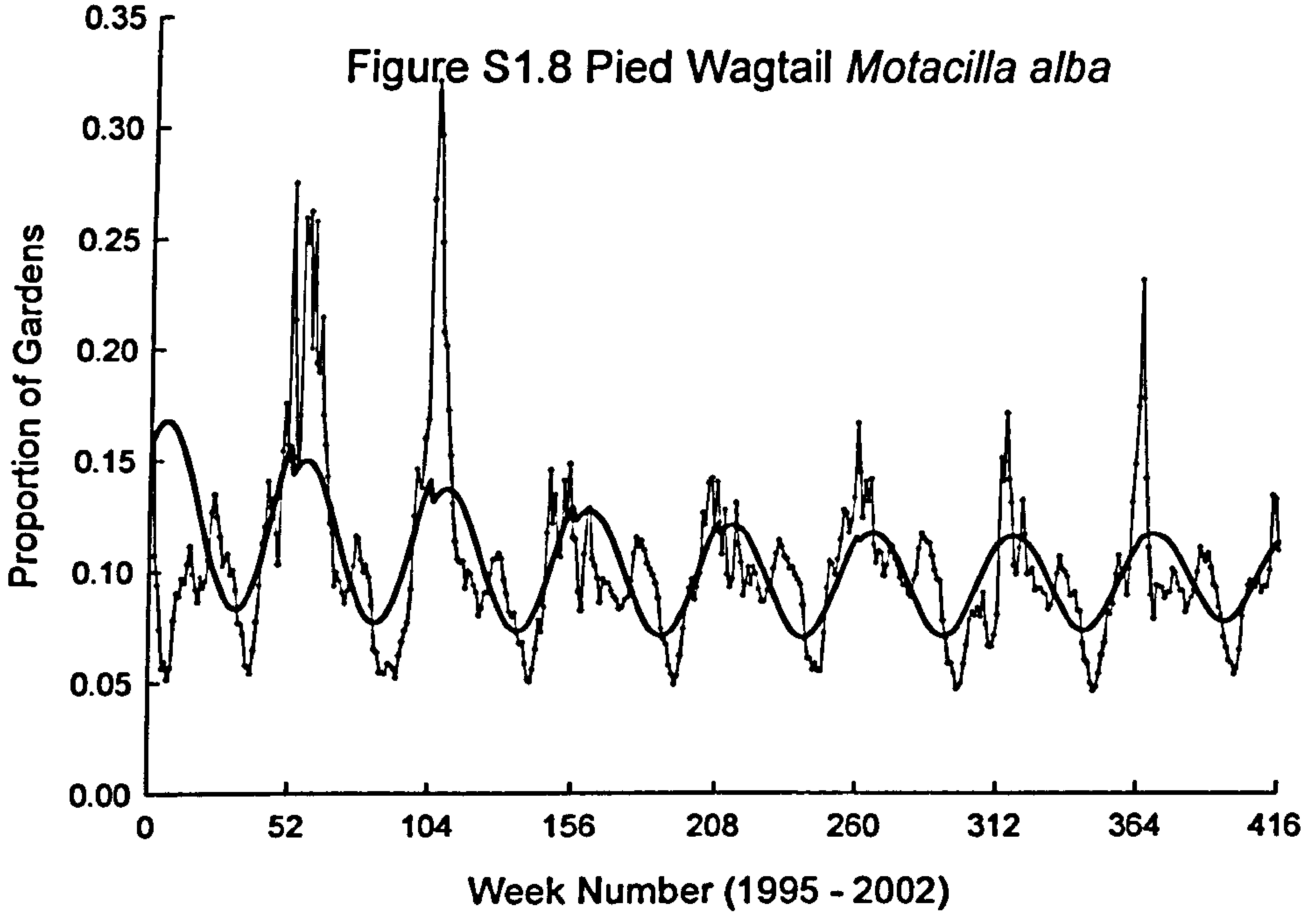


Figure S1.8 Pied Wagtail *Motacilla alba*

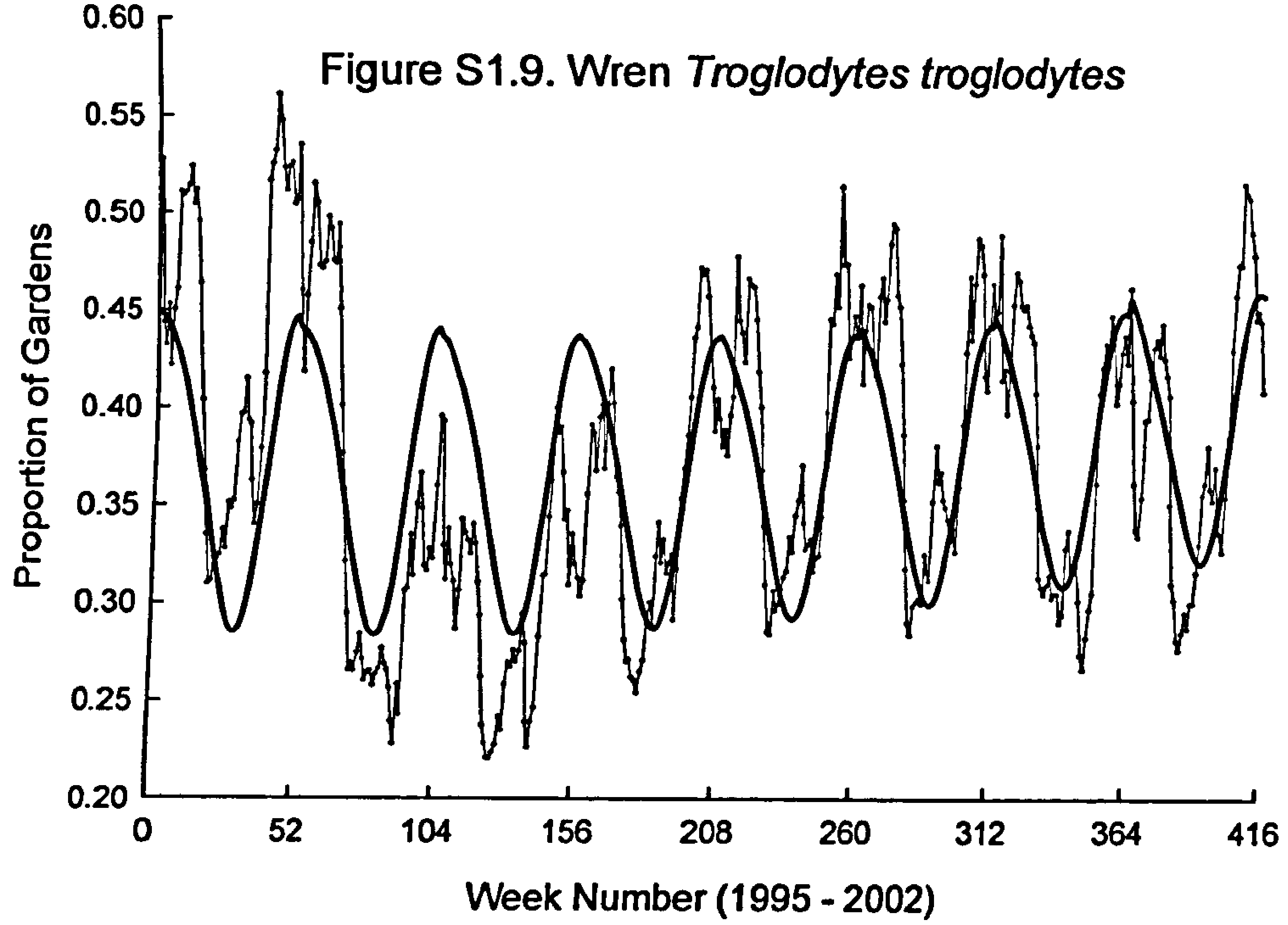


Figure S1.9. Wren *Troglodytes troglodytes*

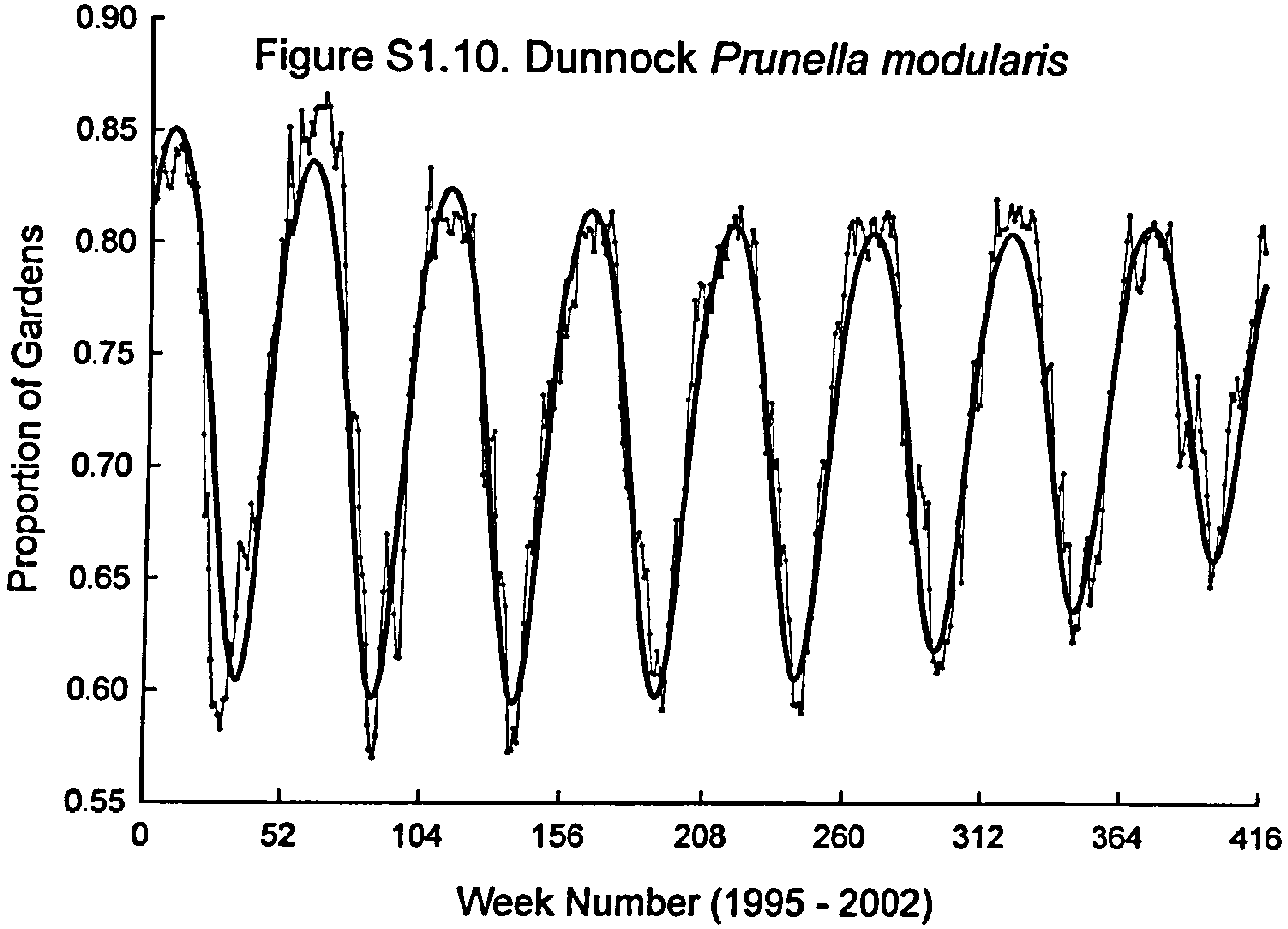


Figure S1.10. Dunnock *Prunella modularis*

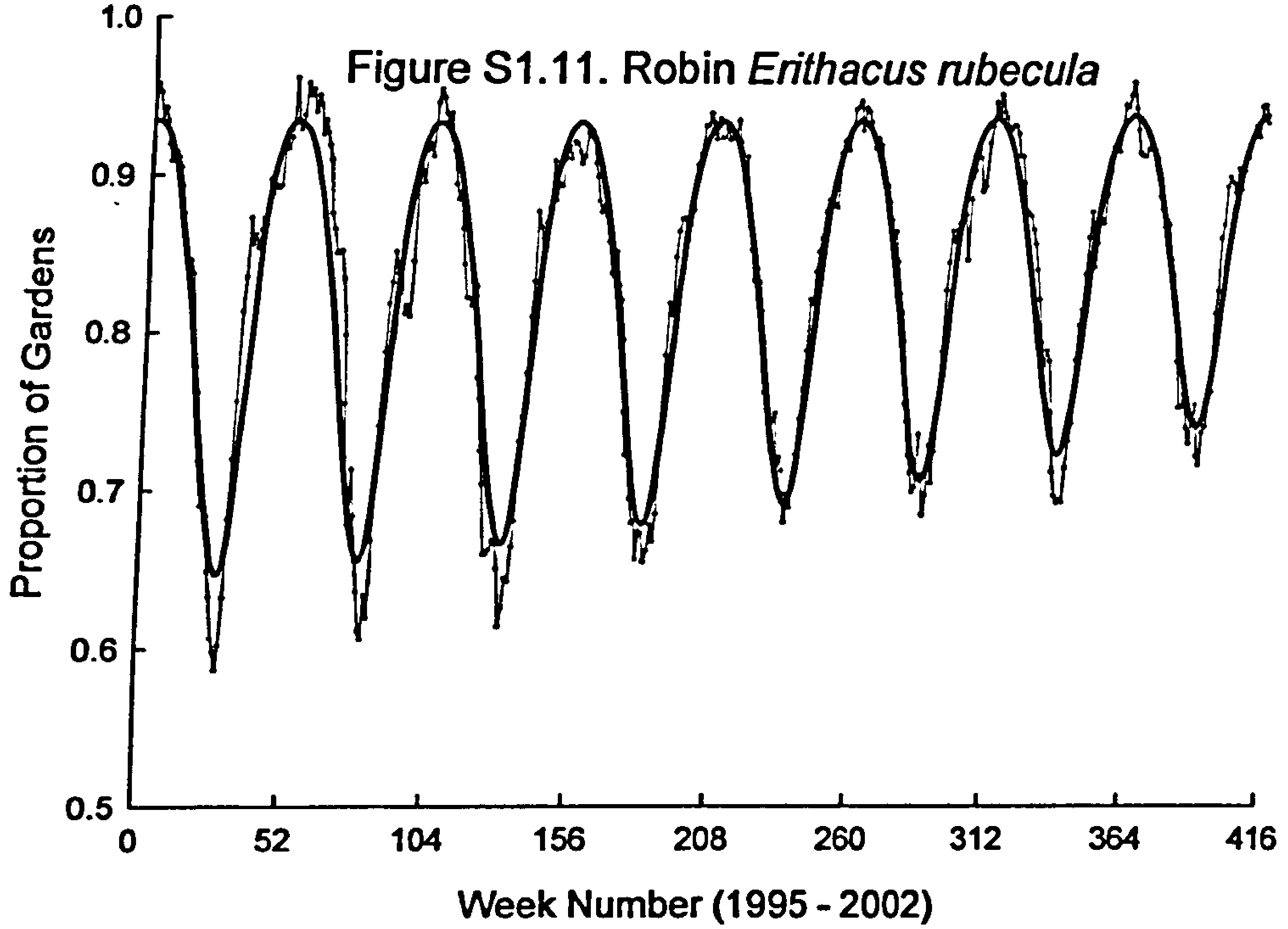


Figure S1.11. Robin *Erithacus rubecula*

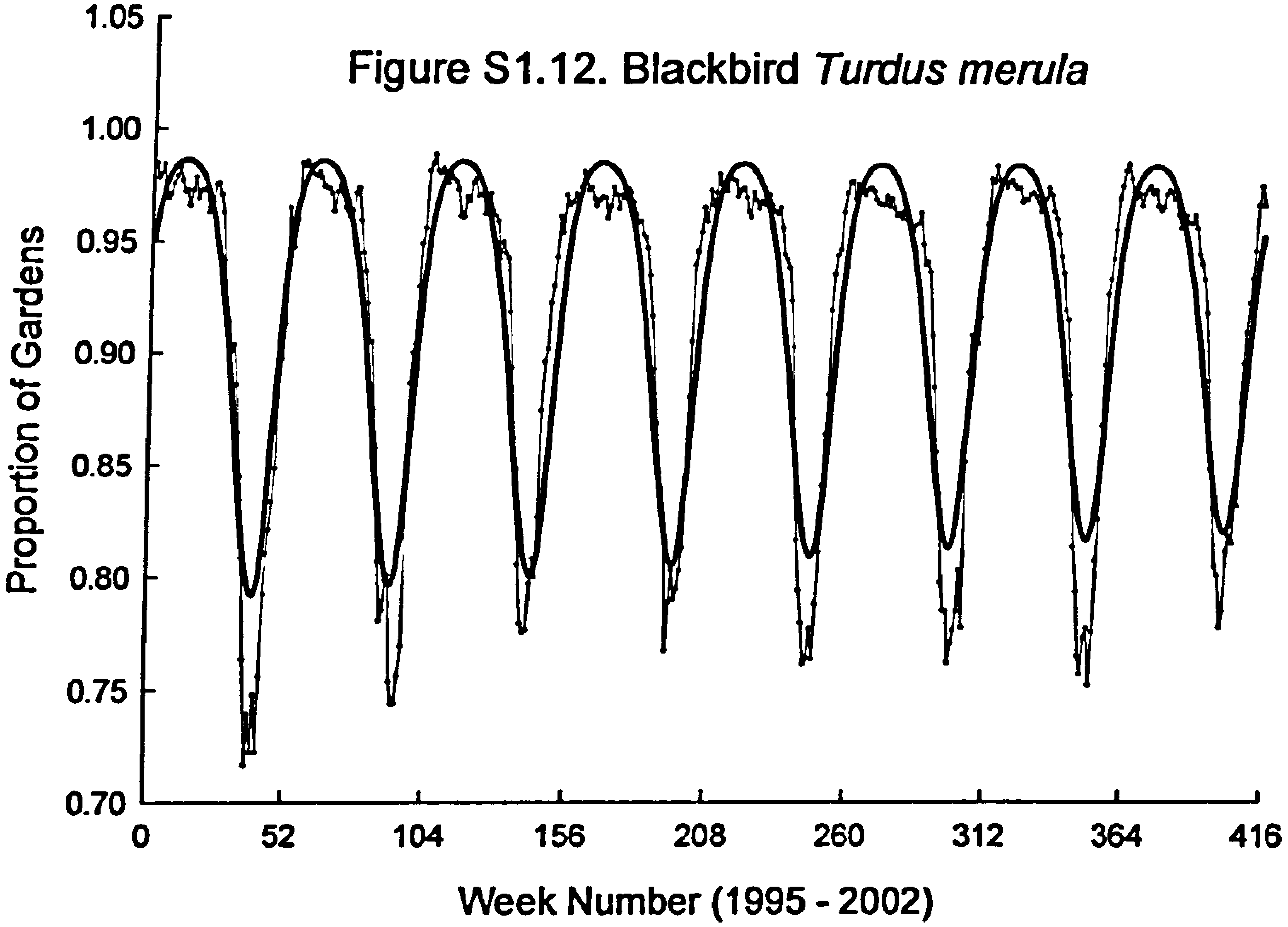


Figure S1.12. Blackbird *Turdus merula*

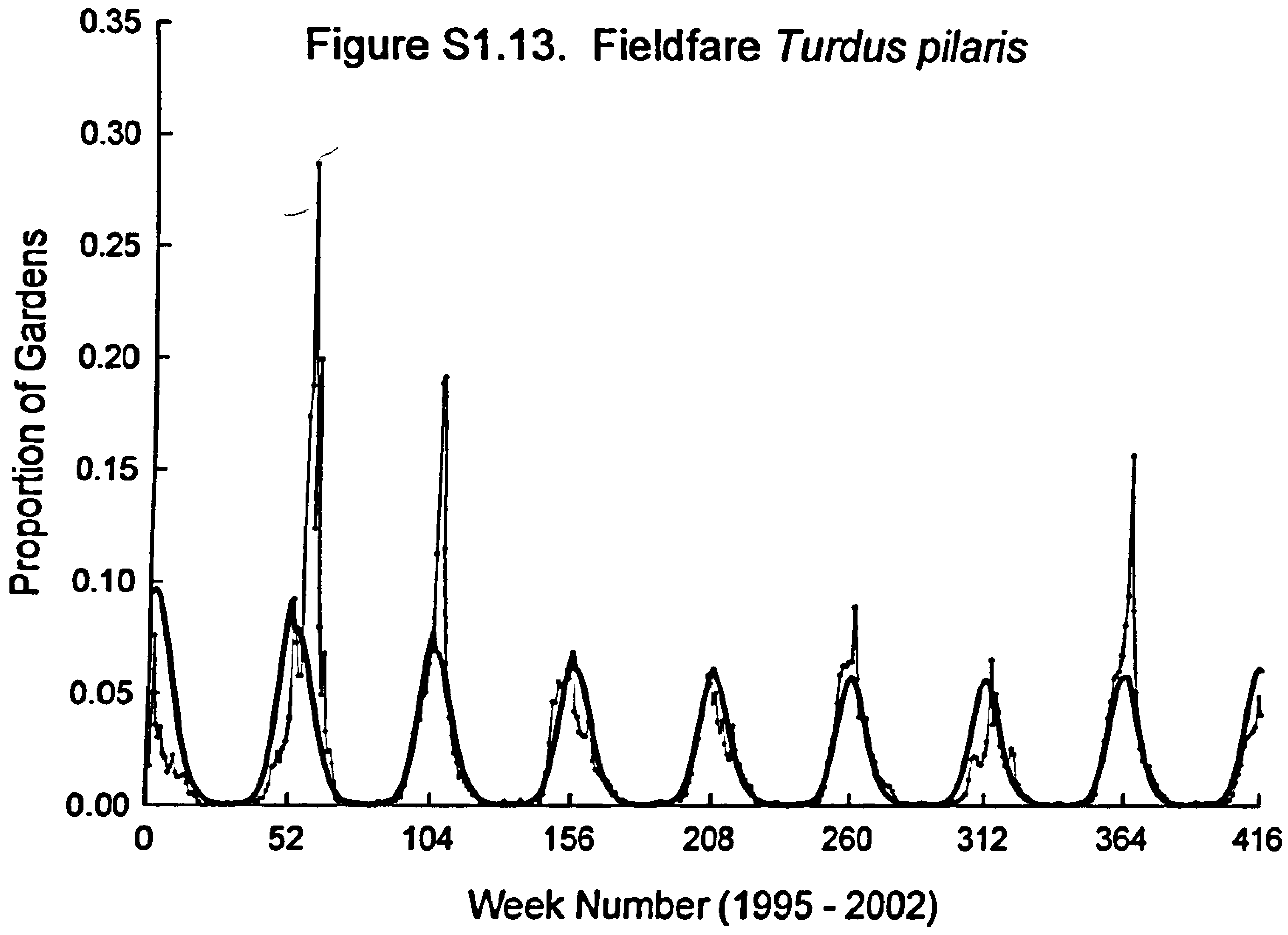


Figure S1.13. Fieldfare *Turdus pilaris*

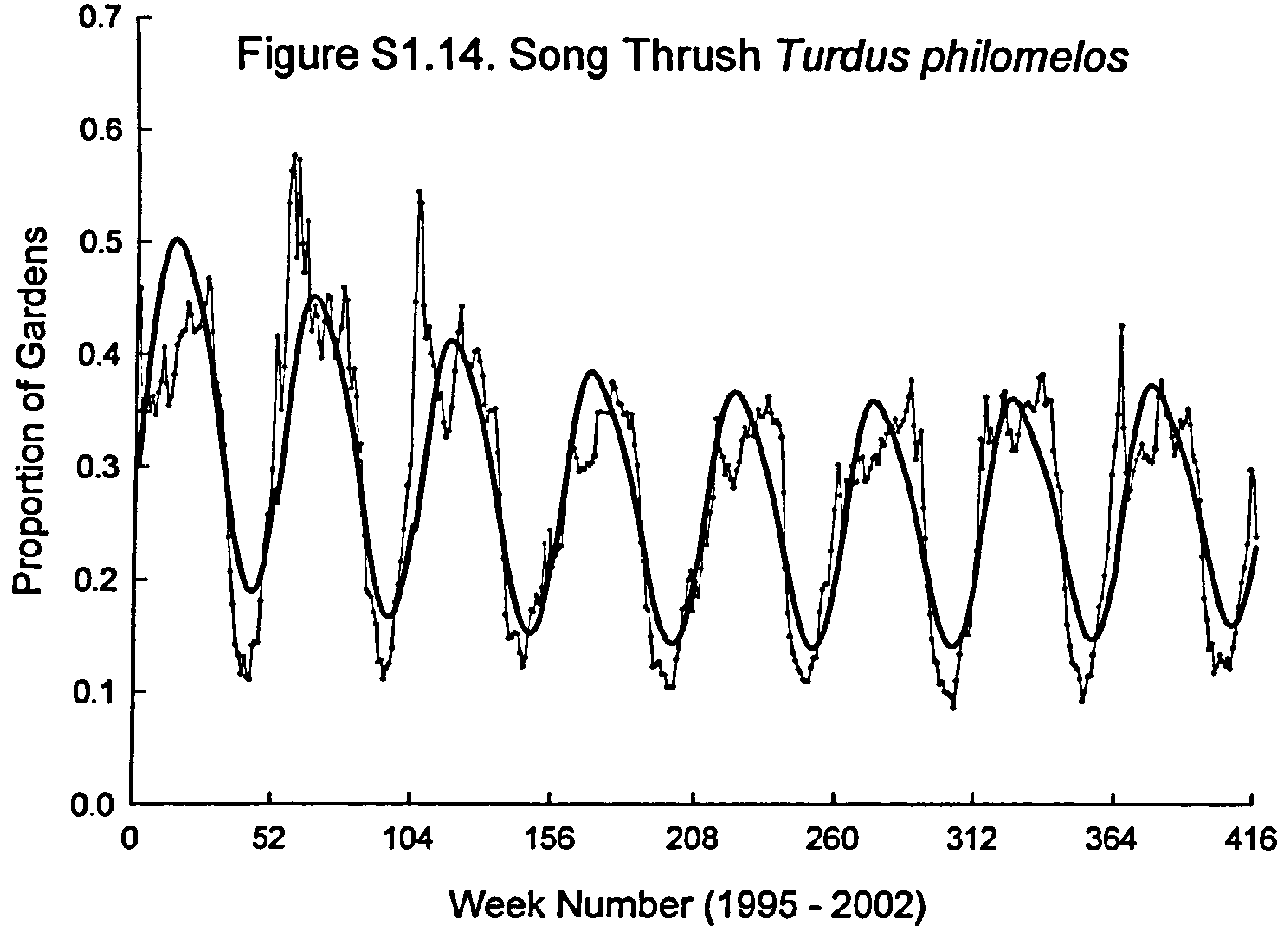


Figure S1.14. Song Thrush *Turdus philomelos*

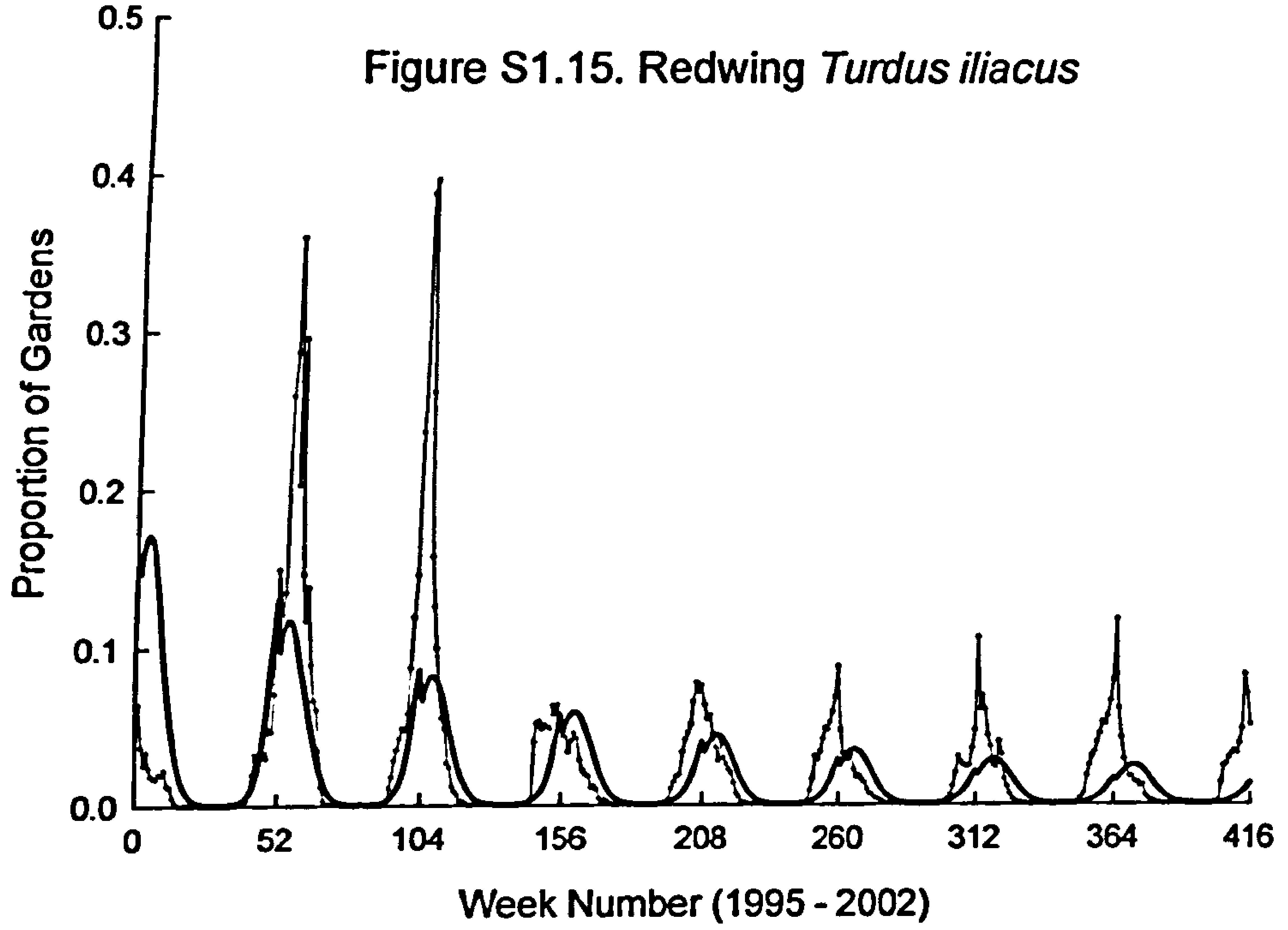


Figure S1.15. Redwing *Turdus iliacus*

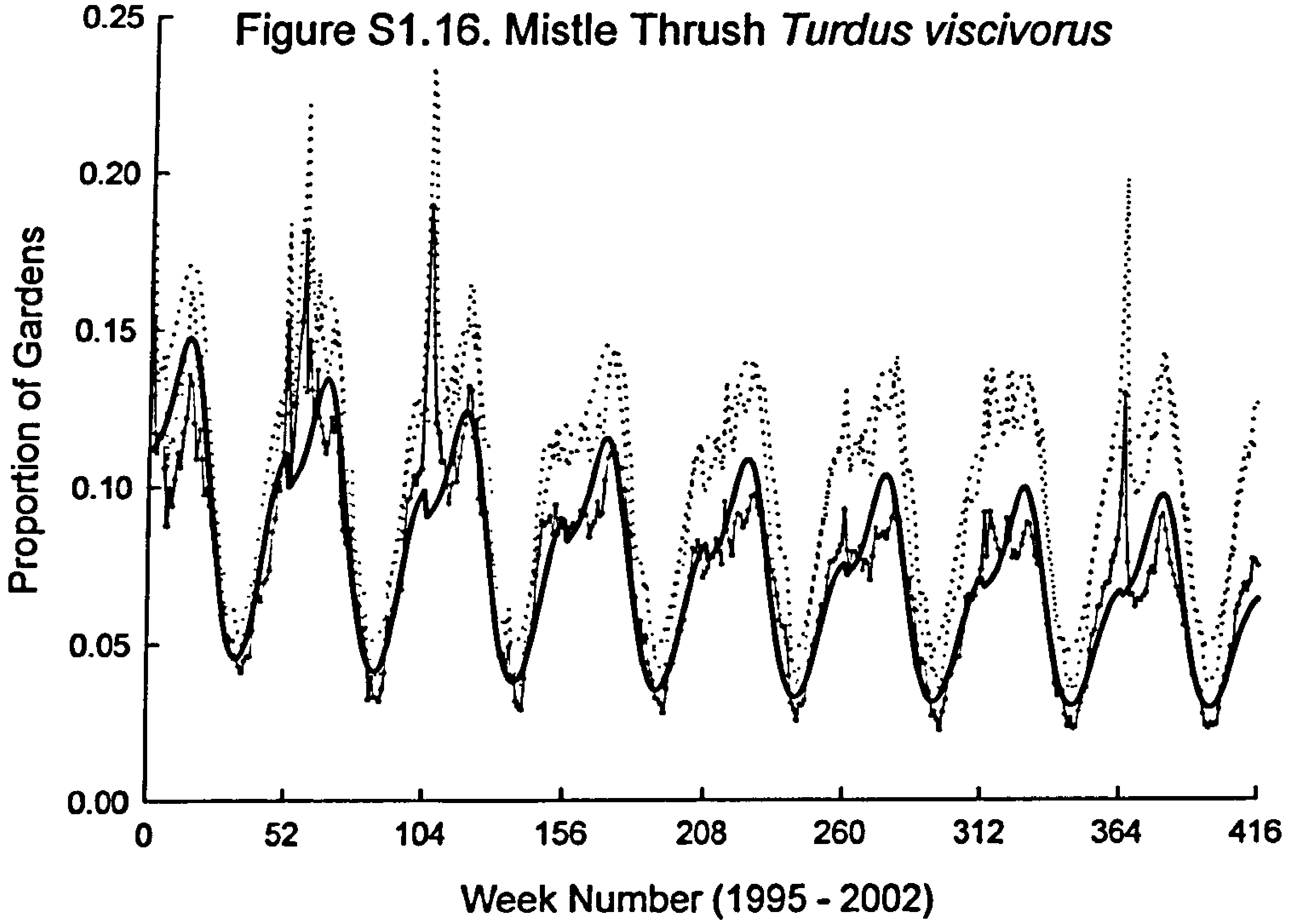


Figure S1.16. Mistle Thrush *Turdus viscivorus*

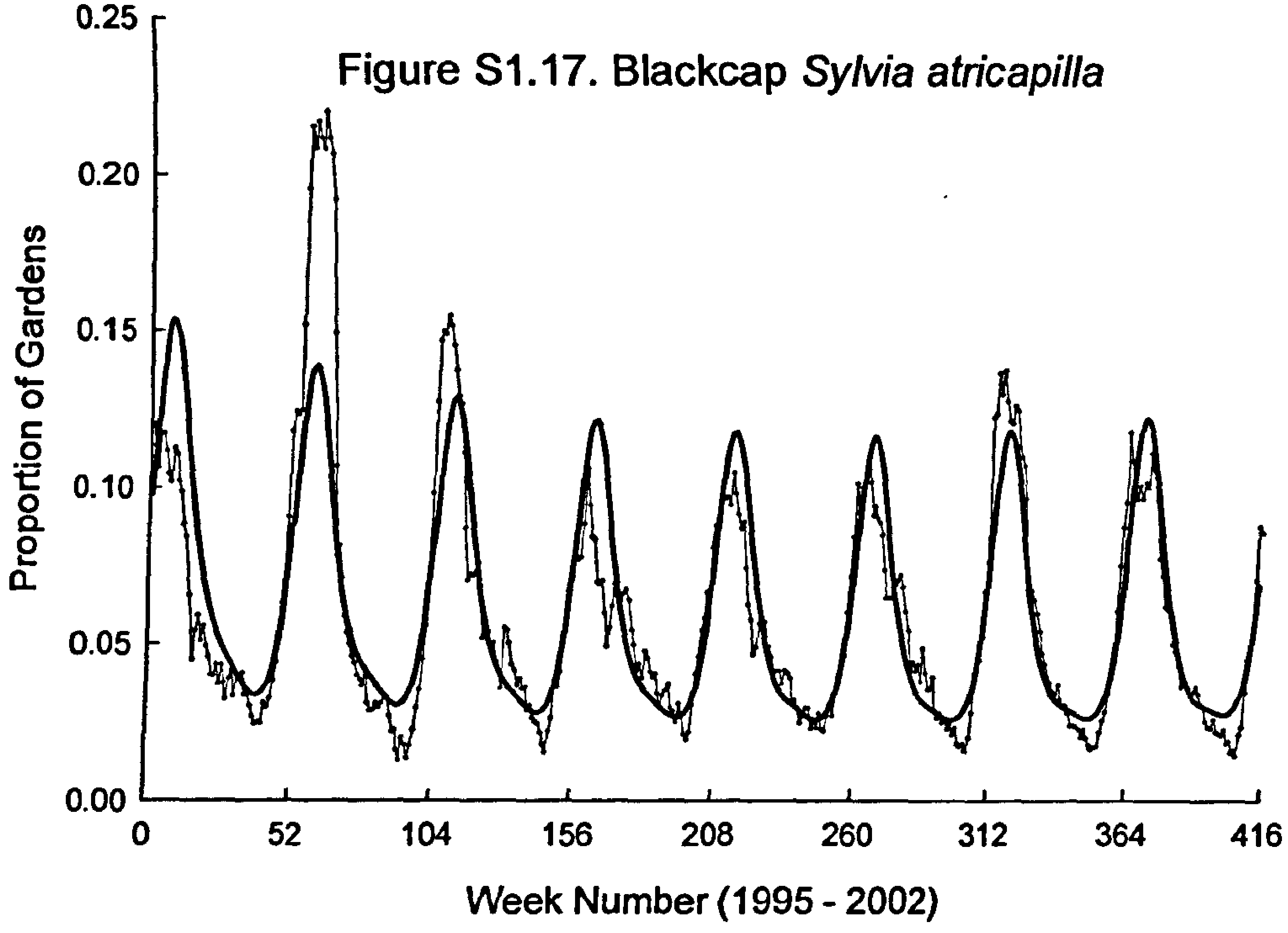


Figure S1.17. Blackcap *Sylvia atricapilla*

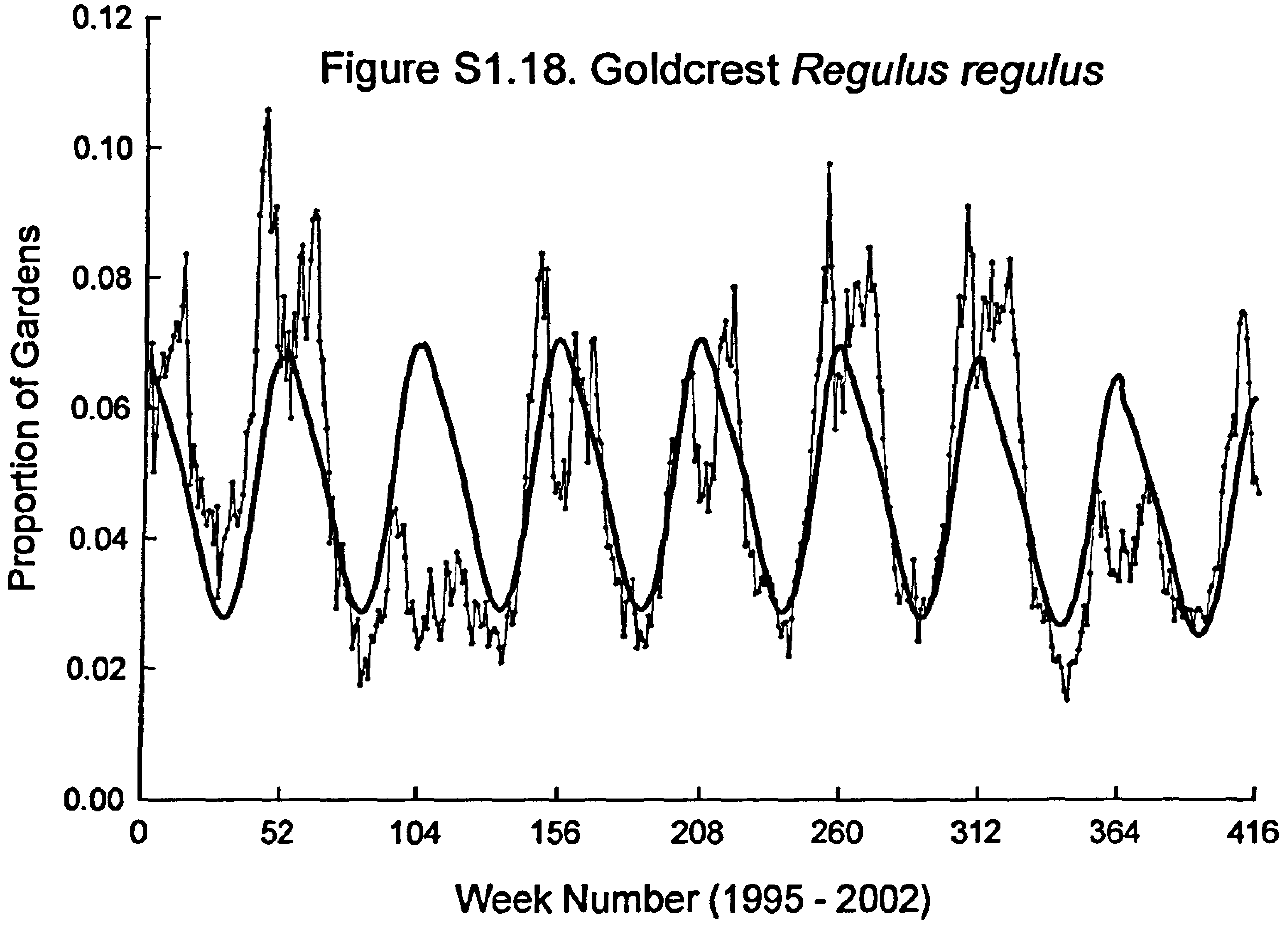


Figure S1.18. Goldcrest *Regulus regulus*

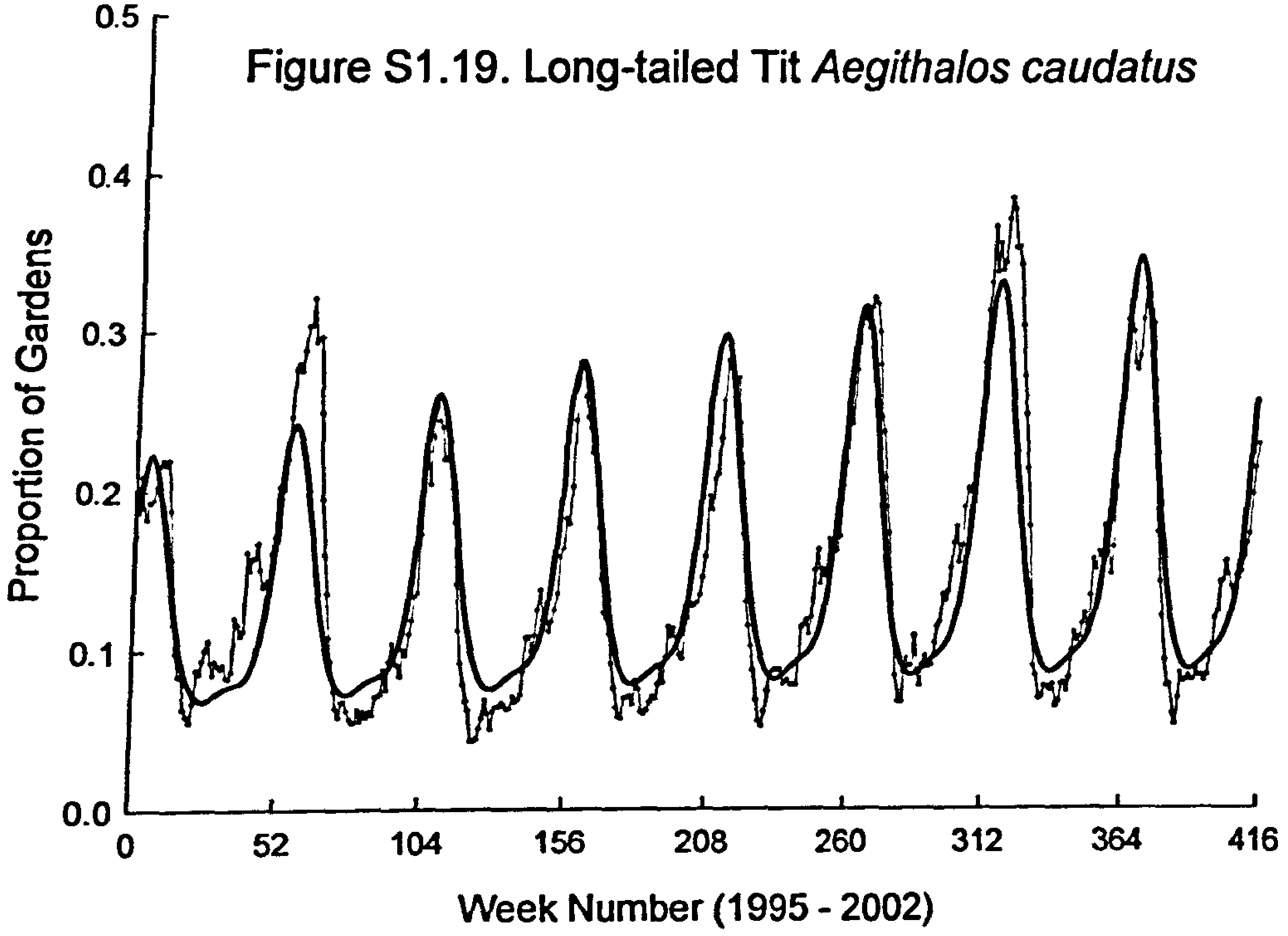


Figure S1.19. Long-tailed Tit *Aegithalos caudatus*

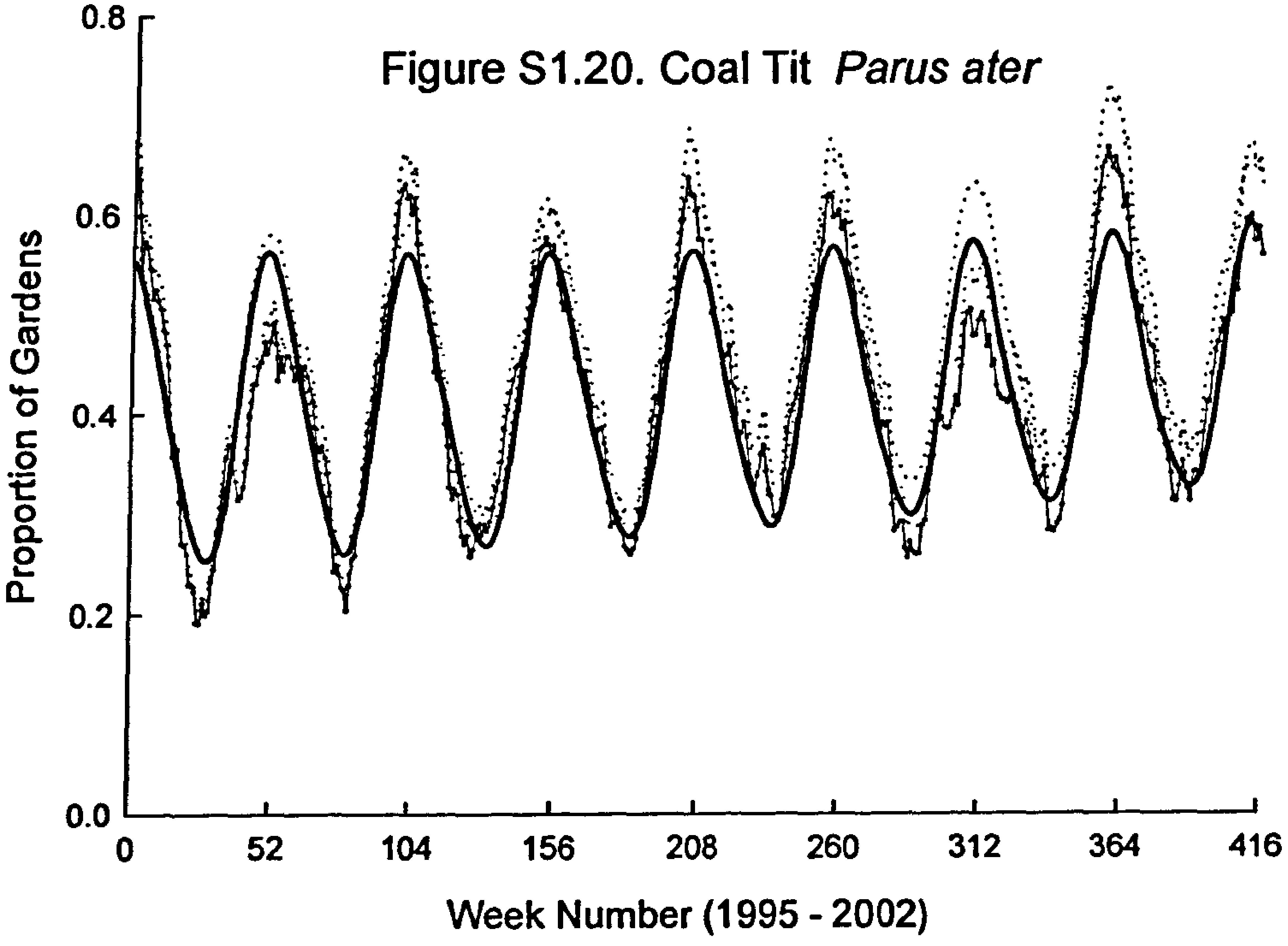


Figure S1.20. Coal Tit *Parus ater*

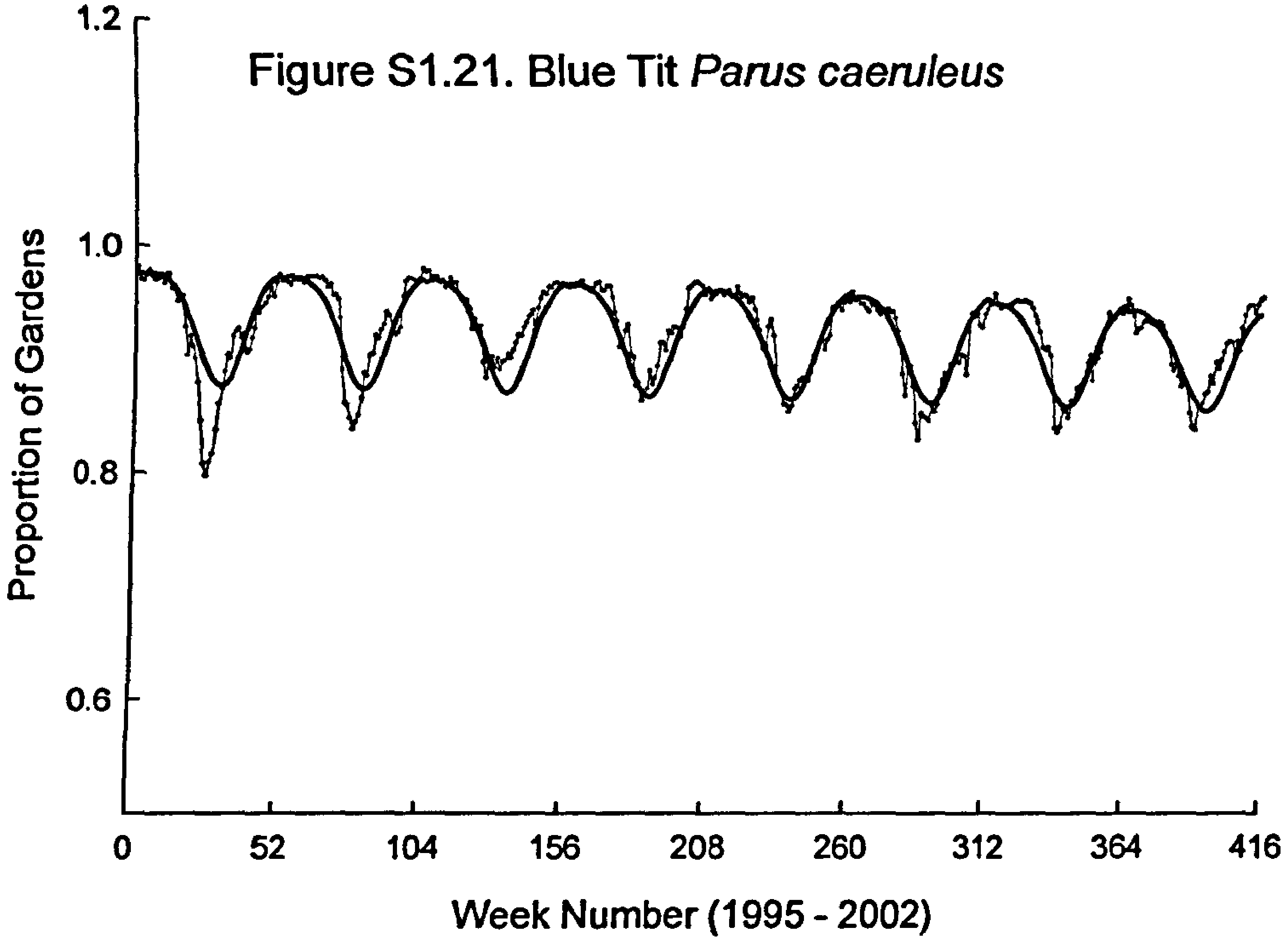


Figure S1.21. Blue Tit *Parus caeruleus*

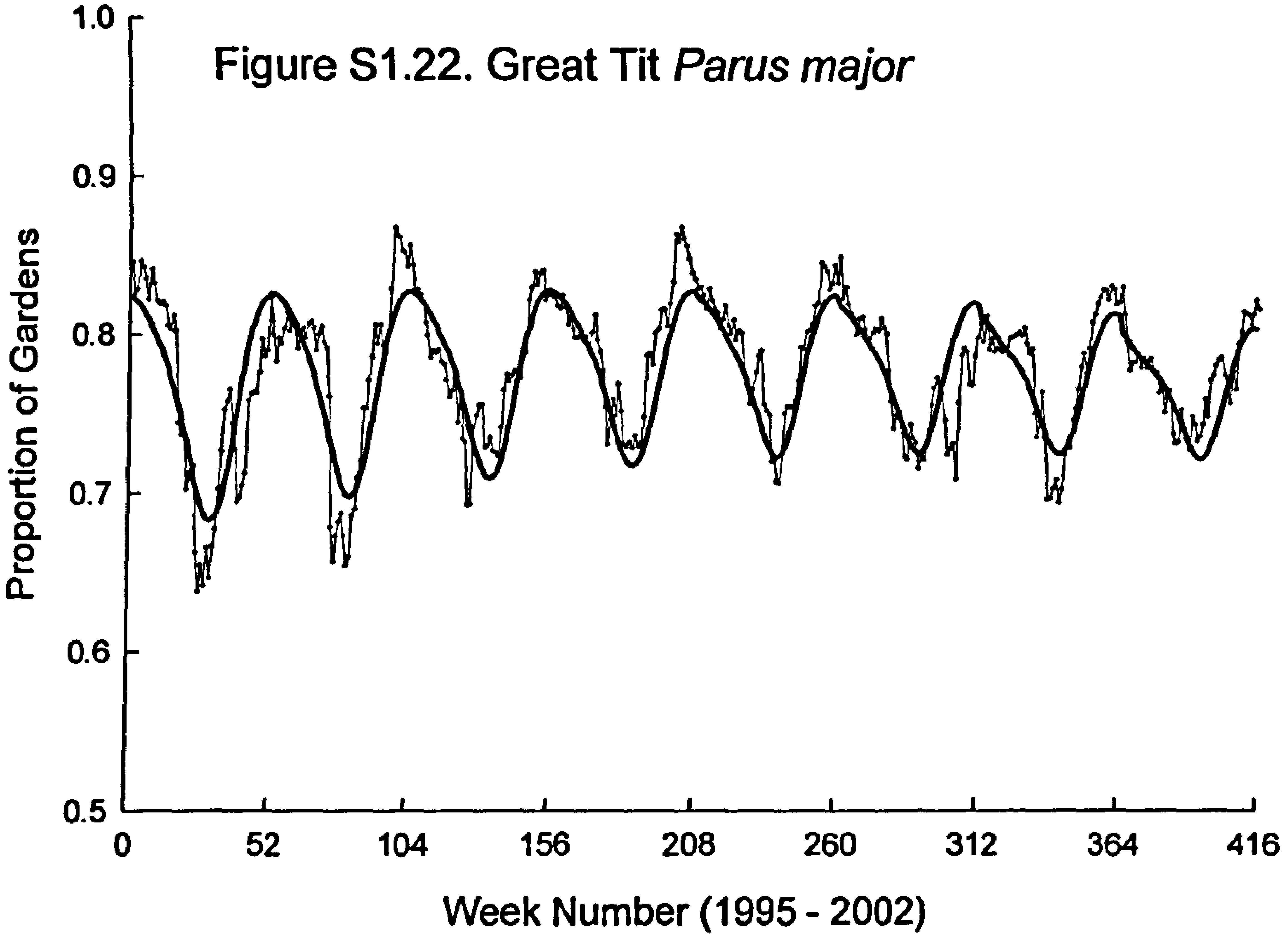


Figure S1.22. Great Tit *Parus major*

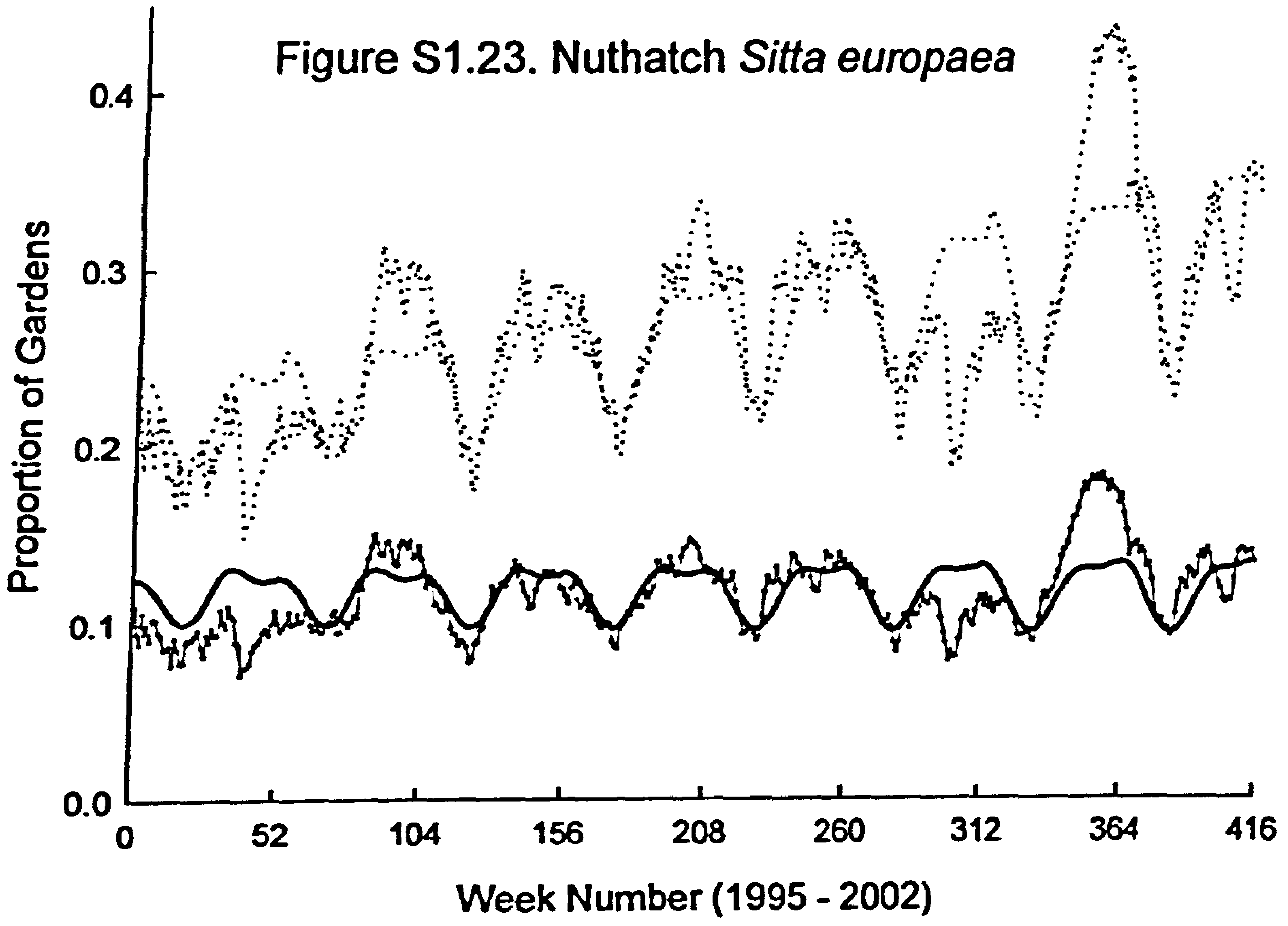


Figure S1.23. Nuthatch *Sitta europaea*

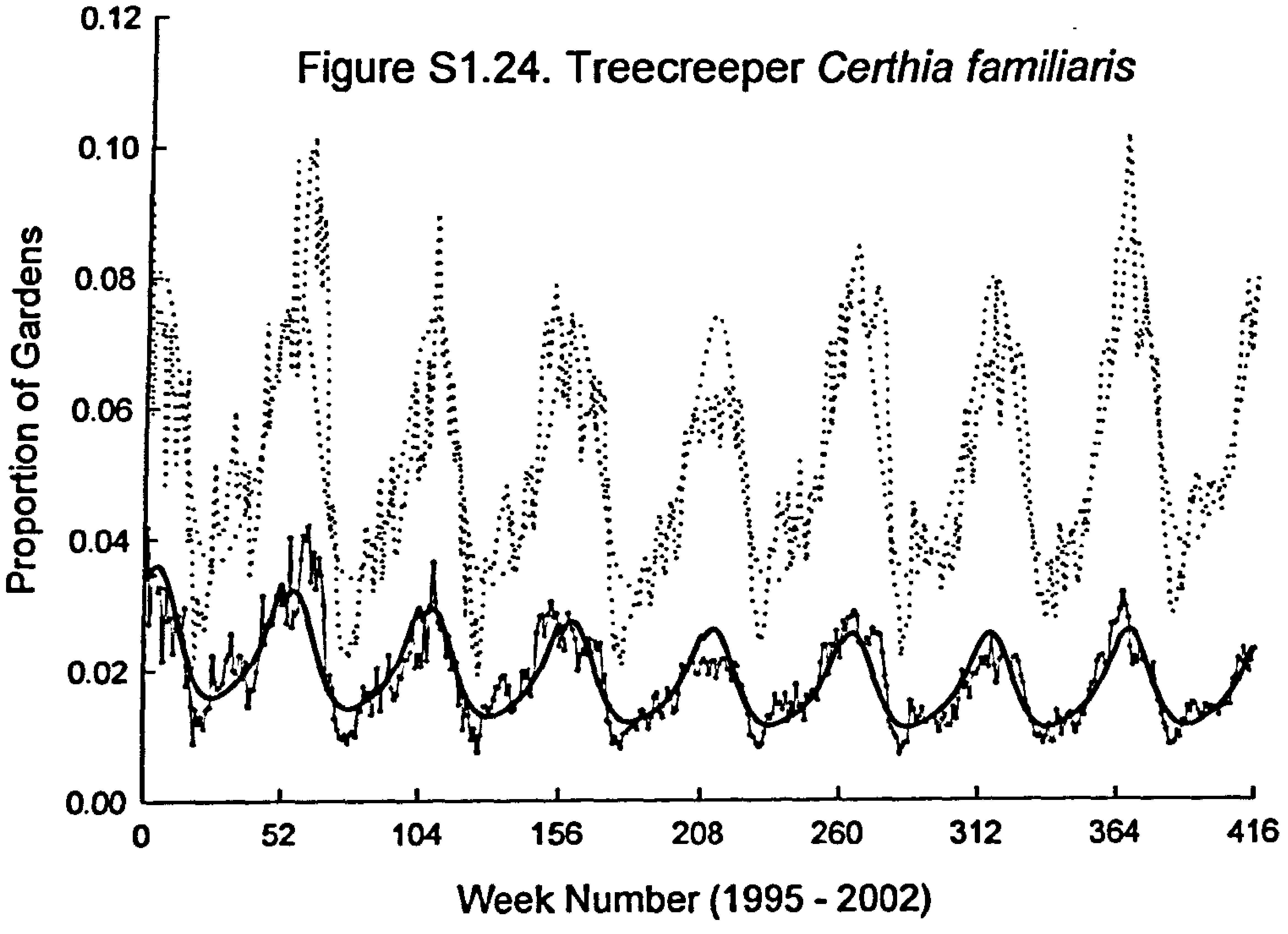


Figure S1.24. Treecreeper *Certhia familiaris*

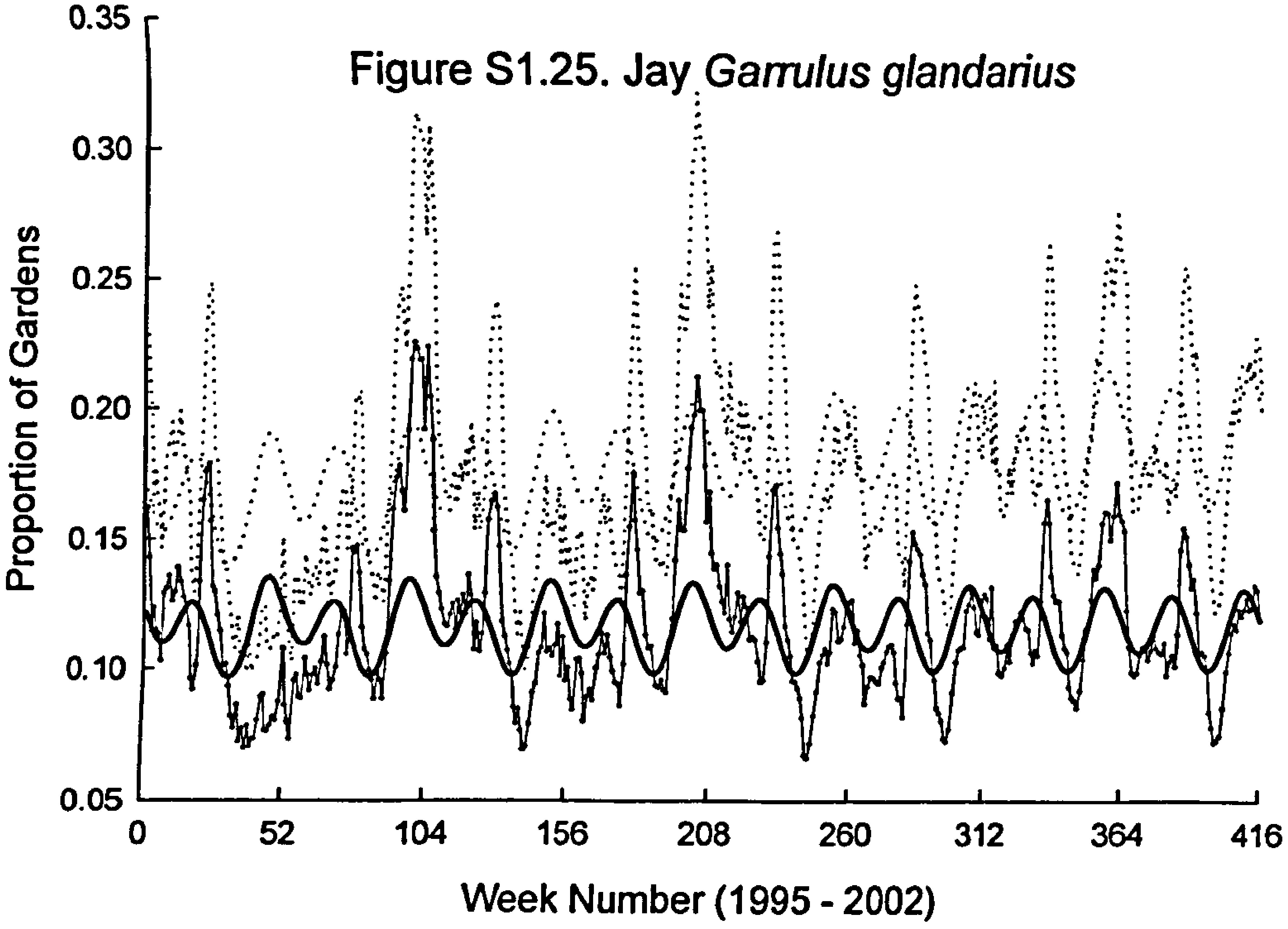


Figure S1.25. Jay *Garrulus glandarius*

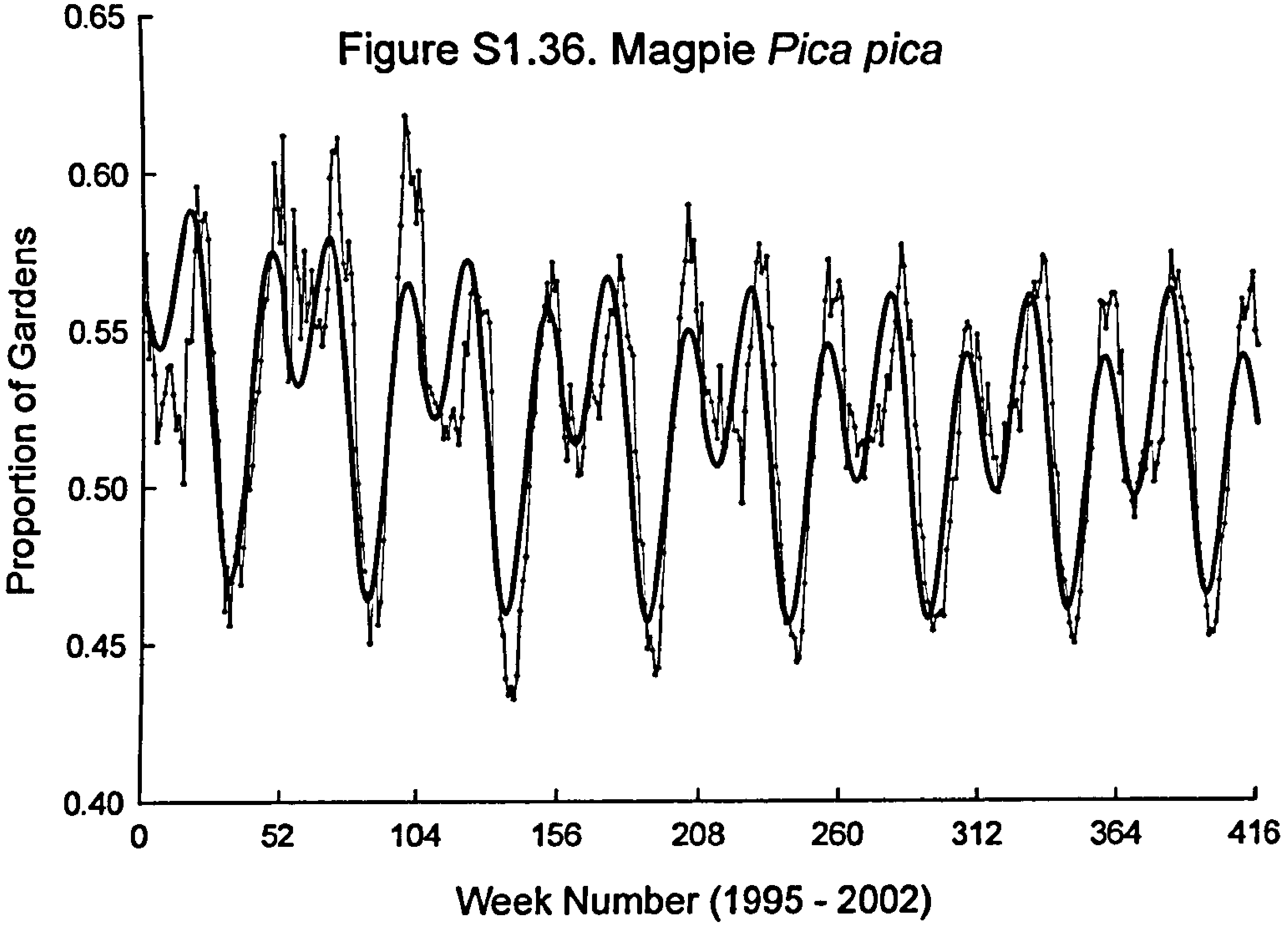


Figure S1.36. Magpie *Pica pica*

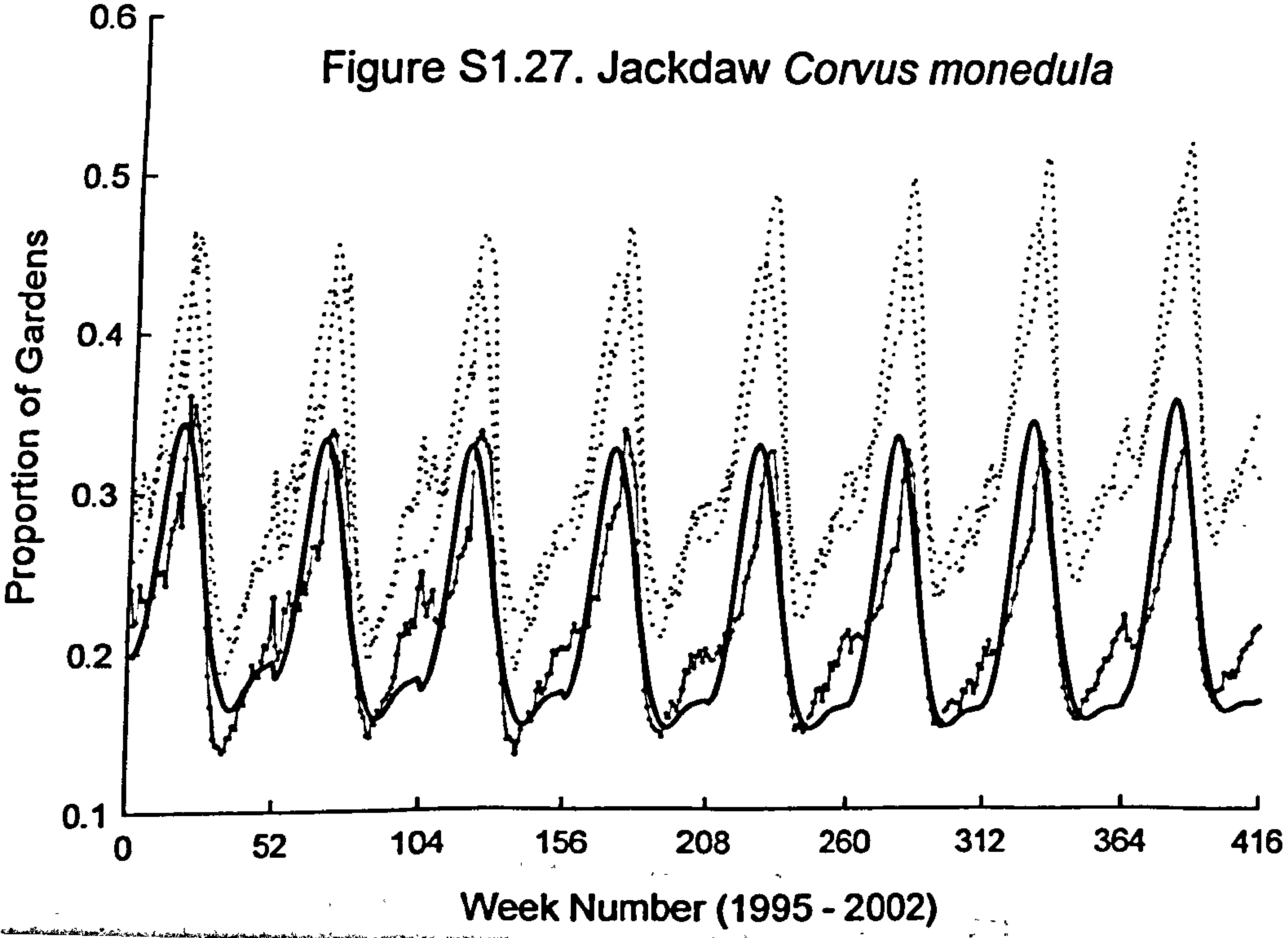


Figure S1.27. Jackdaw *Corvus monedula*

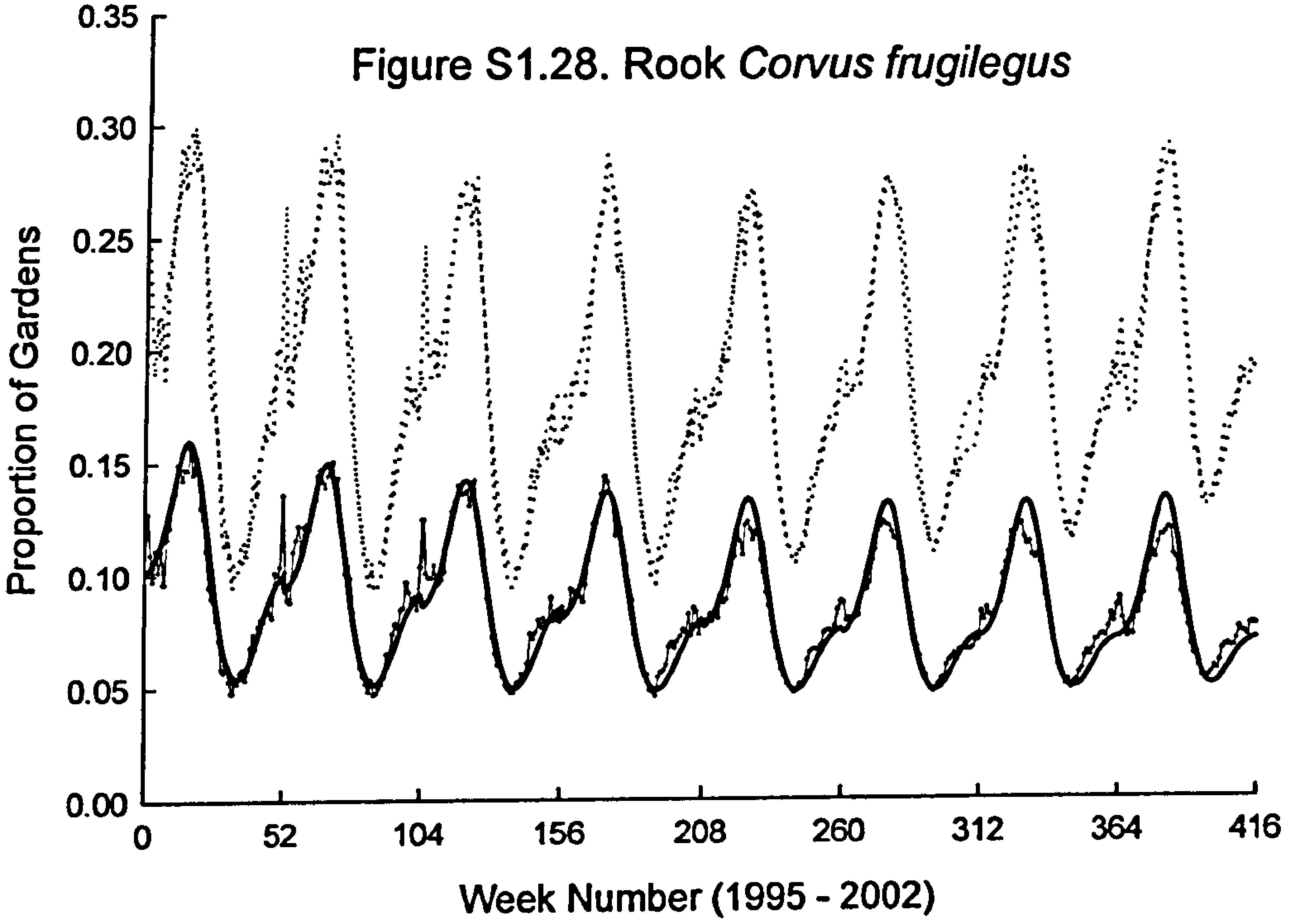


Figure S1.28. Rook *Corvus frugilegus*

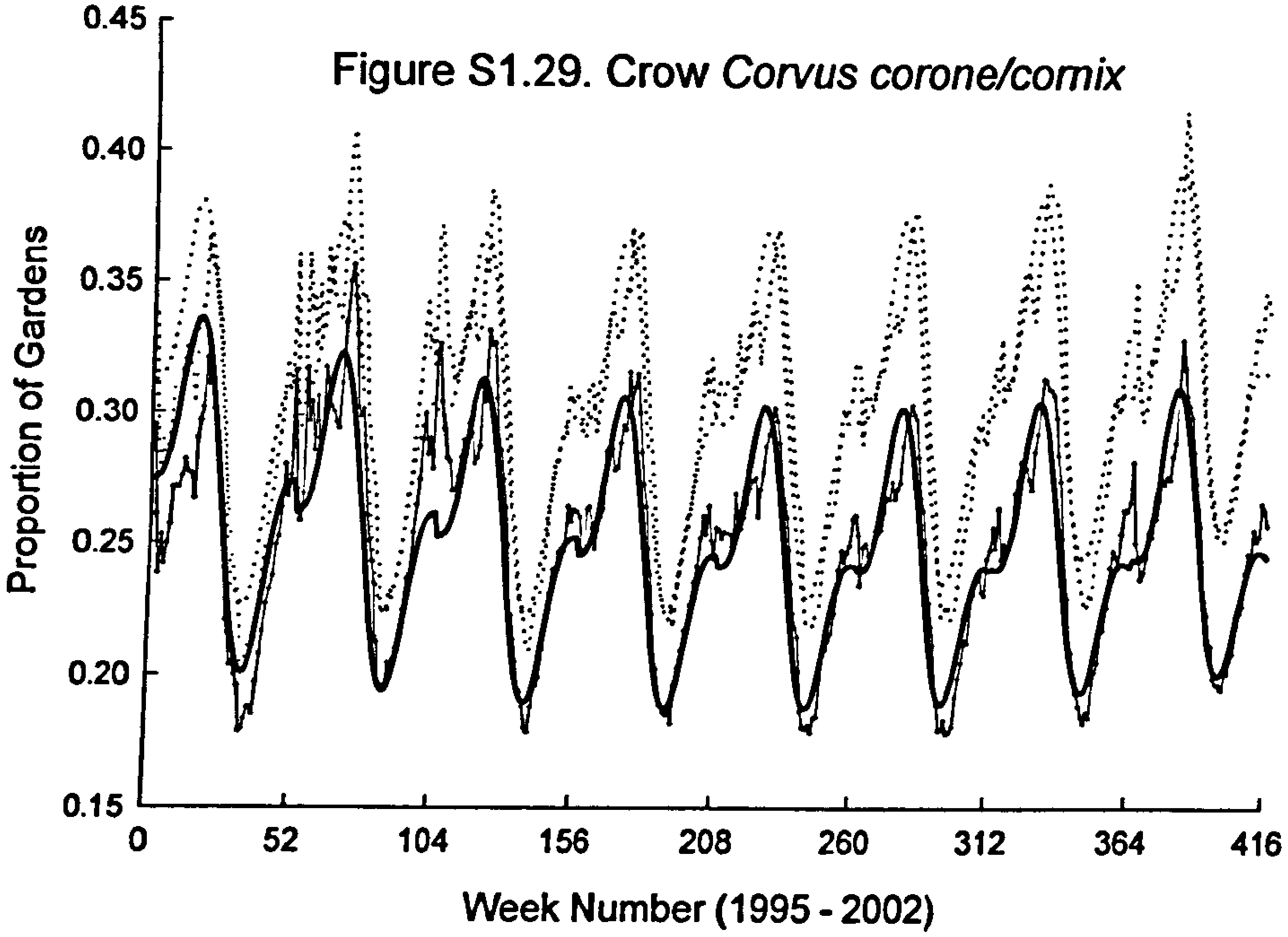


Figure S1.29. Crow *Corvus corone/cornix*

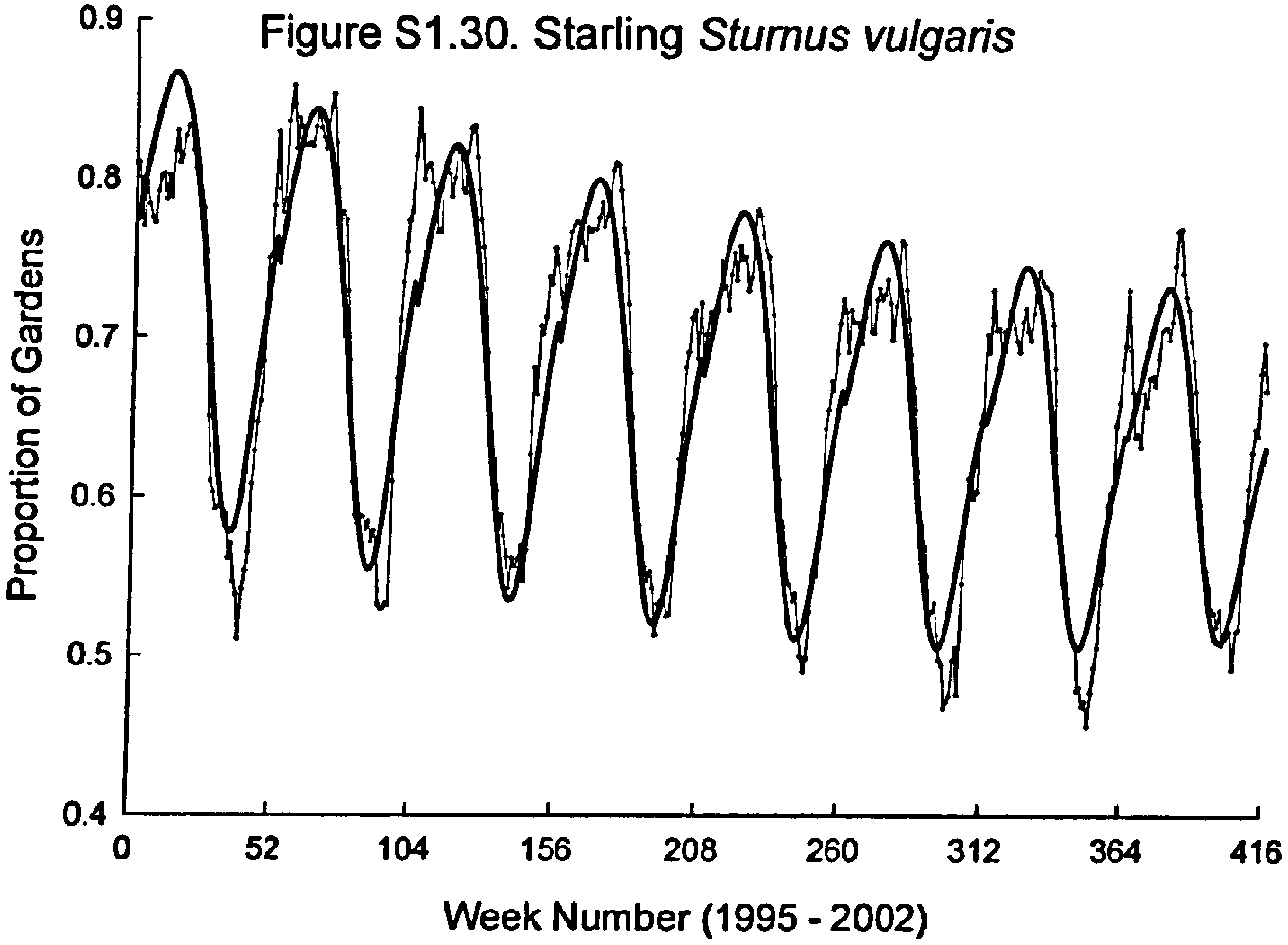


Figure S1.30. Starling *Sturnus vulgaris*

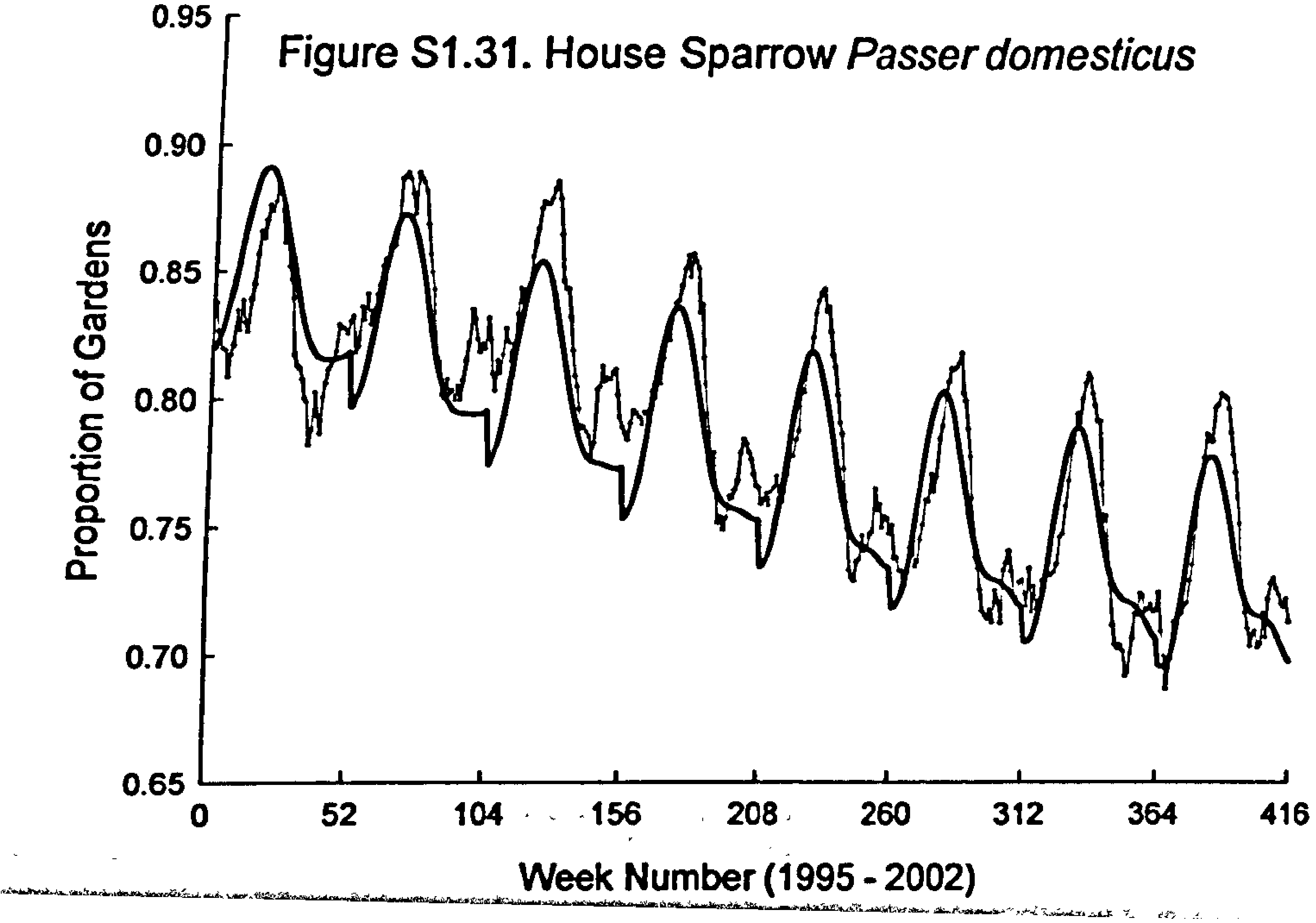


Figure S1.31. House Sparrow *Passer domesticus*

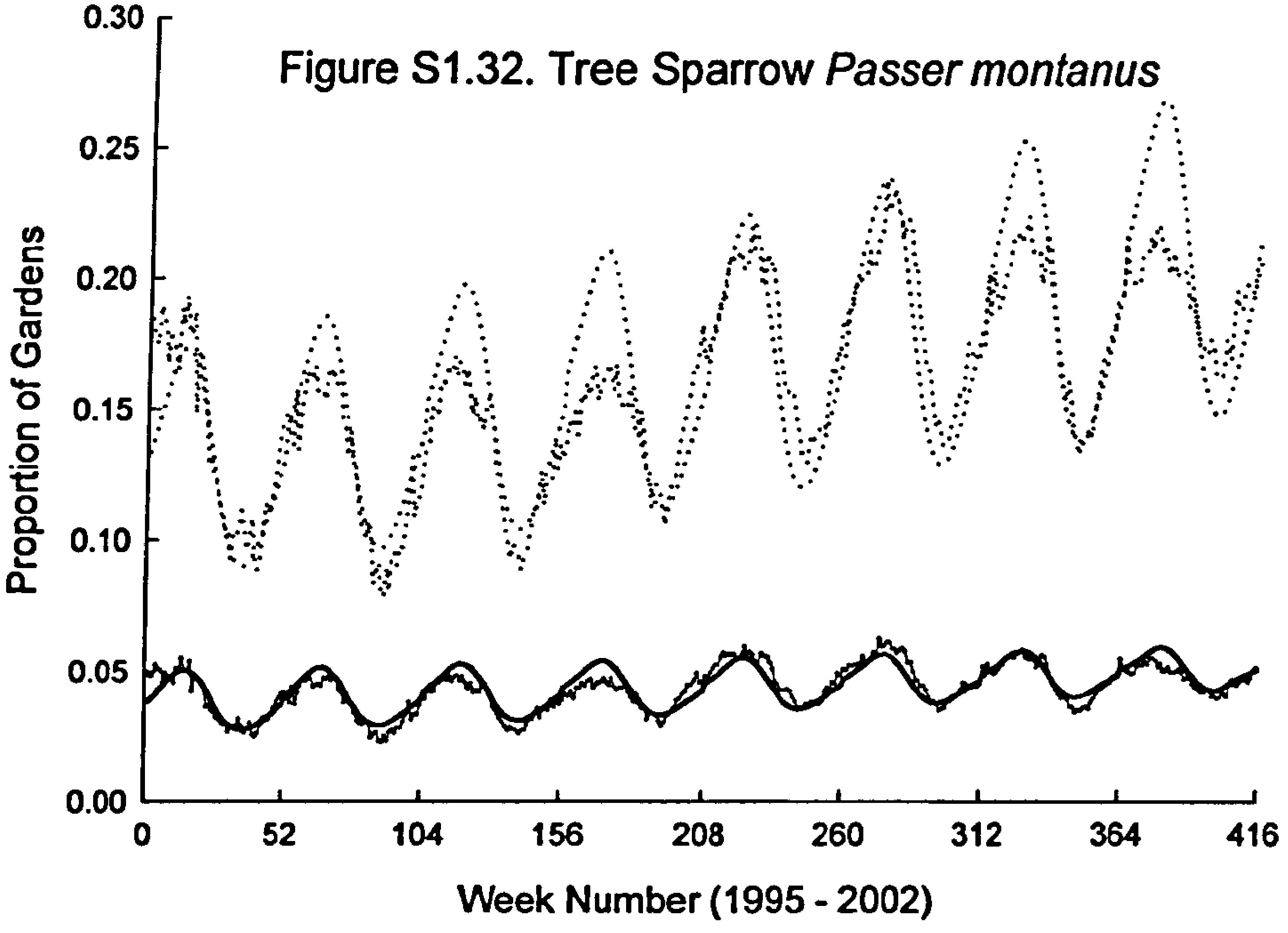


Figure S1.32. Tree Sparrow *Passer montanus*

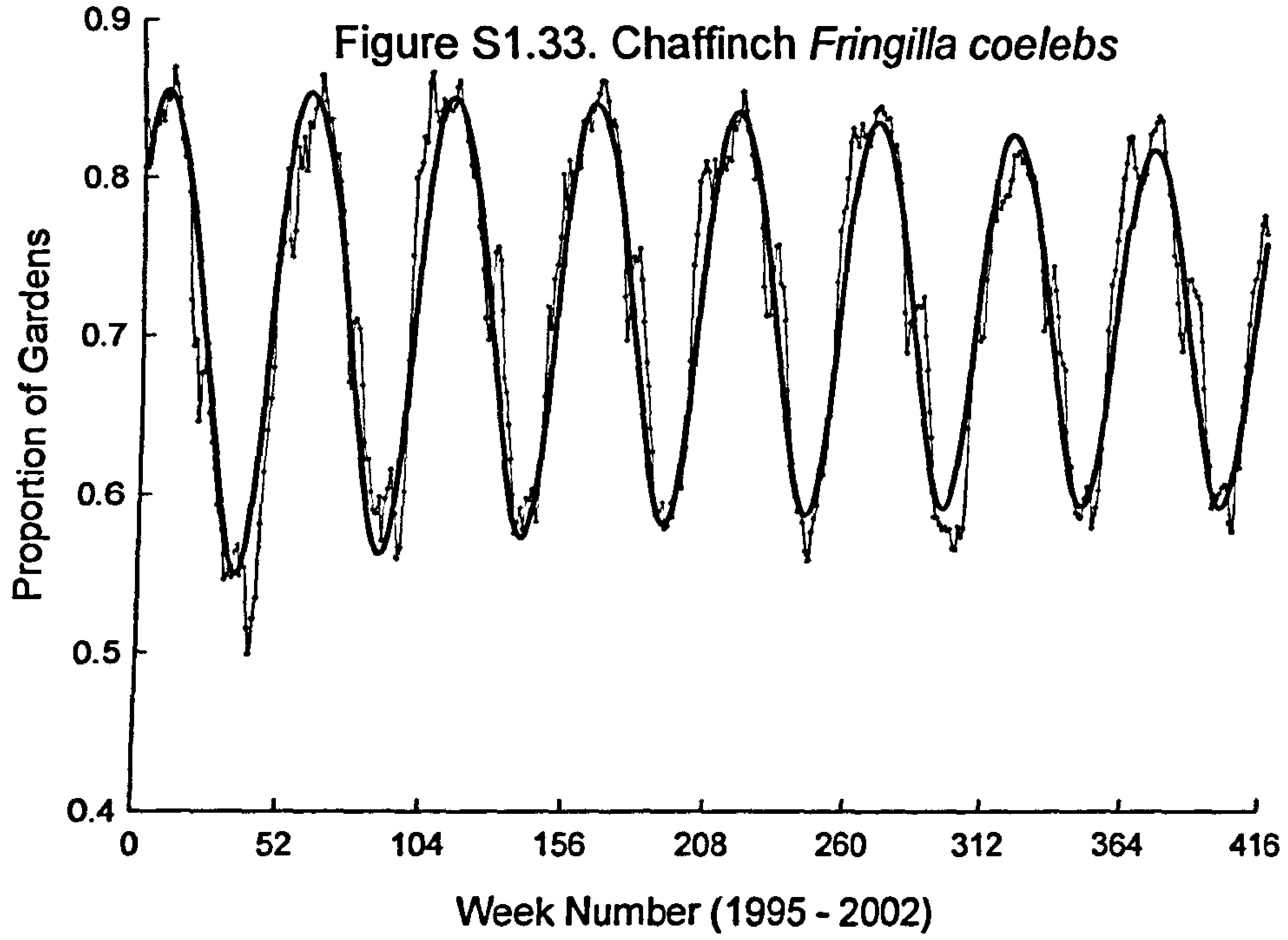


Figure S1.33. Chaffinch *Fringilla coelebs*

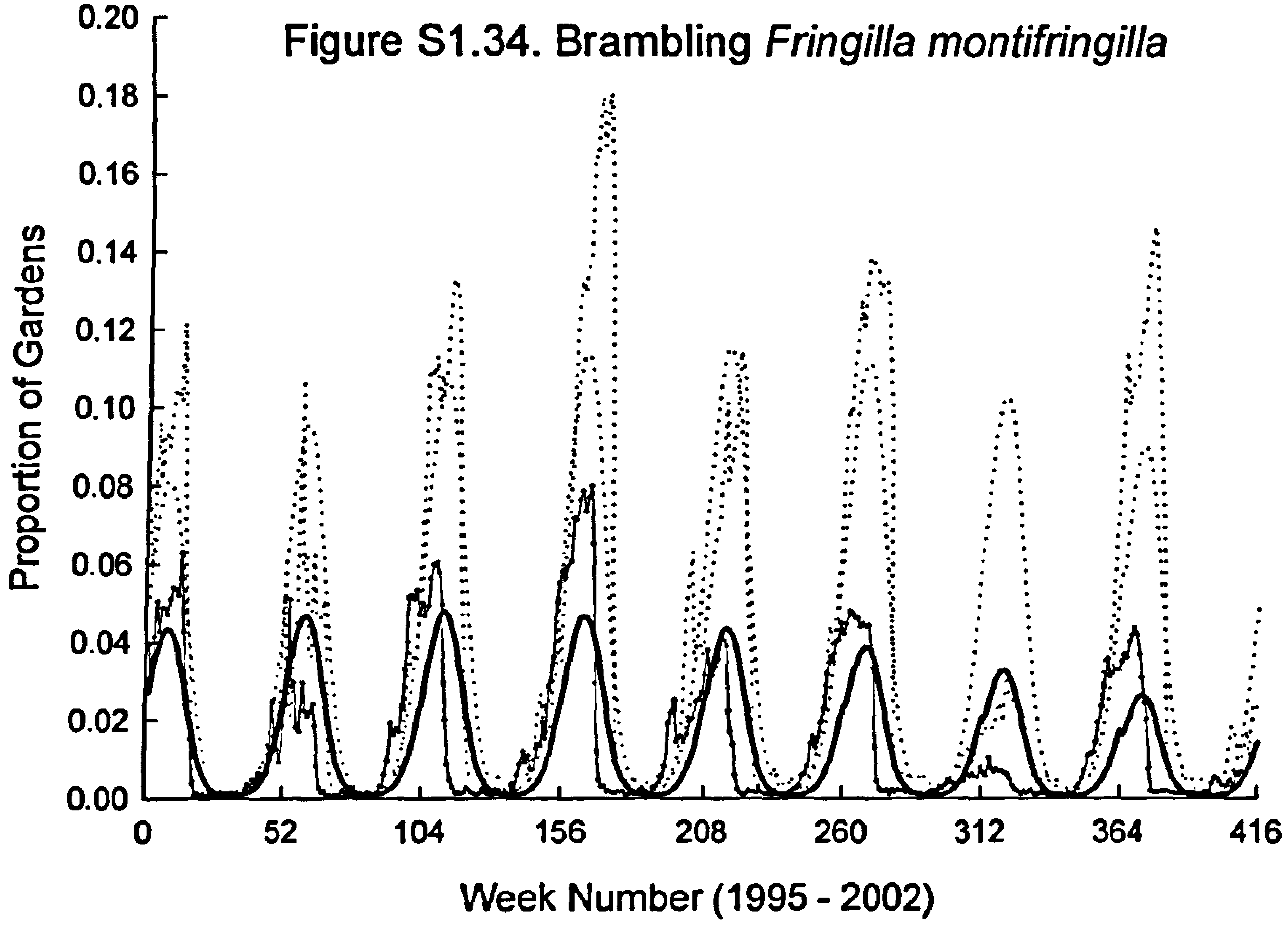


Figure S1.34. Brambling *Fringilla montifringilla*

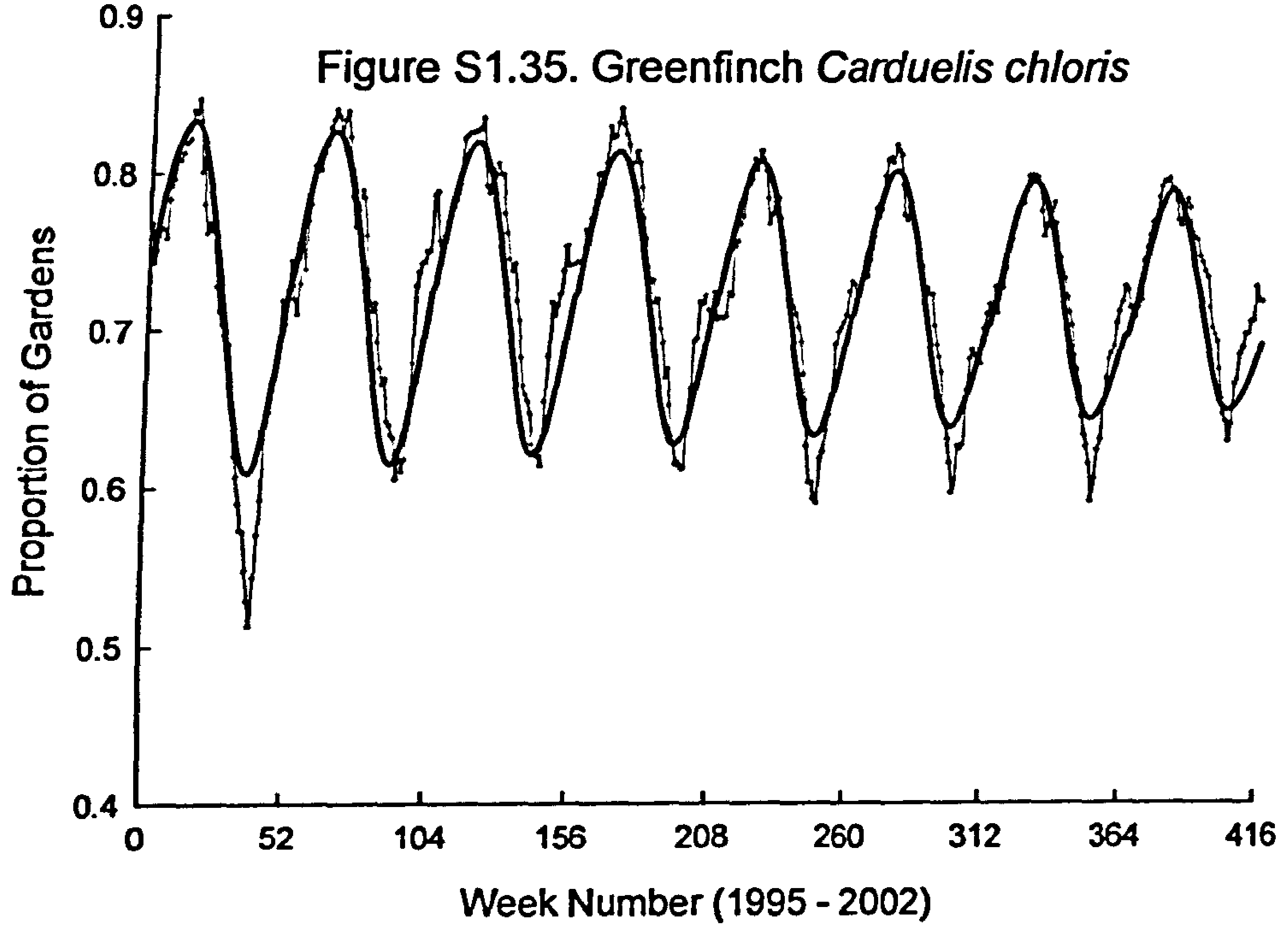


Figure S1.35. Greenfinch *Carduelis chloris*

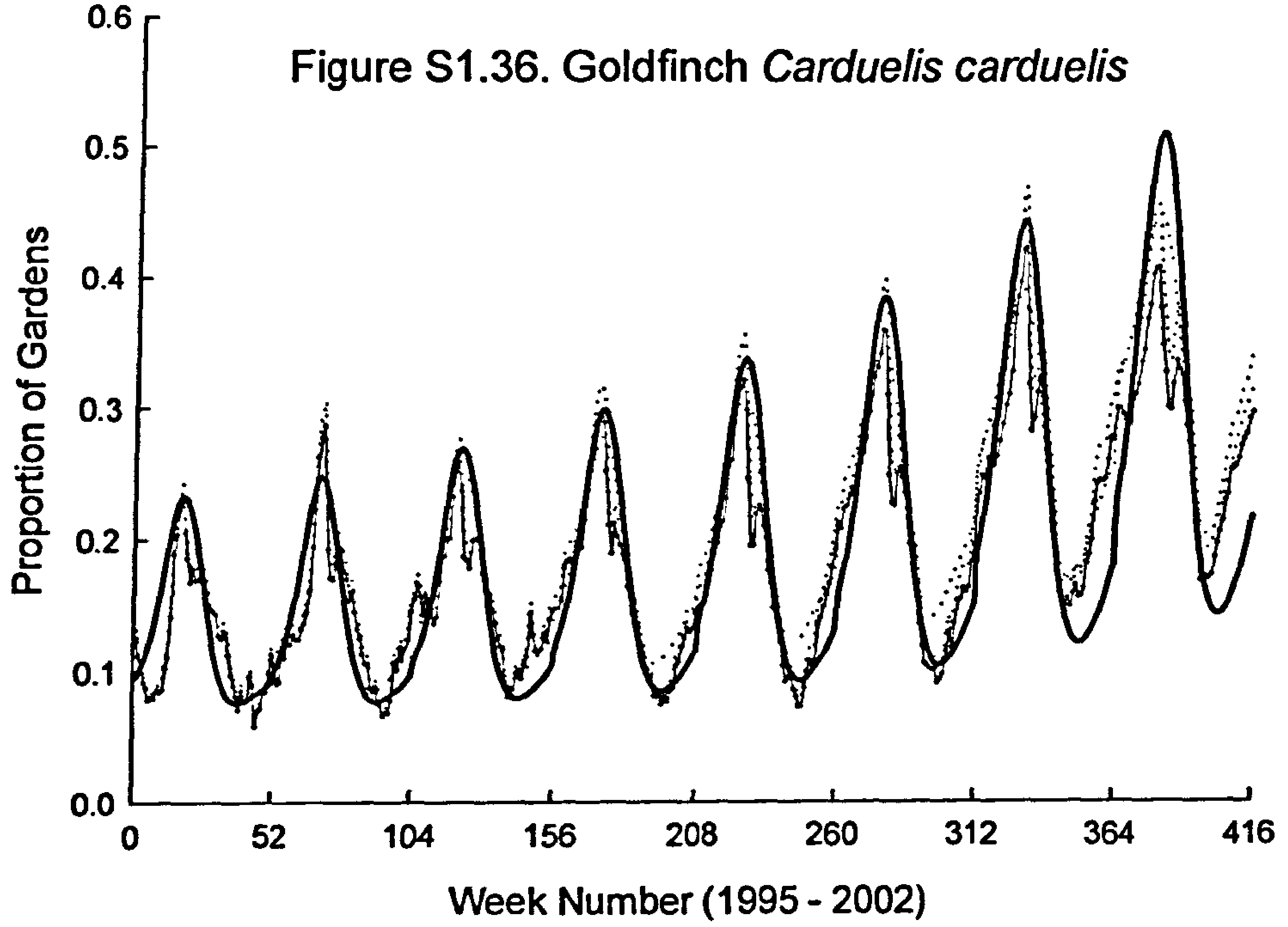


Figure S1.36. Goldfinch *Carduelis carduelis*

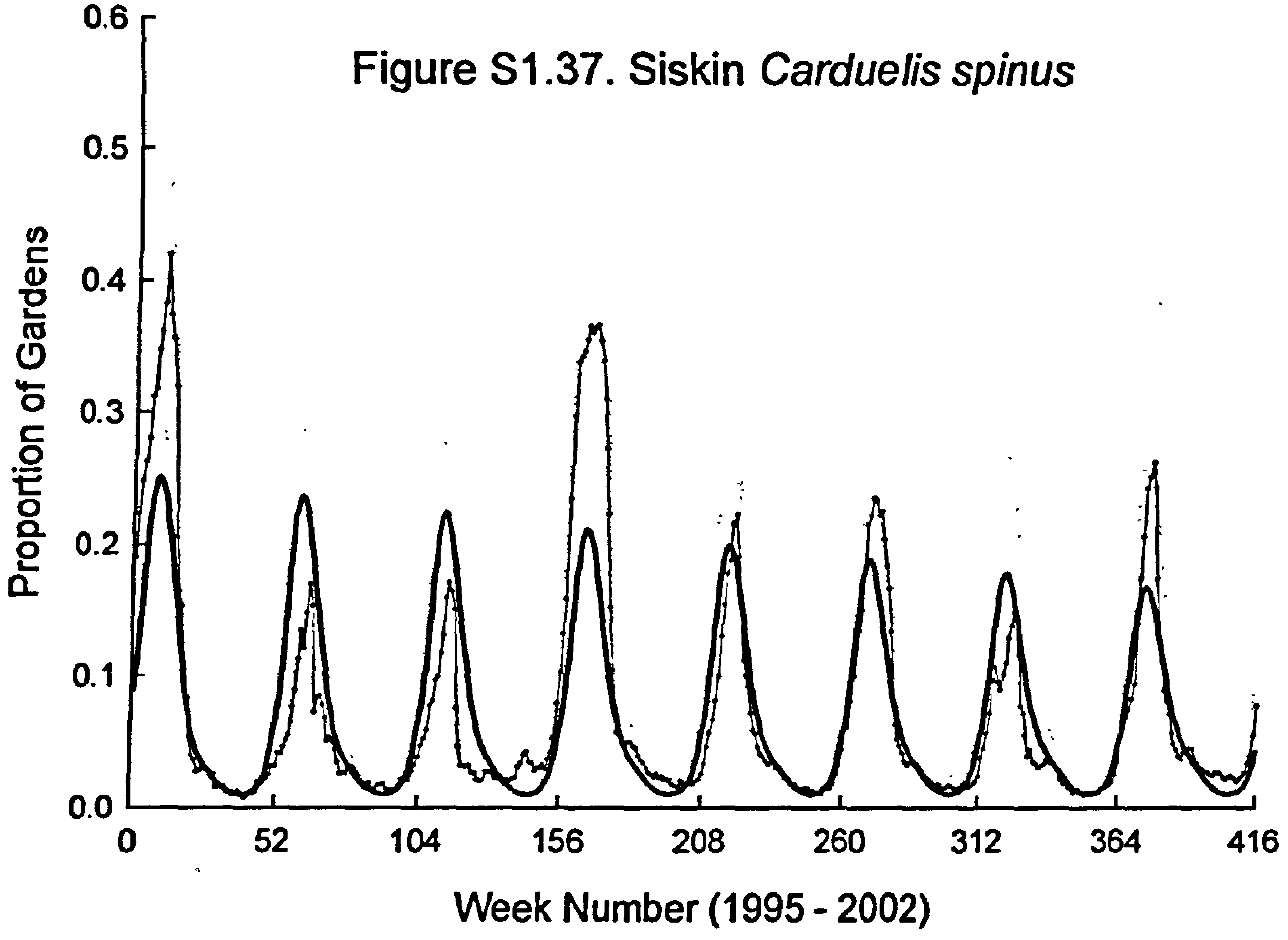


Figure S1.37. Siskin *Carduelis spinus*

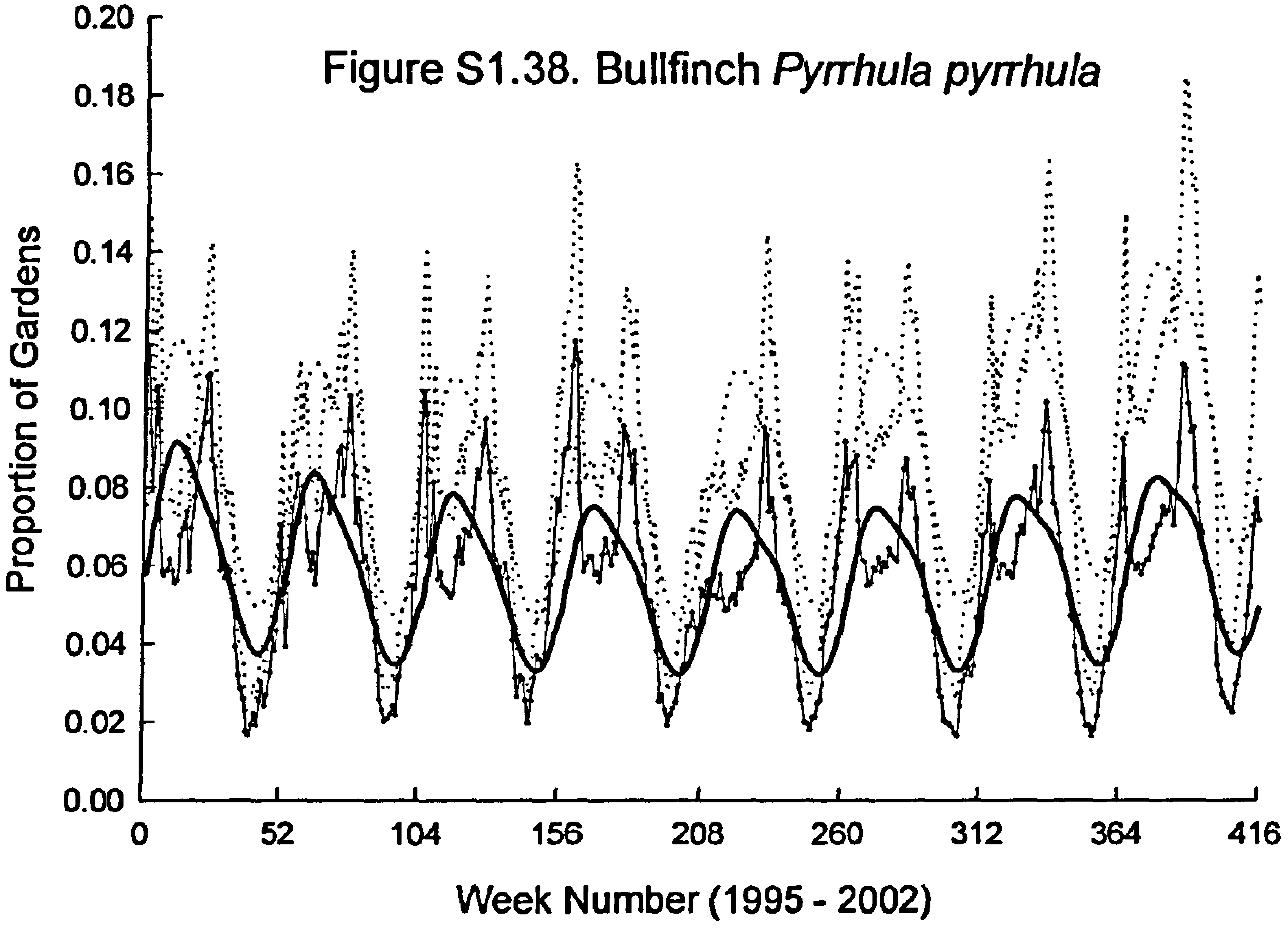


Figure S1.38. Bullfinch *Pyrrhula pyrrhula*

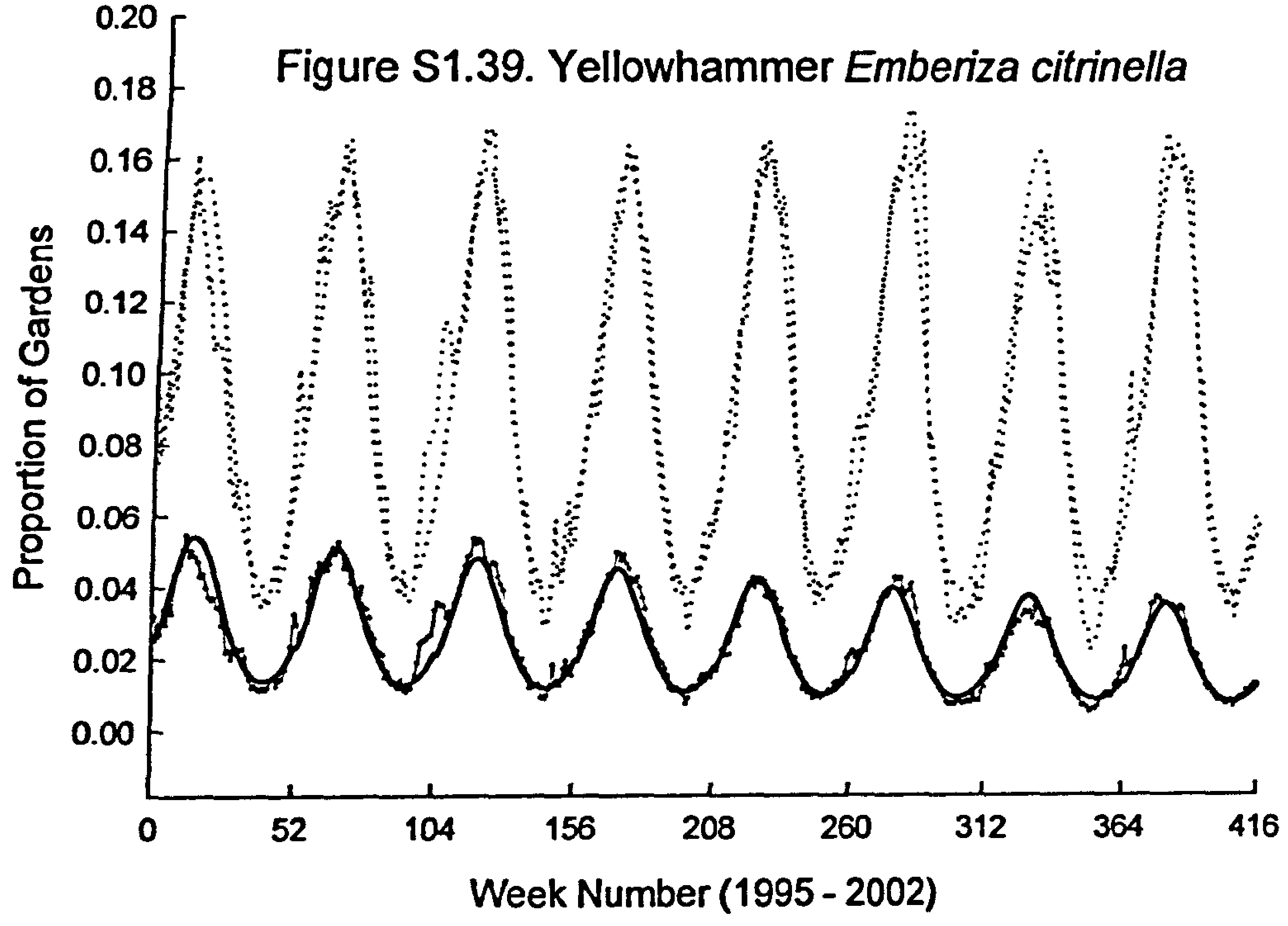


Figure S1.39. Yellowhammer *Emberiza citrinella*

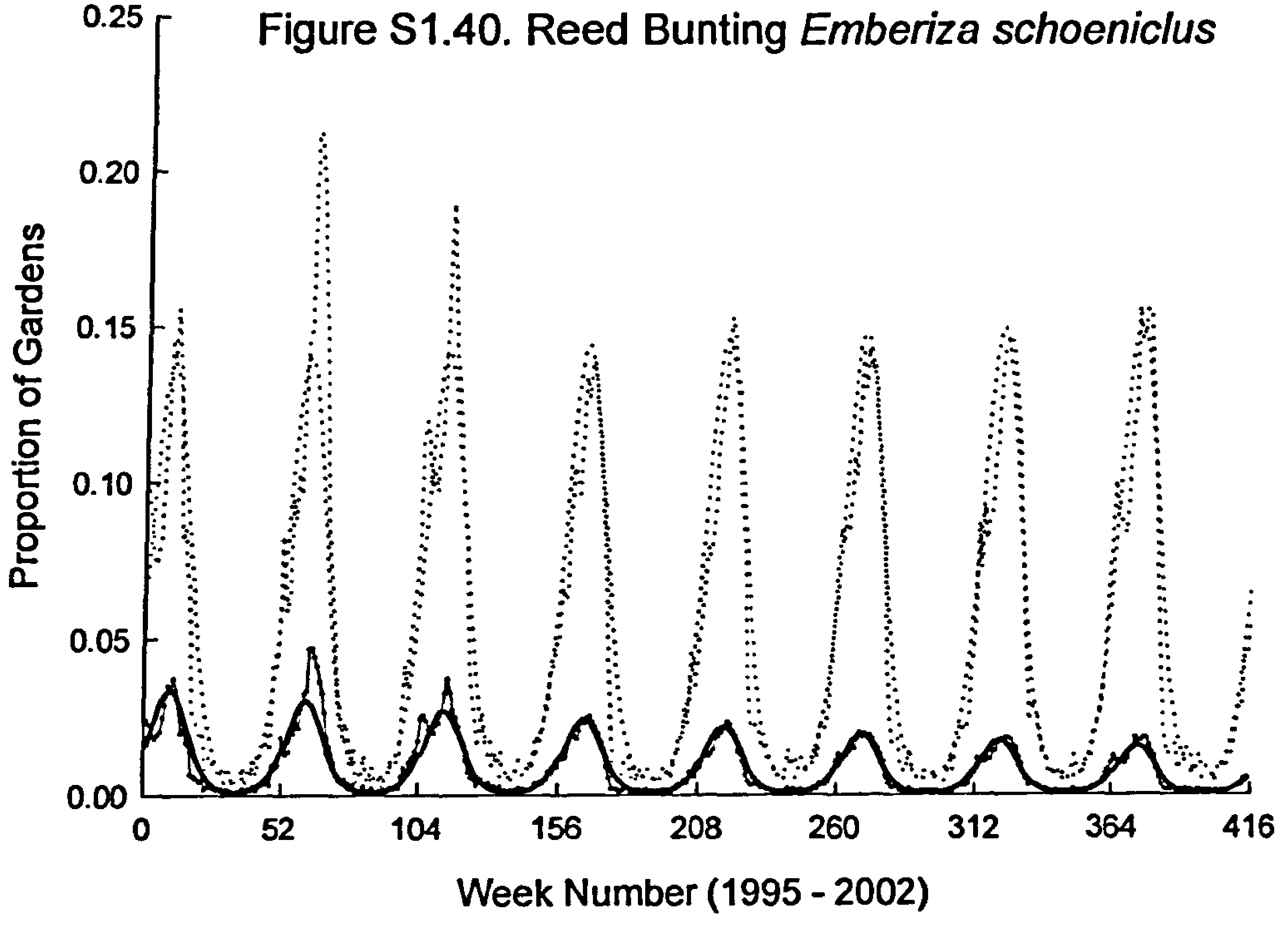


Figure S1.40. Reed Bunting *Emberiza schoeniclus*

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