SPATIAL DISTRIBUTION AND MOVEMENT OF THE COMMON SHREW (*SOREX ARANEUS*) AND THE PYGMY SHREW (*SOREX MINUTUS*) IN A HETEROGENOUS LANDSCAPE

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I'm truly sorry man's dominion

Has broken Nature's social union

Burns, 'To a Mouse'

ABSTRACT

This thesis uses metapopulation theory as a starting point from which to describe the movement and spatial distribution of the Common Shrew, *Sorex araneus* and the Pygmy Shrew, *Sorex minutus*, in a heterogeneous landscape. The study was carried out on a golf-course which provided twelve suitable habitat patches for these two species in the form of the 'rough' (scrub grassland). Each patch was surrounded by unsuitable, homogeneous habitat, the 'fairway'. In this way, the site was similar to a classical metapopulation model.

A regime that involved trapping at the site every two to three months revealed that in the 1997 cohort (the young born in Summer 1997) intra-patch movements were more numerous than inter-patch movements. However, in *S. minutus* males, the ratio of intra-patch movements to inter-patch movements was much less than in *S. minutus* females or in both *S. araneus* sexes. This may have been due to *S. minutus* males having larger home-ranges than *S. araneus*. This has been shown in previous studies and is supported by the present one.

When the trapping intensity was reduced, this pattern was not evident. The 1998 cohort (the young born in Summer 1998) was trapped in Summer 1998 and in April 1999(just before breeding). Due to the very low survival of *S. minutus* over this period, the high rate of inter-patch movement relative to inter-patch movement found in the 1997 cohort, was absent. In *S. araneus*, the same pattern that was found in the 1997 cohort was evident. In addition, *S. araneus* male intra-patch movement was shown to increase with increasing patch size, thus directly indicating that movement was restricted by the patch edges and the unfavourable habitat surrounding the habitat patches. In both cohorts, the most frequently crossed inter-patch distance was also the shortest at the site. Individuals moving between patches almost always moved to a neighbouring patch in the first instance.

In *S. araneus*, there was no difference in inter-patch movement characteristics between those caught for the first time in June 1998 (the June cohort) summer and those born later in August 1998 (the August cohort). However, in females, the June cohort was heavier as juveniles and as adults. However, June cohort adult males were lighter than August cohort males. In both sexes, the June cohort moved greater distances than the August cohort. There was no difference found between the two cohorts in any of the physical characteristics measured although June born females were absent from the two most severe tail-scarring categories.

Microsatellite analysis showed that in *S. araneus* some genetic structuring at the site was evident using F- statistics ($F_{ST} = 0.019$). However, it was small compared to that expected on the basis of the field data. In *S. minutus*, genetic structuring was found to be greater than in *S. araneus* using F-statistics ($F_{ST} = 0.032$). This was also contrary to data collected in the field which showed that gene flow between patches would be expected to be greater in *S. minutus* than in *S. araneus*. However, the result obtained for *S. minutus* may have been due to a particular locus. In *S. araneus*, the difference between the genetic analysis and the field data may be due to landscape history and the mating system of this species.

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DEDICATION

To my parents and

my four grand-parents

DECLARATION

I declare that the work contained in this thesis is my own and that it has not been submitted for any other degree or award.

Alexandra Lewis

Alexandra J. G. Lewis

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CHAPTER 1

INTRODUCTION

1.1 The consequences of a heterogeneous landscape

Landscapes in nature are patchy and heterogeneous (Wiens, 1997). From an organism's point of view, a landscape contains different areas of habitat which vary according to their suitability for life-history processes such as feeding and avoiding predators. Some species have very strict habitat requirements. For them, the landscape will be divided into habitat patches which are either suitable or unsuitable. Other species with less strict requirements will be able to use different habitat types with varying degrees of success.

The spatially heterogeneous nature of landscapes will therefore affect the organisms that inhabit them. Two dramatic effects of a heterogeneous landscape can be the creation of new species (the process of speciation) and the extinction of local populations or sometimes species themselves. Islands found in lakes or oceans present a very clear example of a spatially heterogeneous habitat where for terrestrial species, the islands represent favourable habitat and the water unfavourable habitat. The large stretches of water often found between islands mean that there is limited dispersal both between the island populations themselves and between the islands and any mainland population. Speciation can occur under these circumstances due to 'adaptive radiation', the diversification of species derived from a single common ancestor into many ecological niches (Futuyma, 1986). New islands are colonised and due to lack of gene flow from other populations, lack of competition (Avise, 1996) and different environmental conditions, new species evolve. The results of such a process can be seen in many island archipelagos such as the Galapagos (e.g. Finches, Darwin, 1859) and Hawaii (e.g. Honeycreepers, Freed *et al.*, 1987). Speciation can also occur due to a 'founder effect'. New colonies of a species

become distinct from the parent population as a result of their few founding individuals being an atypical sample (Diamond, 1996). The results of this process are thought to have occurred in, for example, flightless beetles in the Galapagos (Finston and Peck, 1995) and the process itself has been observed in weed plant species on Canadian island lakes (Cody and Overton, 1996).

As well as promoting speciation, heterogeneous landscapes can lead to population or species extinction. When suitable patches of habitat are small, the number of individuals occupying them will be low and the population may enter an 'extinction vortex' (Caughley, 1994). Frequency of mating between close relatives will rise (inbreeding) which will result in a reduction in heterozygosity in the offspring. This may ultimately lead to the exposure of deleterious recessive alleles which decrease fecundity and increase mortality (inbreeding depression). This causes the population to become smaller still which makes it increasingly vulnerable to demographic and environmental stochastic effects.

Such extinction due to small habitat patches can be through natural causes. The ongoing extinction of mammal fauna on mountaintops in the Great Basin of North America is thought to be due to the fact that population numbers are very low and that migration between mountaintops is now impossible (e.g. the Pronghorn, *Antilocapra americana* (Brown, 1971)). Paleontological evidence suggests that the mountains were originally colonised during the Pleistocene when the climatic barriers that currently isolate them were not present (Brown, 1971). However, human influence is more commonly the cause of the decrease in size of suitable habitat patches for many species. This combined with intensive hunting has, for example, caused numbers of a cougar sub-species, the Florida Panther (*Puma concolor coryi*), to become dangerously low (less than 50 individuals now survive, Avise, 1994). The effects of inbreeding are evident: all the animals have a 50 degrees kink in their tail vertebrae and a cowlick on their mid-dorsal back. The species suffers from severe reproductive problems and heart abnormalities are common in captive-bred cubs (Roelke *et al.*, 1993).

1.2 Theories to account for populations in a heterogeneous landscape

1.2.1 Island Biogeography Theory

The Theory of Island Biogeography (MacArthur and Wilson, 1967) states that species richness on oceanic islands is maintained by a dynamic equilibrium. Continuing immigration of species from the mainland or a neighbouring island is balanced by ongoing local extinction on the island itself, primarily due to demographic and genetic stochasticity. The rate of extinction will be strongly influenced by the island's size and the rate of immigration. Many organisms are found only in small areas of suitable habitat which are referred to as 'refuges' which have obvious similarities to oceanic islands (e.g. they are surrounded by habitat that is not suitable for the species occupying the island). Refuge design became an important aspect of conservation biology during the 1970s and 1980s (Diamond, 1975; Wilson and Willis, 1975). Ideas on how best to design refuges were strongly influenced by the Theory of Island Biogeography (MacArthur and Wilson, 1967).

Calculations from the species-area relationship and from empirical studies (e.g. Simberloff and Abele, 1976) showed that two or more islands could hold more species than a single island of the same size. Many of these authors were therefore in favour of creating two smaller refuges instead of one large one. However, Diamond (1975) and Wilson and Willis (1975) claimed that one large, unfragmented refuge was a better strategy. These two viewpoints made up the 'SLOSS' debate (single large or several small) which pervaded conservation biology for much of the 1970s and 1980s. Such differences in opinion arose due to each group of workers having a different conservation goal (Burkey, 1989). Diamond (1975) and Wilson and Willis (1975) aimed to minimise population/species extinction after the refuge had become isolated. As a result, they favoured a single, large refuge which would promote continuing species survival. However, those favouring several smaller refuges aimed to maximise species richness at the time of isolation. The former

view therefore valued population survival both in the present and future whereas the latter view valued the number of species in the refuges only at their time of creation.

In an attempt to evaluate the different approaches to refuge design, Goodman (1987) developed a stochastic simulation model with density dependent reproduction and survival. It also incorporated environmental stochasticity. He concluded that multiple refuges are preferable to a single large one provided that the environmental variation in the separate refuges is at least partially independent. He also stated that is necessary for a small rate of natural or managed migration to occur in order to balance local extinctions.

Using a similar model, Burkey (1989) also modelled the population processes of a hypothetical species in refuges with different degrees of fragmentation but the same total area. The model dealt only with extinction due to demographic stochasticity (the changes in population size brought about by random mortality and reproduction). The results showed that a population with density-dependent dynamics experiences random fluctuations in population size and that these may result in extinction. However, the risk of such extinction was shown to be much greater if the refuge area is discontinuous. He concluded that the fragmentation of habitats has severe effects on population viability and only migration between the fragments can counter this. Empirical work by Fornay and Gilpin (1989) was carried out with the same aim. They used two species of fruit-fly, *Drosophila hydei* and *Drosophila pseudoobscura* which they subjected to three different types of spatial configuration. Their results showed that large, continuous populations are more viable than divided ones but that in divided populations, migration is important for balancing on-going extinctions.

By the late 1980s, the SLOSS debate was therefore losing importance due to an increased emphasis on species/population viability. Conservation biologists began to concentrate on long-term population survival rather than species richness. A

theory encompassing populations occupying fragmented landscapes, and one which was able to offer conditions for persistence was needed.

1.2.2 Metapopulation Theory

The decline in interest in the Theory of Island Biogeography and the SLOSS debate coincided with an increasing interest in metapopulation biology (Hanski, 1997). The term 'metapopulation' was first used by Richard Levins (1969) to describe a population of populations. However, it did not become a driving force in conservation until the early 1990s.

Like the Theory of Island Biogeography, a fundamental assumption of metapopulation theory is that space is discrete and it is possible and useful to distinguish between habitat patches that are suitable for the focal species and the rest of the environment. In a classical metapopulation (Levins, 1969), each suitable habitat patch must be large enough to accommodate a local population but not larger, i.e. there may be one local population per patch. However, certain patches may be vacant at different times. Habitat patches are equal in area and isolation (i.e. each patch is equi-distant to all other patches) and the exchange rate of individuals between these populations is so low that migration into local populations has no real effect on their dynamics. This model is shown, diagrammatically, in Figure 1.1.

In the Levins model, the fraction of habitat patches occupied at time '*t*' is described by the variable $p(t)$. The relevant individual and population processes are represented by two key parameters: *e*, which sets the rate of local extinction and *m*, which sets the rate of local colonization. Equation 1 gives the rate of change of '*p*' and therefore specifies the conditions under which it is greater than zero and the metapopulation extant. Patches are scored as occupied or not and the actual sizes of the local populations are ignored. The rate of colonisation is assumed to be proportional to the fraction of currently occupied patches (source of colonists), *p*, and to the fraction of currently empty patches (colonisation targets), 1-*p*.

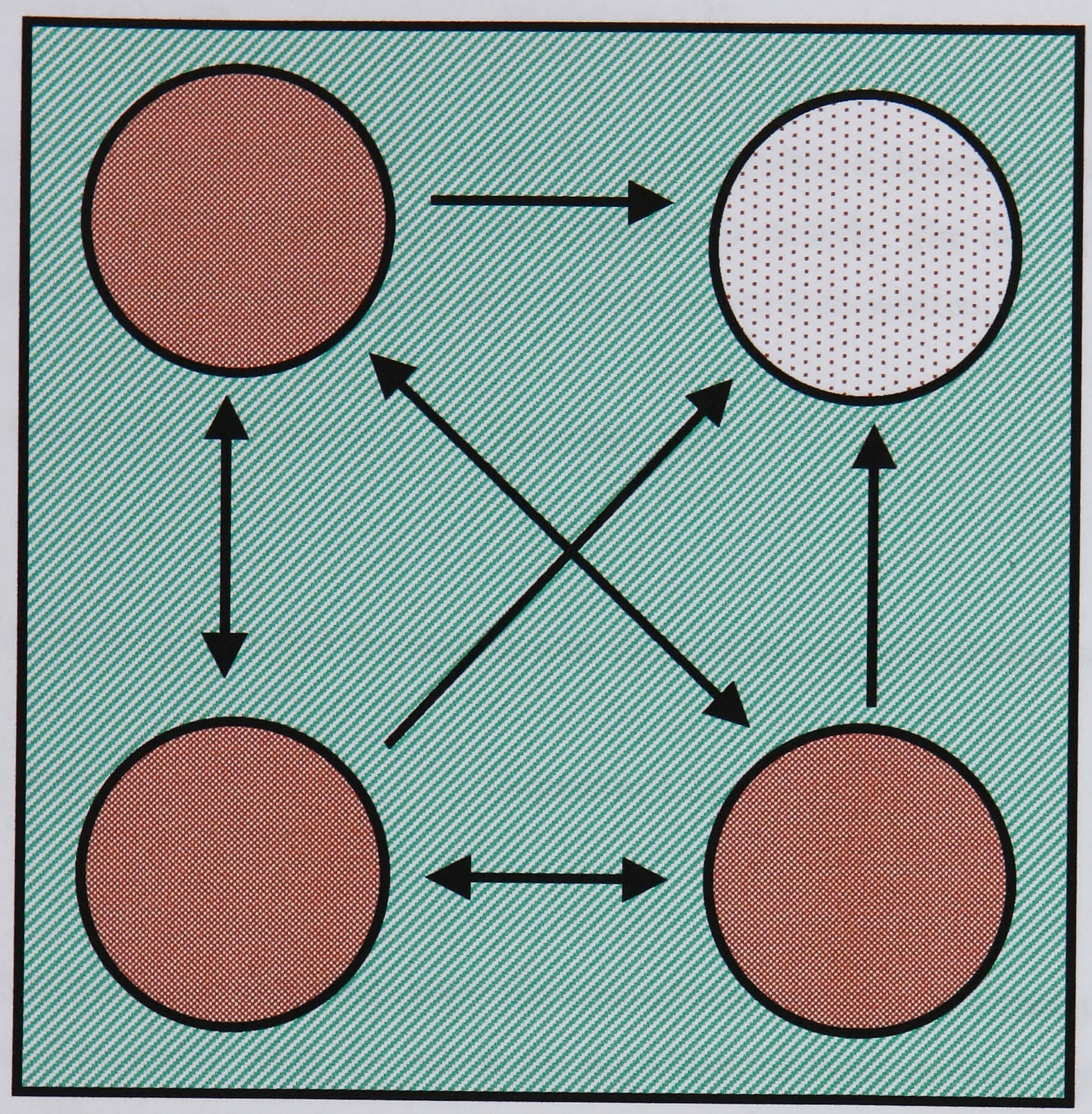


Figure 1.1 Diagrammatic representation of the Levins (1969) metapopulation model. The full brown circles represent the occupied suitable habitat patches, and the dotted circle, an empty suitable habitat patch. They are identical in size and shape, are equi-distant from each other and are embedded in a featureless, unsuitable habitat matrix (hatched green area). The black arrows represent the occasional movement that occurs between patches.

The Levins model is therefore:

$$dp/dt = mp(1-p) - ep \qquad \text{[Equation 1.1]}$$

This equation provides a simple model for metapopulation dynamics analogous to the logistic model as a paradigm of local population growth. The two equations are structurally the same which can be seen if the equation is re-written:

$$dp/dt = (m-e)\, p\, [1 - p/1-(e/m)] \qquad \text{[Equation 1.2]}$$

From this it can be seen that the equilibrium value of the metapopulation is:

$$p^* = 1 - e/m \qquad \text{[Equation 1.3]}$$

The difference $m - e$ therefore gives the rate of increase of p in a metapopulation (i.e. when p is small), while $1 - e/m$ is the equivalent of local carrying capacity, the stable equilibrium point towards which 'p' moves in time. The Levins model therefore predicts that the fraction of occupied habitat at equilibrium increases with a decreasing value of the ratio e/m. It also predicts that the metapopulation will persist (p is positive) as long as e/m is less than 1 (if it is greater than 1, the rate of increase in p becomes negative and the metapopulation declines). The model highlights a key feature of metapopulation dynamics: for the metapopulation to persist, recolonisation of empty habitat patches must occur at a sufficiently high rate to compensate for local population extinction and to allow an increase from small metapopulation size.

Some of the assumptions of the Levins model, such as patches being of equal area and isolation, can be relaxed without the need for major conceptual amendment

(Hanski, 1997). This allows the incorporation of, for example, mainland-island systems. These consist of a system of habitat patches that are located within dispersal distance from a very large habitat patch (mainland) where the local population never goes extinct (and hence, mainland-island metapopulations never go extinct). The inclusion of such systems does not challenge the central concept of metapopulation theory and greatly increases its use in understanding and describing systems found in the natural world. However, Hanski and Simberloff (1997) stress that the most important aspect of the model is the notion of discrete breeding populations occupying spatially separated habitat patches. The spatial arrangement must be such that a small amount of migration between the patches is feasible. If this aspect of a system cannot be defended, a different approach should be used (Hanski and Simberloff, 1997).

1.2.3 Empirical evidence for metapopulations in nature

Support for the classical metapopulation concept has so far been more for its plausibility than as a result of any compelling empirical evidence (Harrison and Taylor, 1997). Only two studies have presented systems representing 'true', 'classical' metapopulations: the pool frog, *Rana lessonae*, in ponds along the Baltic Coast of Sweden (Sjögren, 1991; Sjögren Gulve, 1994) and the butterfly, *Melitaea cinxia*, on granite outcrops in southwest Finland (Hanski *et al.*, 1994; Hanski, 1997). Despite this, the concept provides a very important framework through which to study and understand populations living in patchy, heterogeneous environments. It highlights the important features of an organism's population dynamics and behaviour that may enable it to survive in local populations in fragmented habitat. It has resulted in many studies laying emphasis on important features such as local extinction and migration rates and how these are affected by patch size and isolation. Such studies have been particularly useful in elucidating 'non-equilibrium' metapopulations. These are systems where a previously more continuous population becomes divided into smaller units and no functional metapopulation is created. The system exists as an assemblage of populations all slowly declining to extinction

(Hanski and Simberloff, 1997). Beier (1993), for example, studied cougars, *Puma concolor*, in the Santa Ana Mountains of California in a metapopulation context. He showed that at present, the species exists as a collection of small populations loosely linked by riparian corridors. His radio-telemetry data on movement, combined with a simulation model, showed how loss of particular populations and corridors would affect the entire system making it non-equilibrium and therefore non-viable.

1.2.4 Metapopulation Theory and genetics

Geneticists have been interested in the effect of spatial local division, local extinction and re-colonisation since 1931 (Wright, 1931; Wright, 1940; Wright, 1978). Since 1970 (Levins, 1970), the genetic consequences of metapopulation structure itself have been explored. However, it remains unclear what patterns in genetic variation are associated with such a system (Hastings and Harrison, 1994). Wright (1931) originally proposed that local, differential rates of extinction could drive natural selection at the among-population level. However, Slatkin (1985) argued that this was unlikely because ongoing local extinction implies ongoing re-colonisation and this constitutes gene flow. This will prevent local populations from becoming differentiated. Wade and McCauley (1988) showed that the outcome depends on how the new populations are founded. If colonising propagules are large and contain individuals from many populations, turnover will have the homogenising effect described by Slatkin. However, if groups of colonising organisms tend to be small, homogeneous and coming from only one or a few source populations, then the turnover of local populations can actually enhance their differentiation. However, it is important to note that the latter effect would not increase total variation in a metapopulation, only re-distribute it from within to among populations.

Under natural circumstances, the combination of high rates of local extinction and low rates of gene flow (c.f. Wright, 1931) seems unlikely. 'Weedy' species with naturally high rates of local extinction tend to show low values of differentiation

among populations due to their being good dispersers (Godt and Hamrick, 1991; Broyles and Wyatt, 1993). Natural metapopulation systems would therefore be expected to have low levels of differentiation among local populations.

In recently created (often human-made) metapopulations, local populations also show low rates of population differentiation. Population turnover accelerates genetic drift because alleles are lost when populations disappear and recently separated populations will not tend to be such efficient dispersers. As a result, the genetically effective size of a metapopulation may be only a tiny fraction of its consensus size (the actual number of individuals making up the population) (Gilpin, 1991). Because the total genetic variation of the metapopulation is depleted, this will result in low variation among local populations in absolute terms (Hastings and Harrison, 1994). In natural and/or recently created metapopulation systems, therefore, low variation between local populations would be expected. However, the overall genetic variation is expected to be lower in recently created systems than that found in natural metapopulation systems.

Many of the above-mentioned theories remain to be tested in the field. An added complication to testing such theories is the influence of the past history of the population on its present day genetic structure. However, the general conclusion is that in either type of metapopulation system (natural or human induced) some differentiation between the local populations is expected. This prediction can be used to help determine how a system is functioning. If there is no differentiation, the population may be acting as one, large, panmictic population. If there is differentiation between the local population, the population is more likely to be somewhere on the continuum between a 'patchy population' and a Levins (1969) metapopulation (as defined by Harrison and Taylor, 1997). However, such predictions must always be interpreted in combination with field data if reliable conclusions are to be reached (Koenig *et al.*, 1996).

1.2.5 Metapopulations and conservation in the 1990s

The focus on metapopulations, combined with that on genetics has further served to emphasize the population and the species as the dominant levels of concern in conservation (Hanski and Simberloff, 1997). However, such an approach carries with it many problems. An increasing amount of money is required for species conservation as habitat is continually lost. This will not be available to manage all the individual species that require such funds. A more recent view is that conservation should be carried out through the management of entire ecosystems (Swank and Van Lear, 1992): if the ecosystem is kept 'healthy', the component species will thrive (e.g. Morrisey *et al.*, 1994). Although the concept is laudable, it too is associated with many problems. There is, for example, no consensus definition of the term 'ecosystem management' (Grumbine, 1994; Soulé, 1994) and 'ecosystem health' is ill-defined; even the various US federal agencies have different working definitions (Morrisey *et al.*, 1994).

The recognition that some ecosystems have 'keystone species' whose activities govern the well-being of many other species suggests an approach that may unite the best features of single-species management and ecosystem management (Simberloff, 1998). Such an approach is focused on an understanding of the mechanisms that underlie the function and structure of an ecosystem. However, it is also focused on the population viability of the keystone species. Recent work by Kellman and colleagues (eg. Kellman *et al.*, 1998) showed how birds (in this case the keystone species group) helped to maintain tree diversity in tropical forest fragments in Belize and Venezuela. They compared fragments created by recent deforestation with old forest fragments of the same size that became disconnected from larger areas of forest during the Pleistocene drought. These old fragments contained as many tree species as areas of continuous forest, and richness accumulated from hectare to hectare within and among fragments (Tackaberry and Kellman, 1996). However, recently created fragments lost species very fast due to fire, displacement of resident

species by weedy species and the vulnerability of small populations due to chance extinction. By comparing the patches, it was possible to understand the processes operating in the older patches that maintain tree species diversity. In the older patches, for example, fire-tolerant species were concentrated around the edge and they protected the rest of the fragment. Such species were absent from the new fragment edges. A major reason for the high species diversity in the old fragments was that bird-dispersed species dominated the tree flora. Birds therefore played a major part in the conservation of forest fragment species richness. Bird vagility enriched individual fragments by seed exchange among fragments.

A metapopulation approach is helpful to determine how bird species will react to a new spatial arrangement of forest fragments. For example, are the fragments big enough to support viable bird populations from which dispersers can move to other fragments; are the fragments close enough so that birds can move between the fragments; and most importantly, will they move between the fragments? These questions must be answered as best as possible under each new fragmentation regime. Species dependent on mammal dispersal were absent from the fragments studied by Kellman and his colleagues and this is probably due to the scale of fragmentation being too great in relation to their dispersal distance (Brokaw, 1998). The size of fragment required for population persistence for the bird species and the distance that they will migrate must set the scale of a planned series of forest fragments.

It is not enough to say that bird migration will automatically maintain species diversity in newly created forest fragments. Response to landscape structure is notoriously species specific as are area requirements for population viability. Tropical bird species generally disperse very low distances. In Papua New Guinea, for example, distinct sub-species of several bird species are found on mountains only a few kilometres apart (Diamond, 1973). Other species, for example the antbirds of Panama, simply will not cross areas of water 100 metres wide (Willis, 1974). This

has caused species to go locally extinct on Barro Colorado Island, an island recently created by the making of the Panama Canal (Willis, 1974).

1.2.6 Landscape ecology and the metapopulation concept

Due to the importance of the metapopulation concept and its increasing use in conservation biology, there is a demand for it to become more spatially realistic. The assumption of homogeneous patches of favourable habitat in a homogenous matrix of unfavourable habitat no longer meets the demand for understanding population processes in real landscapes. The discipline of landscape ecology has the potential to give greater depth and realism to the metapopulation concept. Figure 1.2 shows the Levins (1969) model in a more realistic landscape context. The matrix itself is spatially structured and the spatial relationships between the patches play an active role in determining the dynamics within them. Patches are viewed as components in a landscape mosaic and what happens within and among the patches may be contingent on the composition and dynamics of other elements of the landscape mosaic (Wiens *et al.*, 1993; Andren, 1994; Wiens, 1995; 1996).

In terms of metapopulation dynamics, the most obvious effect of this underlying landscape structure is on individual movement patterns among patches and therefore on patch re-colonisation. Studies have shown that patch context is very important. The presence of red squirrels (*Sciurus vulgaris*) in wooded fragments in the Netherlands was positively correlated with the total amount of hedgerow surrounding the fragments (Verboom and van Apeldoorn, 1990). In Australia, the occupancy of corridors by arboreal marsupials could not be predicted by habitat features within the corridor but required additional information on the composition of the surrounding landscape (Lindenmayer and Nix, 1993). What happens within a patch is therefore often contingent on its location relative to the structure of the surrounding mosaic.

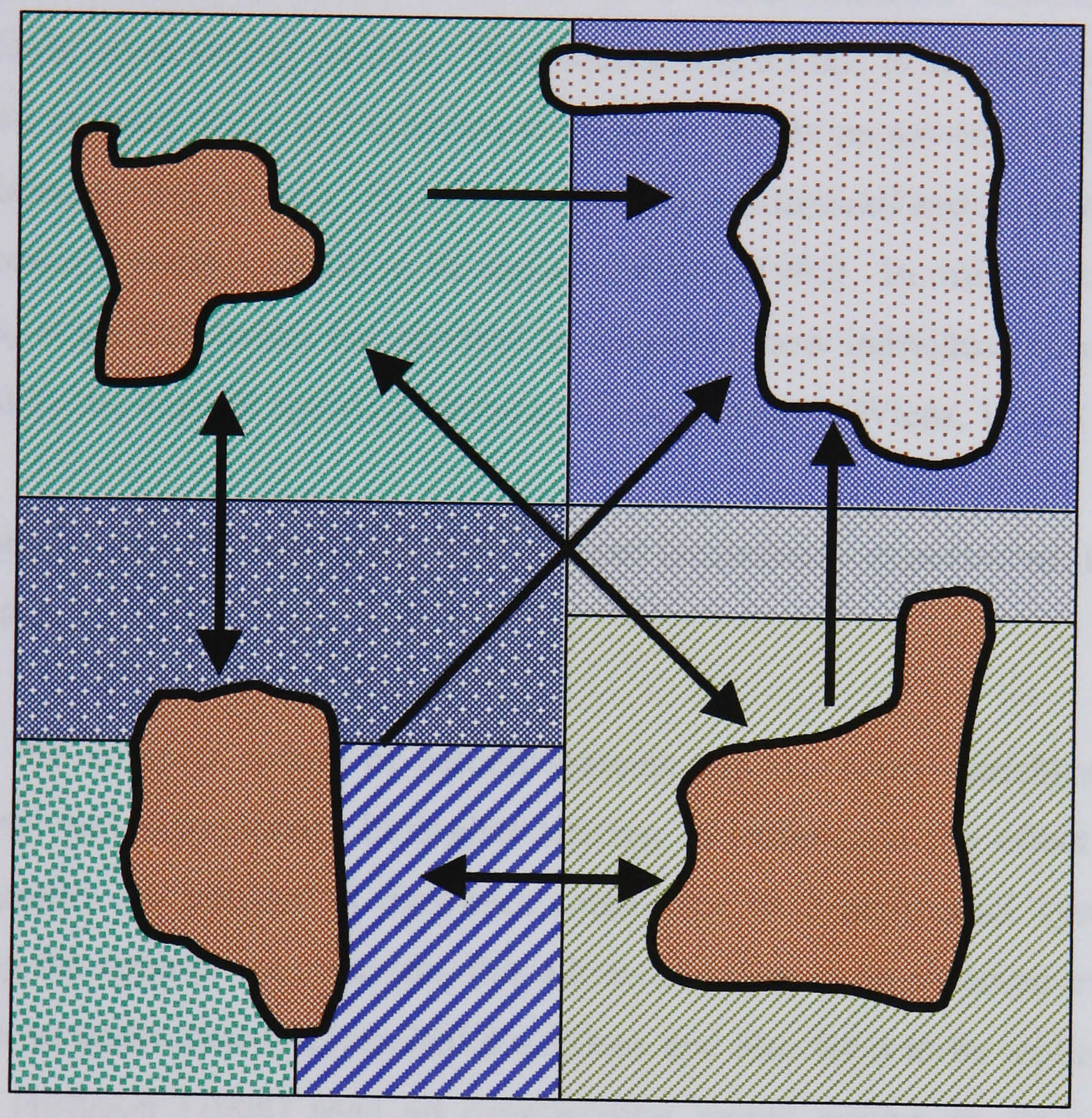


Figure 1.2 Diagrammatic representation of a metapopulation in a more realistic landscape context. Each different habitat type (which may be, for example, a coniferous woodland, a meadow, a lake) is represented by different colour and shading. The full brown areas represent the occupied suitable habitat patches, and the dotted brown area, an empty suitable habitat patch. The black arrows represent the occasional movement that occurs between patches. Movement between patches and the probability that migrating individuals will reach the patches, are affected by the explicit spatial configuration of the landscape.

Such studies indicate that landscape structure may often be an important component of organism movement and therefore population dynamics. Whether or not a spatially divided population functions as a metapopulation depends on how individuals move among patches. How individuals do this is affected by landscape structure in many ways and understanding these effects on movements is therefore of fundamental importance. However, as yet, the synthesis of metapopulation theory and landscape ecology is still to be realised (Wiens, 1995). In order to expedite this process, empirical studies are required to determine how individual movements are affected by the explicit spatial patterning of environments (Wiens, 1997).

1.3 Studying populations in a heterogeneous landscape - experimental model systems

Due to the complex nature of natural systems and the many variables involved, ecologists and evolutionary biologists striving to understand the effect of spatial heterogeneity on population dynamics often turn to experimental systems. By choosing the appropriate organism, this allows a system to be observed over several generations under strictly controlled conditions and also for it to be replicated many times. Huffaker (1958) used an experimental model system to show that in a predator-prey system, spatial heterogeneity may dampen population oscillations and promote the persistent co-existence of the two populations. Such studies are relatively easy and cheap to carry out and can provide much information. Kareiva (1987), for example, used a natural but manipulated system and found that increased spatial heterogeneity in aphid populations resulted in more frequent local population explosions and therefore less stable dynamics. He showed that this difference was due to the specific characteristics of the organism and warns against making robust generalisations about the effect of spatial heterogeneity on population dynamics.

More recently, Gonzalez *et al.* (1998) looked at the effect of landscape fragmentation in a miniature, moss-based ecosystem. Such a system is semi-natural

and easily manipulated at a scale that is large relative to the size and dispersal abilities of the animal populations that live in it. Their results showed that fragmentation resulted in a decline in the abundance and distribution of the multi-species animal community and the extinction of many species. However, when patches were connected by habitat corridors, an immigration 'rescue effect' prevented this from occurring. The results demonstrate the importance of metapopulation dynamics and landscape connectivity for the persistence of populations in fragmented landscapes. Like Kareiva's work (1987), the results are also important because the manipulation was not carried out under purely laboratory-based conditions.

In small organisms such as aphids and *Drosophila* which have short life-cycles and small area requirements, it is possible to link the effect of movement with population dynamic processes. In larger organisms, which cannot be manipulated so effectively and have longer generation times, this is not so easy. Usually, the effect of landscape heterogeneity on organism movement is studied and tentative suggestions about its effect on population dynamics are based on this. Wiens (eg. Wiens *et al.*, 1993) has looked at the movement of beetles (*Eleodes* spp.) in their semi-arid grassland habitat in artificially constructed mosaics of bare soil and grass. An individual beetle was released near the centre of a plot (either 5 x 5 metres or 20 x 20 metres) and its location recorded at five second intervals (Wiens and Milne, 1989). From this, a trajectory was re-constructed and summary statistics for ensembles of beetles computed. Analysis has shown that landscape structure does influence beetle movement: there is a significant tendency to avoid regions of the microlandscape with particular local fractal dimensions of bare soil. Other work (Crist *et al.*, 1992) has also demonstrated that variation in vegetation structure within 5 x 5 metre plots had significant effects on beetle movements and that these effects differed among *Eleodes* species. However, the relative complexity (fractal dimension) of the movement pathways was insensitive to variation among species or habitat type. Using fractal dimensions as a measure of complexity allows comparisons to be made between species. When beetle pathways were compared

with harvester ants and grasshoppers, the fractal dimensions of their movement were very different (Wiens *et al.*, 1995). This showed that they differ fundamentally in their response to heterogeneous landscapes.

A critical premise of such an experimental approach is that processes in one particular species at one particular scale may be compared with similar processes in another species at another spatial scale. Ims and Rolstad (1993), for example, compared space use responses of individual male capercaillie (*Tetrao urogallus*) from twelve years of field data with those of the root vole (*Microtus oeconomus*) which was studied under experimental conditions. Areas of homogeneous meadow were enclosed with steel sheets and mown to provide two large habitat patches (675 m^2) and two small ones (250 m^2) surrounded by very short mown grass. Laboratory bred voles were released into these plots and monitored for one month and the results were compared with the capercaille movement data. The results showed that when subject to habitat fragmentation on the same scale relative to their home-range requirements, voles and capercailles behaved similarly. This was the first study showing that space use response can be constant for such different taxa as birds and mammals over different absolute spatial scales. The advantage of such a model system can be seen from the fact that it took one month to gather more data than was collected for capercaillie in twelve years. Such an approach may therefore be able to identify fragmentation patterns that are likely to affect space use of a given species most strongly. It is then possible to speculate more effectively on how space use responses will affect population process and therefore population viability.

1.4 Species included in this study

Sorex araneus and *Sorex minutus*

Shrews belong to the family Soricidae. This family is divided into two sub-families, Soricinae ('red-toothed shrews') and the Crocidurinae ('white-toothed shrews'). *Sorex* is the most species-rich genus in the subfamily Soricinae and it includes both

Sorex araneus (the Common Shrew) and *Sorex minutus* (the Pygmy Shrew) (Churchfield and Searle, in press).

1.5 *Sorex araneus*

1.5.1 Distribution, habitat and abundance

S. araneus is widely distributed across most of Europe except for the Mediterranean region and Ireland. In Western Europe it is replaced by *Sorex coronatus* (Millet's Shrew). *S. araneus* occurs North to the Arctic coast and East into Siberia as far as Lake Baikal. Within these areas it is found almost everywhere if there is low vegetation cover available, but it is most abundant in thick grass, bushy scrub, hedgerows and deciduous woodland (Churchfield and Searle, in press). Population densities vary according to habitat and time of year but they can be up to 69 individuals per hectare (Shillito, 1963).

1.5.2 Life-cycle, spatial organisation and dispersal

S. araneus is an annual species. Generally, individuals are born in the summer, mate and produce offspring in the following early summer and die in the following autumn. Few individuals disperse far from their natal range in the year of their birth. It is essential to establish a territory in which to over-winter if they are to survive to breed the following spring (Shillito, 1963; Michielsen, 1966; Churchfield, 1980). Their territories are relatively stable, over-lapping and have a diameter of approximately 30 metres (Shillito, 1963; Michielsen, 1966). However, some long-distance dispersal by immatures has been recorded (e.g. Tegelström and Hansson, 1987).

During the breeding season, female home-ranges expand in size and overlap slightly. Early maturing males also extend their range and occupy areas with a high density of females. Later maturing males occupy more peripheral areas and may move very

large distances (up to 200 metres) in search of mates (Stockley *et al.*, 1993). *S. araneus* females have been shown to mate with many different males at each oestrus (Searle, 1989). The genetic diversity of the subsequent litter (which can contain up to ten individuals) will therefore be higher than that of a female mating with only one male. This strategy of 'multiple mating' is thought to reduce the probability of inbreeding (Stockley *et al.*, 1993). Due to *S. araneus* dispersal characteristics, mating between close relatives does occur and therefore the more males a female mates with, the lower the probability of her mating entirely with related ones.

1.5.3 Genetic diversity

Prior to the development of microsatellite primers for this species, work on their genetic population structure was carried out using protein electrophoresis. This method depends on the fact that non-denatured proteins with different net charges migrate at different rates through starch or acrylamide gels to which an electric current is applied. Their resulting position on the gel can be viewed by eye and so differences between individuals and populations can be detected. The charge of the proteins is due to the three amino-acids with positive side chains (lysine, arginine and histidine) and the two with negative side chains (aspartic acid and glutamic acid). The net charge of a protein determines the protein's movement toward the anode (positive pole) or cathode (negative pole) in the gel (Avise, 1994). This method was the first relatively easy way in which genotypic differences between individuals could be established. Such studies on *S. araneus* were stimulated by the extensive chromosomal polymorphism it displays over most of its geographical range (Searle and Wojcik, 1988). However, despite extensive chromosomal variations, there was no comparable differentiation at the allozymic level. Variation at protein loci was usually very low both within and among populations sampled in geographical proximity, regardless of karyotypic race (Frykman *et al.*, 1983; Wojcik and Wojcik, 1994). An exception to this is the difference between the Valais and Vaud races in the Alps where at least two diagnostic protein loci differentiate each chromosome race, thus indicating that there is limitations to gene flow (Hausser *et*

al., 1991; Neet and Hausser, 1991). Other karyotypic races occurring in the Alps are unable to be distinguished from one another by protein electrophoresis.

Protein polymorphism does not, therefore, offer the resolution required for elucidating population structure over short geographical distances. The development of microsatellite primers for this species has greatly improved the resolution at which population structure can be studied (Wyttenbach *et al.*, 1997; Balloux *et al.*, 1998). Previous studies have shown that heterozygosity is high at *S. araneus* microsatellite loci and this has enabled many chromosomal hybrid zones to be re-studied and genetic differences found between the different karyotypic races (e.g. Lugon-Moulin *et al.*, 1996; Wyttenbach *et al.*, 1999). Such studies have so far been restricted to hybrid zones.

1.6 *Sorex minutus*

1.6.1 Distribution, habitat and abundance

S. minutus has a similar global distribution to *S. araneus* but it is present in Ireland and a few other British islands where *S. araneus* is absent (Churchfield and Searle, in press). It is widespread in all types of habitat with preference for sites offering plenty of ground cover (O'Keeffe and Fairley, 1981). It is usually less abundant than *S. araneus* except in moorland habitats (Butterfield *et al.*, 1981). Although this species is largely ground dwelling, it can climb up into aerial vegetation (pers. obs.). Population densities vary according to habitat and time of year but can be up to 42 individuals per hectare (Ellenbroek, 1980).

1.6.2 Life cycle, spatial organisation and dispersal

The life-cycle and territorial system in this species is thought to be similar to that of *S. araneus* (Churchfield and Searle, in press). However, this species is thought to be more mobile than *S. araneus* and disperse larger distances (Michielsen, 1966).

1.6.3 Genetic diversity

No work on genetic population structure in *S. minutus* has previously been carried out. As a result, allozyme diversity is unknown. However, of the eight microsatellite primers developed for *S. araneus*, five have been shown to amplify microsatellite loci in *S. minutus* (Wyttenbach *et al.*, 1997). Thus there is potential for analyzing genetic population structure over a small geographical scale in this species.

1.7 Inter-specific competition between *S. araneus* and *S. minutus*

S. araneus and *S. minutus* are often caught in the same location as they have similar habitat requirements (e.g. Michielsen, 1966; Shore and Mackenzie, 1993). Indirect studies aiming to determine the relationship between these two species have produced differing results. Ellenbroek (1980) studied populations of *S. minutus* in Holland where they occur sympatrically with *S. araneus* and also in Ireland where *S. araneus* is absent. He found that during the summer and early autumn, population density, territory sizes and surface activity were the same in both *S. minutus* populations and he therefore concluded that there was no competition occurring between them. However, Malmquist (1986) carried out a similar study during the winter. He found that *S. minutus* populations that occur in sympatry with *S. araneus* were at lower densities than those that were not and therefore concluded that inter-specific competition was occurring between the two species.

A more recent study aimed to study the nature of their co-existence more directly. Dickman (1991) used field observations and field enclosures and concluded that inter-specific competition did exist and that it occurred due to 'interference competition' (Case and Gilpin, 1974). Although no direct encounters were observed, *S. minutus* actively avoided contact with *S. araneus* on an instantaneous basis and hourly removals of *S. araneus* from enclosures produced hourly increases

in the numbers of *S. minutus* that were captured. The rate of prey-capture by *S. minutus* also increased immediately after removal of *S. araneus*. Dickman (1991) suggests that as both species usually inhabit physically complex habitats, *S. minutus* may avoid contact with *S. araneus* by hiding. *S. araneus* can be a noisy animal when it moves through undergrowth and it also emits occasional squeaks. This may alert *S. minutus* to its presence and enable it to avoid an encounter (Dickman, 1991).

A difference in prey selection and prey habitat is often cited as the reason for the co-existence of the two species. *S. araneus* depends largely on earthworms for food and therefore often forages in burrows. *S. minutus*, on the other hand feeds mainly on arthropods which occur towards the surface. There is therefore a spatial separation between the two species which allows them to co-exist without numerous encounters (Rudge, 1968; Pernetta, 1976; Grainger and Fairley, 1978). Although this may be true to a certain extent, both species are caught readily in Longworth traps which are placed on the surface of the vegetation. This spatial segregation of the two species may therefore be over-emphasised.

1.8 Shrews as model species

In many habitats, shrews are relatively abundant and easy to trap. As a result, they have been used as model species in various ways.

1.8.1 Shrews as indicators of ecosystem change

A study by Shore and Mackenzie (1993) looked at the effect of catchment liming on *S. araneus* and *S. minutus* at three sites in Britain. The results not only indicated the effect on the two shrew species themselves but also on other components of the ecosystem. Catchment liming is sometimes used to improve water quality in upland regions. However, prior to their study there was concern that such treatment may be detrimental to the terrestrial ecosystem (e.g. Woodin and Skiba, 1990). *S. araneus* and *S. minutus* dominate the small mammal fauna on blanket bog and moorland

(Butterfield *et al.*, 1981; Yalden, 1981) and they eat a wide variety of invertebrates (Rudge, 1968; Pernetta, 1976; Churchfield, 1990). They are, therefore, an important component of the terrestrial ecosystem and any changes in their abundance or activity may indicate other, underlying changes.

The results of the study showed that in *S. minutus*, liming reduced abundance and surface activity. This was directly related to a decline in prey abundance at limed sites. In *S. araneus*, the results were less severe. Although surface activity was reduced for a short period, abundance was not affected. These results can be interpreted in terms of the different prey species taken by the two species. *S. araneus* and *S. minutus* feed on similar invertebrate groups but *S. araneus* also takes lumbricids and enchytraeids which were probably not affected by the liming process (Persson *et al.*, 1989; Shore and Mackenzie, 1993). Blanket bog is also an important habitat for birds which feed on invertebrates (Coulson and Whittaker, 1978) many of whose young feed extensively around pools (Tyler, 1989). Thus a knowledge of prey species taken by *S. araneus* and *S. minutus* combined with a study on their movement and abundance can be important in indicating environmental change induced by human management regimes.

1.8.2 Island Biogeography Theory and shrews

The distribution of shrews on small islands (less than 2 km^2) in Lake Sysma, Finland has been useful in illustrating the Theory of Island Biogeography (MacArthur and Wilson, 1967; Hanski, 1986). As island area increases, so does the number of shrew species occupying it (*Sorex caecutiens* was also included in this study), i.e. there is a species-area relationship, as predicted by the theory. As well as this, a compensatory effect was found in *S. araneus* between island area and isolation. This species was found on every island greater than 1.6 hectare and absent on every island smaller than 0.63 hectare. Of the 20 islands that were in the range 0.63-1.6 hectare, ten were occupied and these tended to be the less isolated ones. However, on larger islands (27 – 132 km^2), the theory did not explain distribution patterns

(Peltonen *et al.*, 1989). This highlighted the possible importance of 'historical contingency' as a major factor influencing shrew distribution, such as human-aided transport in ships.

Such studies have provided important information on the ability of shrews to disperse over water or ice (Diamond, 1987). However, they are specific to mainland-island situations (in the literal sense) and are not directly applicable to terrestrial fragmented habitats where a 'mainland' may not be present. They also concentrate on explanations of patterns and do not focus on conditions for persistence of the overall population.

1.9 Aims of the thesis

This thesis aims to use metapopulation theory as a starting point from which to assess spatial structure and movement patterns of *S. araneus* and *S. minutus* in a heterogeneous landscape. It is important to determine whether or not movement in *S. araneus* and *S. minutus* is affected by landscape structure as this will indicate whether, in a terrestrial setting, areas of suitable habitat have the potential to become 'island equivalents' if they are surrounded by unsuitable habitat. Their spatial distribution relative to the landscape structure can have a direct influence on their population viability. The effect of landscape structure on individual movement can be assessed by determining how often individuals move between areas of suitable habitat.

In addition, general ecological characteristics of the two species will be addressed. Due to their abundance in the British mammalian fauna and their readiness to enter traps, these species also make good model organisms to study more generally how landscape structure may affect movement. However, it is also important in its own right to discover how landscape structure affects these species. The aims will be realised through a live-trapping regime which will give direct information on spatial arrangement and movement. In addition, genetic analysis of individuals will be

undertaken which will give indirect information on spatial arrangement and movement.

1.10 The study site

The study site chosen for this work was Fulford Golf Course in Heslington, York. The landscape structure at the site can be viewed as a terrestrial version of a series of islands in a lake and can be seen in Figure 1.3. A traditionally managed British golf course consists of two main habitat types. The greens and tees are subject to concentrated golf-playing pressure and receive intensive management in order to maintain the quality and smoothness of their surface. This involves regular mowing, rolling and spraying. The fairways are usually about 35 metres wide and are also mown frequently. The greens, tees and fairways therefore make up 'unfavourable' habitat from a shrew's point of view. These areas provide absolutely no cover from predators and no habitat for their invertebrate prey. Figure 1.4 shows the very short grass of the fairway. The remainder of the course consists of various gradations of grassland 'rough' which is more or less unmanaged (Tobin and Taylor, 1996). Such areas can be viewed as 'favourable' habitat and can be seen in Figure 1.5. These areas provide cover from predators and habitat for invertebrate prey. Table 1.1 shows the major plant species making up these favourable patches and Table 1.2 shows the details of their size and distance to neighbouring patches.

This study site provides a unique opportunity to study animal movement in a terrestrial heterogeneous landscape. The classification of the area into two main habitat types also enables such a study to be carried out without the complication of an unmanageable number of landscape variables. Figures 1.6 – 1.7 show the sharply defined border between these two main habitat types. Although the patches vary slightly in vegetational composition, both shrew species have been shown to be insensitive to the successional stage of grassland (Churchfield et al., 1997). The golf-course has been in place since 1906, a time-span which is equivalent to 92 generations of shrews.

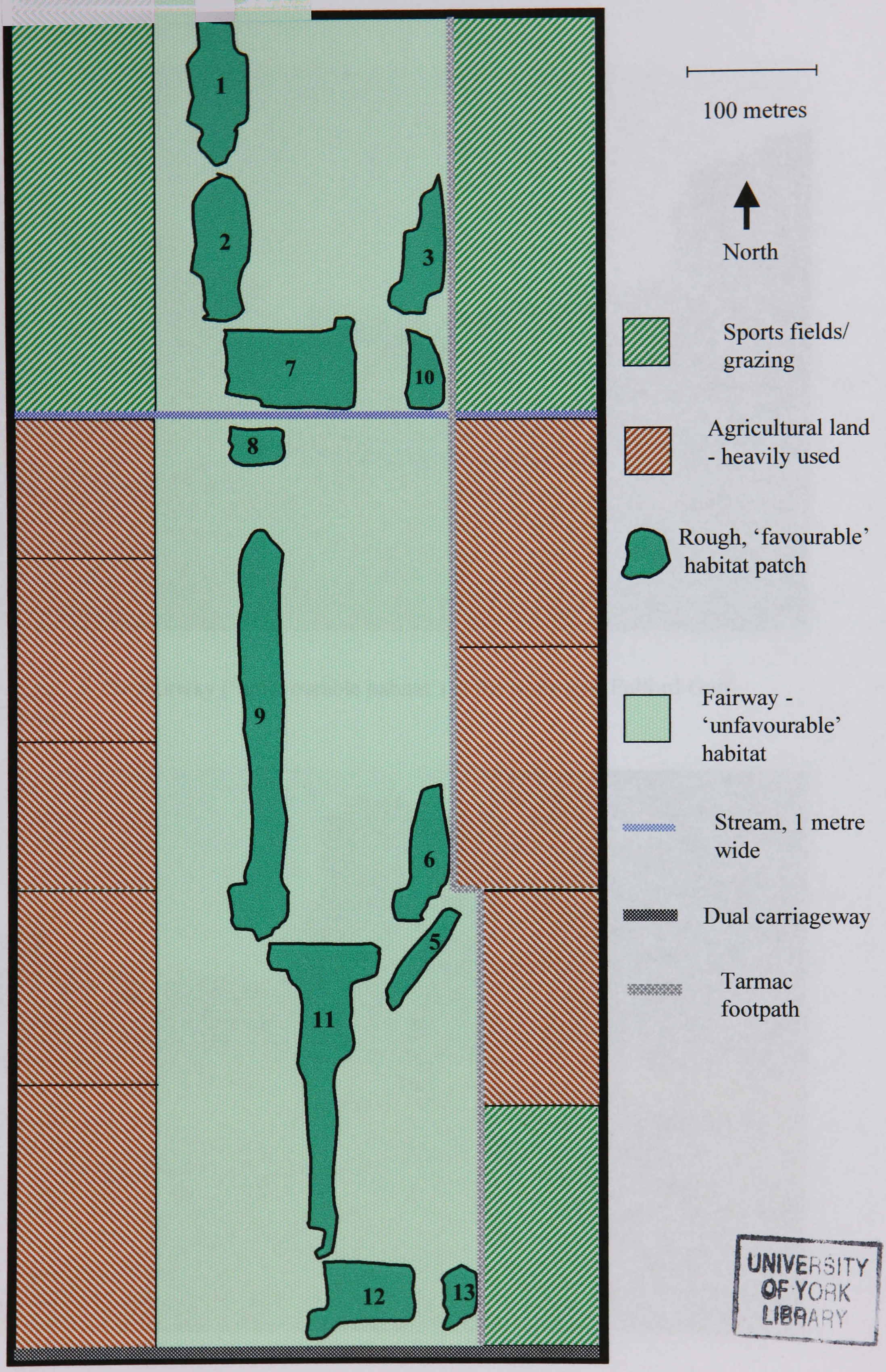


Figure 1.3 A map of the study site, Fulford Golf-Course, showing the patches of rough, 'favourable' habitat embedded in the 'unfavourable' habitat of fairway. To the North of the site is a built up area

Figure 1.4 The Fairway ('unfavourable habitat') at the study site, Fulford Golf-Course

Figure 1.5 A rough patch ('favourable habitat') surrounded by the fairway ('unfavourable habitat') at the study site, Fulford Golf-Course.

SPECIES	COMMON NAME
TREES	
Betula pendula	Silver birch
Fagus sylvatica	Beech
Pinus sylvestris	Scots Pine
Quercus robur	Oak
SHRUBS	
Crataegus monogyna	Hawthorne
Hedera helix	Ivy
Pteridium aquilinum	Bracken
Rubus fruticosus agg.	Bramble
Ulex europaeus	Gorse
GRASSES/FORBS	
Agrostis spp.	Bent grasses
Dactylis glomerata	Cocksfoot
Holcus lanatus	Yorkshire Fog
Lolium perenne	Perennial Rye Grass
Poa trivialis	Rough meadow Grass
Ranunculus repens	Creeping Buttercup
Rumex obtusifolius	Broad-leaved Dock
Taraxicum officinale agg.	Dandelion
Trifolium repens	White (Dutch) Clover

Table 1.1 A list of the most common plant species making up the rough habitat patches at the study site, Fulford Golf-Course.

PATCH NO.	PATCH SIZE (AREA, m^2)	DISTANCE TO NEAREST NEIGHBOUR (m)	NEAREST NEIGHBOUR
1	3,184	25	Patch 2
2	2,220	13.5	Patch 7
3	2,725	19	Patch 10
5	1,683	5	Patch 6
6	2,165	5	Patch 5
7	2,806	11	Patch 8
8	1,000	11	Patch 7
9	7,840	15	Patch 11
10	1,100	19	Patch 3
11	6,758	2	Patch 12
12	3,688	2	Patch 11
13	1,508	25	Patch 12

Table 1.2 The area, nearest neighbour and distance to nearest neighbour of the twelve favourable habitat patches at the study site, Fulford Golf-Course.

Figure 1.6 The sharp contrast between the 'favourable' and 'unfavourable' habitat at the study site, Fulford Golf-Course.

Figure 1.7 The 'unfavourable' habitat (fairway) between two adjacent 'favourable' habitat patches

The course is bordered by sports fields and grazing land (Figure 1.8), heavily worked agricultural fields (Figure 1.9) and a dual carriage-way which do not provide suitable habitat for either species. Although some immigration into the site from the surrounding areas is inevitable, it is anticipated to be low due to the lack of large areas of suitable habitat. The study site thus provides an excellent opportunity to study how landscape structure in a terrestrial setting affects spatial distribution and movement in *Sorex araneus* and *Sorex minutus*.

1.11 Thesis structure

Chapter 2 describes the results of an intensive trapping regime carried out over ten months (November 1997 – August 1998) which was designed to investigate spatial structure and movement in the two shrew species at the site. This Chapter concentrates on individuals from the 1997 cohort. It also aims to determine whether or not movement is actually restricted by landscape structure so as to be able to extrapolate the results to other locations. Chapter 3 focuses on the 1998 cohort. The trapping regime was begun in June 1998 and therefore animals were captured very soon after they had left the nest. This allows general ecological characteristics to be examined. It also enables life-time movement patterns to be examined in a landscape context. Chapter 4 involves *S. araneus* only and aims to determine whether or not timing of birth affects movement and other associated characteristics. This chapter also explores the consequences of its findings for current theories explaining *S. araneus* reproductive strategies. Chapter 5 uses microsatellite loci to examine the genetic population structure of the two species of shrew. Chapter 6 provides a summary discussion of the main findings of the work.

Figure 1.8 The sports fields which border some of the study site, Fulford Golf-Course.

Figure 1.9 An agriculturally worked field, typical of those surrounding the study site, Fulford Golf-Course.

CHAPTER 2

SPATIAL STRUCTURE AND MOVEMENT OF INDIVIDUALS

2.1 INTRODUCTION

Destruction of natural habitat is occurring at an alarming rate and poses the single greatest threat to the long-term survival of species on earth (Barbault and Sastrapradja, 1995). One consequence of such destruction is the increased level of habitat fragmentation, i.e. the remaining habitat is found in ever smaller and more isolated discrete fragments (patches) (Hanski, 1999). It is therefore important to understand the dynamics of populations living in such patchy environments. Metapopulation theory (Levins, 1969) is becoming increasingly popular as a way to do this. This chapter aims to use this theory as a starting point to assess the spatial structure of *S. araneus* and *S. minutus* at the study site.

The first premise of metapopulation theory is that the landscape contains suitable habitat patches for the species concerned (Hanski and Simberloff, 1997, Hanksi, 1999). In a metapopulation sense, a patch is defined as 'a continuous area of space with all necessary resources for the persistence of a local population and separated by unsuitable habitat from other patches (at a given time a patch may be occupied or empty)' (Hanski and Simberloff, 1997). The second premise is that the individuals making up the populations are responding to the landscape structure such that the population is operating as a series of local populations occupying the patches rather than as one large population utilising all the patches. In this context, a local population is defined as 'a set of individuals that live in the same habitat patch and therefore interact with each other' (Hanski and Simberloff, 1997).

The usefulness of the metapopulation approach is therefore dependent on the rate of migration between local populations occupying the habitat patches. The more that occurs, the less useful it is to classify them as separate. Levins (1969) stated that the

migration rate must be so low that it plays no role in the dynamics of existing local populations. However, the recent extension of the metapopulation concept to systems that do not rigorously adhere to the Levins (1969) model has meant that more migration than this can be acceptable and the concept still useful. Source-sink systems, for example, are now included in the metapopulation concept. This refers to a system of patches in which the population growth rate at low density and in the absence of immigration is negative (sinks) and patches in which the growth rate at low density is positive (sources) (Hanski and Simberloff, 1997). Such a concept has been particularly useful in elucidating processes occurring in endangered species such as Bachman's sparrow (*Aimophila aestivalis*), an endangered North American passerine (Pulliam *et al.*, 1992) and the Red Squirrel in Europe (Celada *et al*, 1994). However, Hanski and Simberloff (1997) state that if migration is very high, i.e. more than fifty percent, a metapopulation approach is unlikely to be helpful.

The aim of this chapter is to examine the spatial structure and movement patterns of *S. araneus* and *S. minutus* individuals relative to the habitat patch structure found at the study site i.e. to see whether or not the habitat patches each contain a local population of individuals. It is particularly important to look at this in two closely related species which share similar habitat requirements. Two such species will often be affected by the same habitat destruction but may differ in their response to the resulting landscape structure.

2.2 METHODS

2.2.1 Live-trapping

Small mammal live-trapping was carried out on Fulford Golf-Course during November 1997 and March, June and August 1998. Longworth live-traps (Chitty and Kempson, 1949) were placed in 10 metre grids over the entire area of each patch with one trap at each trap point. The range in the number of traps therefore varied according to patch size (see table 1.2). This is illustrated in Figure 2.1. Each trap contained hay for bedding and was baited with a mixture of rolled oats, carrots and blowfly puparia. They were all set

to a tripping weight of 2 g. Traps were left in place for 5 days. During November 1997 and March 1998, traps were set in the late afternoon (so that the last trap was set just before dusk) and checked early in the morning. During June and August 1998, traps were not set overnight because of the danger of retaining lactating females for long periods of time. Traps were therefore set at 7.30am and checked 3 hours later.

Due to the size and number of patches at the site, it was not possible to trap all of them at the same time. One hundred traps were placed on three patches for 5 days and these traps were then moved to a different set of three patches within 24 hours. Trapping of the whole site (all 12 patches) was always completed within 24 days. This regime is illustrated in Figure 2.2. No pre-baiting was done as this would have increased the time it took to trap the whole site, thus making the results from each set of three patches within a trapping session less comparable.

Captured animals were identified, sexed (according to Searle, 1985), aged as adults or sub-adults, weighed (using a Pesola spring balance accurate to 0.1 g) and assigned to the trap and patch in which they were caught. Individuals were marked using toe-clipping (under Home Office licence).

2.2.2 Movement

The extent of movement between habitat patches was quantified and inter-patch movement was compared with intra-patch movement to see if there was evidence to suggest that the habitat borders of the patches were restricting movement. In order to ascertain if movement between patches should be expected, the movement distances were compared with the inter-patch distances using a Mann-Whitney U-test. The movement distance values used were the maximum straight-line distances between each individual's furthest two points of capture.

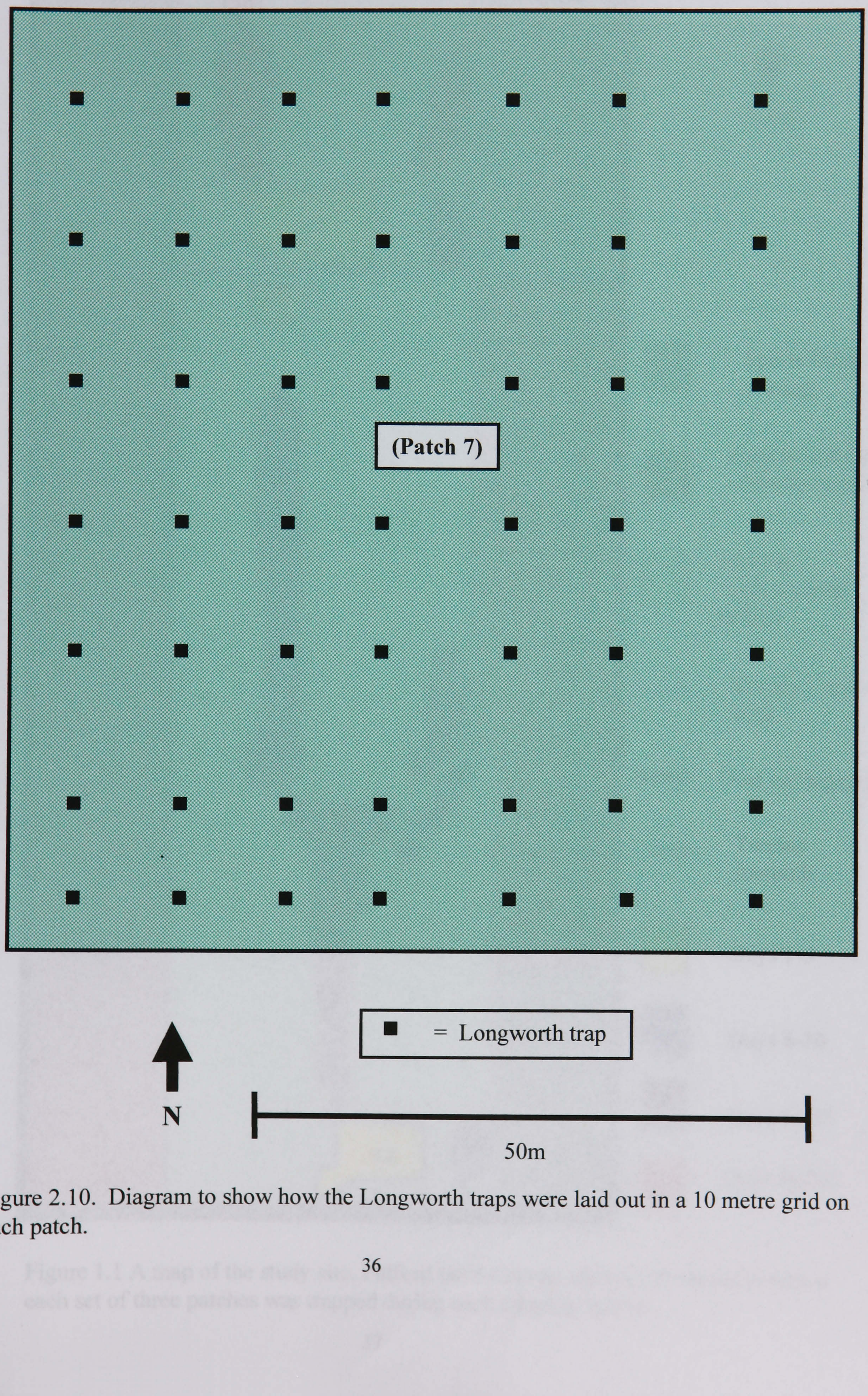


Figure 2.10. Diagram to show how the Longworth traps were laid out in a 10 metre grid on each patch.

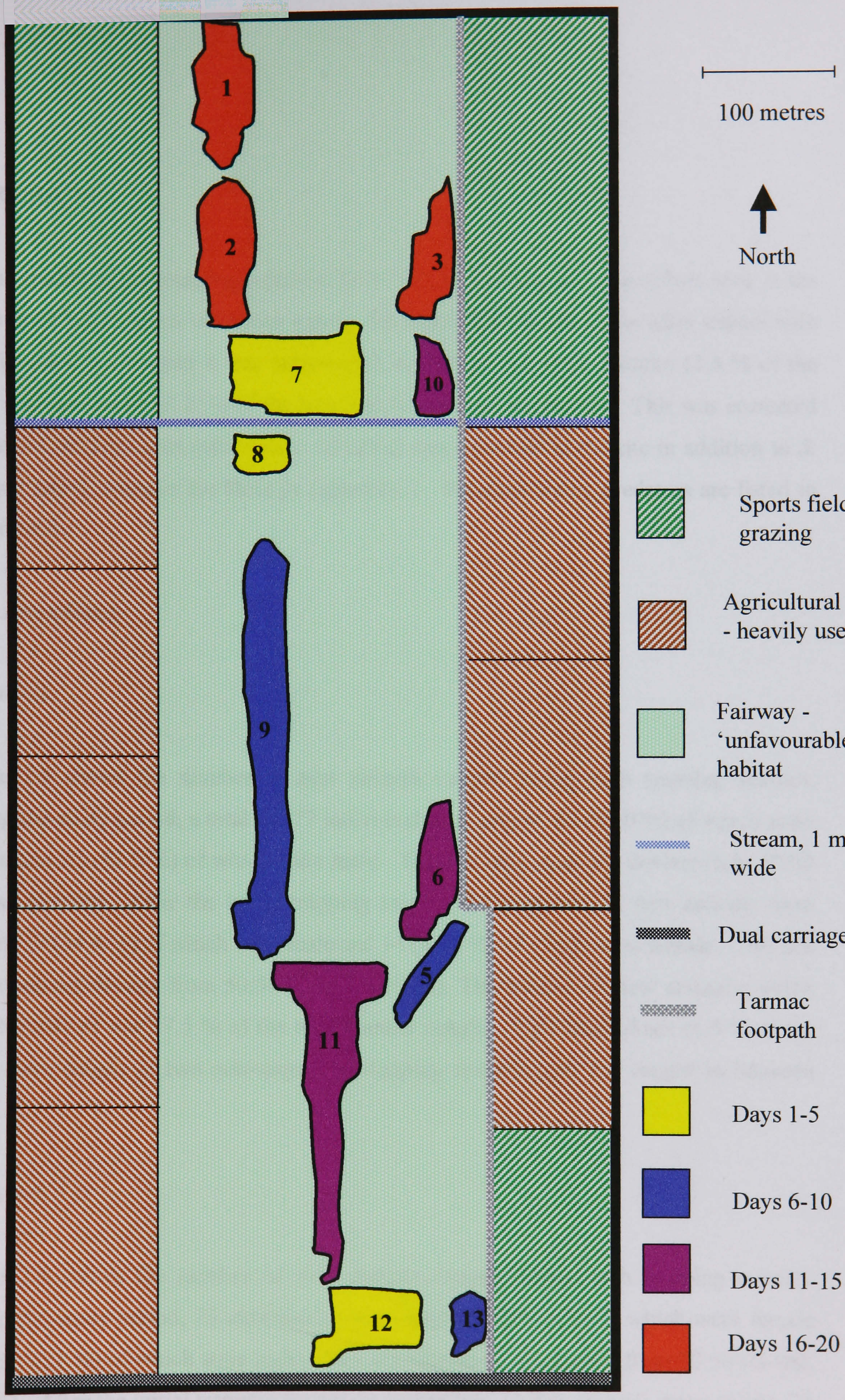


Figure 1.1 A map of the study site, Fulford Golf-Course, showing the order in which each set of three patches was trapped during each trapping session.

2.3 RESULTS

All the results of the trapping regime refer to the 1997 cohort (i.e. the cohort born in the Summer of 1997) unless otherwise stated. By comparing the sex of the adult animal with that recorded for it when it was immature it was found that three females (3.5 % of the total) and two males (2.2 %) of the total had been sexed incorrectly. This was corrected before any analysis was carried out. Mammal species found at the site in addition to *S. araneus* and *S. minutus* are listed in Appendix 1. Potential shrew predators are listed in Appendix 2.

2.3.1 Abundance

S. araneus

Figure 2.3 shows the number of new animals caught during each trapping session. During the study period, a total of 177 individuals was caught, 85 (48.0 %) of which were female and 92 (52.0 %) of which were male. This sex ratio does not deviate from 50:50 (G-test, $p>0.05$). After the initial trapping session in November, 31 new animals were caught, 17 (54.8 %) of which were male and 14 (45.2 %) of which were female. This sex ratio does not deviate from 50:50 (G-test, $p>0.05$). The number of new animals caught after November was 17.5 % of the total number caught. Eight individuals (4.5 % of the total) were caught in two non-sequential trapping sessions and not caught in between them.

S. minutus

Figure 2.4 shows the number of new animals caught during each trapping session. During the study period, 73 individuals were caught, 35 (47.9 %) of which were female and 38 (52.1 %) of which were male. This sex ratio does not deviate from 50:50 (G-test, $p>0.05$). After the initial trapping session in November, 46 new animals were caught, 21

(45.7 %) of which were female and 25 (54.3 %) of which were male. This sex ratio does not deviate from 50:50 (G-test, $p>0.05$). The number of new animals caught after November is 63.0 % of the total number caught. There were no individuals caught in non-sequential trapping sessions but not in the middle session.

2.3.2 Habitat suitability

Patch 4 was destroyed prior to the start of the live-trapping regime. Patch 8 was destroyed after March 1998.

S. araneus

The pattern of captures in each patch for this species is shown in Figure 2.5. Individuals of this species were present in all patches at some point during the study period. They over-wintered in all patches except 5 and 8. Over-wintering is defined as being caught in a patch in November 1997 and then again in the same patch during one of the 1998 trapping sessions. Juvenile animals (offspring of the 1997 cohort) were caught in all patches during Summer 1998 (June and August) and therefore it was assumed that breeding was occurring in all patches.

S. minutus

The pattern of captures in each patch for this species is shown in Figure 2.6. Individuals of this species were present in all patches apart from 5 and 8 at some point during the study period. They over-wintered in all patches except for 2, 3, 5, 6, 8 and 10. Juvenile animals (offspring of the 1997 cohort) were caught in all patches during Summer 1998 except for 3, 5 and 10.

2.3.3 Inter- and intra-patch movement

The results of the movement recorded during the trapping regime can be seen in Table 2.1.

S. araneus

Of the 85 females caught during the study period, only one individual was found to have moved from one patch to another. There were therefore 84 individuals (98.8 %) caught in one patch only. Of the total number caught, 57 (67.1 %) were caught twice or more. Of these, one individual (1.8%) was found to have moved between patches.

Of the 92 males caught during the study period, eight individuals were found to have moved from one patch to another. There were therefore 84 individuals (91.3 %) caught in one patch only. Of the total number caught, 57 individuals (62.0%) were caught twice or more. Of these, eight individuals (14.0%) were found to have moved between patches. There was a significant difference between the number of males that moved between patches and the number of females that moved between patches in this species (Fisher's Exact Test, $p<0.05$).

Of all movement recorded in this species, only 5.3 % was between patches. Figure 2.7 shows all the inter-patch movement that was recorded in this species during the study period. Figure 2.8 shows all the intra-patch movement recorded within one of the patches (Patch 7) during the study period. There was a significant difference between the number of inter- and intra-patch movements in males and females in this species (Fisher's Exact Test, $p<0.05$).

S. minutus

Of the 35 females caught during the study period, four individuals (11.4 %) were found to have moved from one patch to another. There were therefore 31 individuals (88.6 %) caught in one patch only. Of the total caught, 21 individuals (60.0 %) were caught twice or more. Of these, four individuals (19.0 %) were found to have moved between patches.

Of the 38 males caught during the study period, 12 individuals (31.6 %) were found to have moved from one patch to another. There were therefore 26 individuals (68.4%) caught in one patch only. Of the total caught, 22 individuals (57.9 %) were caught twice or more. Of these, 12 individuals (54.5 %) were found to have moved between patches. There was a significant difference between the number of males and females that moved between patches in this species (Fisher's Exact Test, $p<0.001$).

Of all movement recorded in this species, only 19.7 % was between patches. Figure 2.9 shows all the inter-patch movement recorded in this species during the study period. Figure 2.10 shows all the intra-patch movement recorded within one of the patches (Patch 7) during the study period. There was also a significant difference between the number of inter- and intra-patch movements in males and females in this species (Fisher's Exact Test, $p<0.001$).

Inter-specific comparisons

There was a significant difference between both the number of individuals that moved (Fisher's Exact Test, $p<0.001$) and the number of intra- versus inter-patch movements (Fisher's Exact Test, $p<0.01$) in male *S. araneus* and *S. minutus*. In females, there was a significant difference between the species in the number of individuals that moved between patches (Fisher's Exact Test, $p<0.05$) but not in the number of inter- versus intra-patch movements made (Fisher's Exact Test, $p>0.05$).

2.3.4 Patch isolation

Patch isolation is measured in terms of the difference in distributions between the movement distances of the animals relative to the nearest-neighbour inter-patch distances. The nearest-neighbour inter-patch distance for each patch is the distance to its nearest neighbouring patch. These distances are listed in Table 1.2 (Chapter 1). This is important because it ensures that the study is being carried out at the correct spatial scale. It is equivalent to comparisons made in similar studies, such as those looking at the effect of roads on individual movement. Richardson *et al.* (1997), for example, state that individuals moved along the road-side verge at distances equivalent to the distance across the road. This ascertains that it is not dispersal tendencies which are preventing individuals crossing the unfavourable habitat.

S. araneus

For the 114 *S. araneus* individuals caught twice or more, the maximum straight-line distance between the furthest two points of capture was calculated (Figure 2.11). There was a significant difference between the distances moved by this species and the inter-patch distances in both males and females (Mann-Whitney U-test: females and males, $p<0.01$). The medians show that the distances moved were greater than the inter-patch distances (females, 20 m, males, 22 m; nearest-neighbour inter-patch distances, 12 m). There was no significant difference between the distances moved by males and females in this species (Mann-Whitney U-test $p>0.05$).

The three outlying values for movement distances (all undertaken by males: 238m, 545m and 1, 026 m) were substantially larger than the other values and therefore excluded so as not to bias the analysis.

S. minutus

For the 43 *S. minutus* individuals caught twice or more, the maximum straight-line distance between the furthest two points of capture was calculated (Figure 2.12). There was a significant difference between the distances moved by this species and the inter-patch distances in both males and females (Mann-Whitney U-test: females and males, $p<0.01$). The one outlier was excluded from this analysis. The medians show that the distances moved were greater than the inter-patch distances (females, 32 m, males, 95 m; inter-patch distances, 12 m). A significant difference was found between male and female movement distances in this species (Mann-Whitney U-test, $p<0.05$). The median movement distances (females, 32 m and males 95 m) show that male movement distances tended to be greater than female movement distances.

2.3.5 Inter-patch distance

Figures 2.7 (*S. araneus*) and 2.9 (*S. minutus*) show graphically the movements made by the two shrew species during the study period.

S. araneus

The most frequently crossed inter-patch distance for this species was between patches 11 and 12. The distance between these two patches is 2 metres and is the shortest inter-patch distance at the site. Twelve inter-patch movements were made and of these, six (50%) were between these patches.

S. minutus

The most frequently crossed inter-patch distance for this species was also between patches 11 and 12. In *S. minutus*, 25 inter-patch movements were made and of these, eight (32.0 %) were between these patches.

Is not possible to deduce any other patterns, such as the influence of increasing inter-patch distance with movement frequency, from these results. This is because of the low number of inter-patch movements made by individuals in both species and the spatial nature of the patches at the site.

2.3.8 Spatial nature of movement

S. araneus

Only one individual (a male) was found to have moved back and forth between two patches. The distance covered was 2 metres, between patches 11 and 12. All other inter-patch movement was uni-directional (i.e. the individual did not return to its original patch). The only female that moved between patches, moved to an adjacent patch. Five males also moved to adjacent patches. However, three males moved further than the adjacent patch.

S.minutus

Four individuals were found to have moved back and forth between patches. Two of these moved between patches 11 and 12. One other individual moved between patches 13, 12, and 11. This individual was last caught in its original patch (patch 13). Another individual moved between patches 3, 7, 10 and 2 but did not return to its original patch. Three females moved to adjacent patches and only one to a non-adjacent patch. Of the 12 males that moved between patches, seven moved to an adjacent patch. Five moved to non-adjacent patches.

2.3.7 The effect of age-class on response to landscape structure

S. araneus

Only one female moved between patches and this occurred when the animal was adult. Of the eight males that moved from one patch to another, four did so when they were adults. Two of these individuals also moved when they were sub-adults. Three individuals only moved while they were sub-adults. With one individual, it is not possible to tell when it moved due to the time between captures.

S. minutus

Three females moved between patches. In all cases, the animals were adult. Of the thirteen males that moved between patches, eight did so when they were adult. Of these, one also moved when it was sub-adult. Five individuals moved when they were sub-adults. Movement could not be assigned to an age-class in five individuals due to the time between captures.

2.3.8 The influence of weight on inter-patch dispersal

The weight of those animals that moved between patches was compared with animals in the same age class that did not using a Mann-Whitney U-test. No difference was found in the weight of these two groups of individuals ($p>0.05$ in all cases).

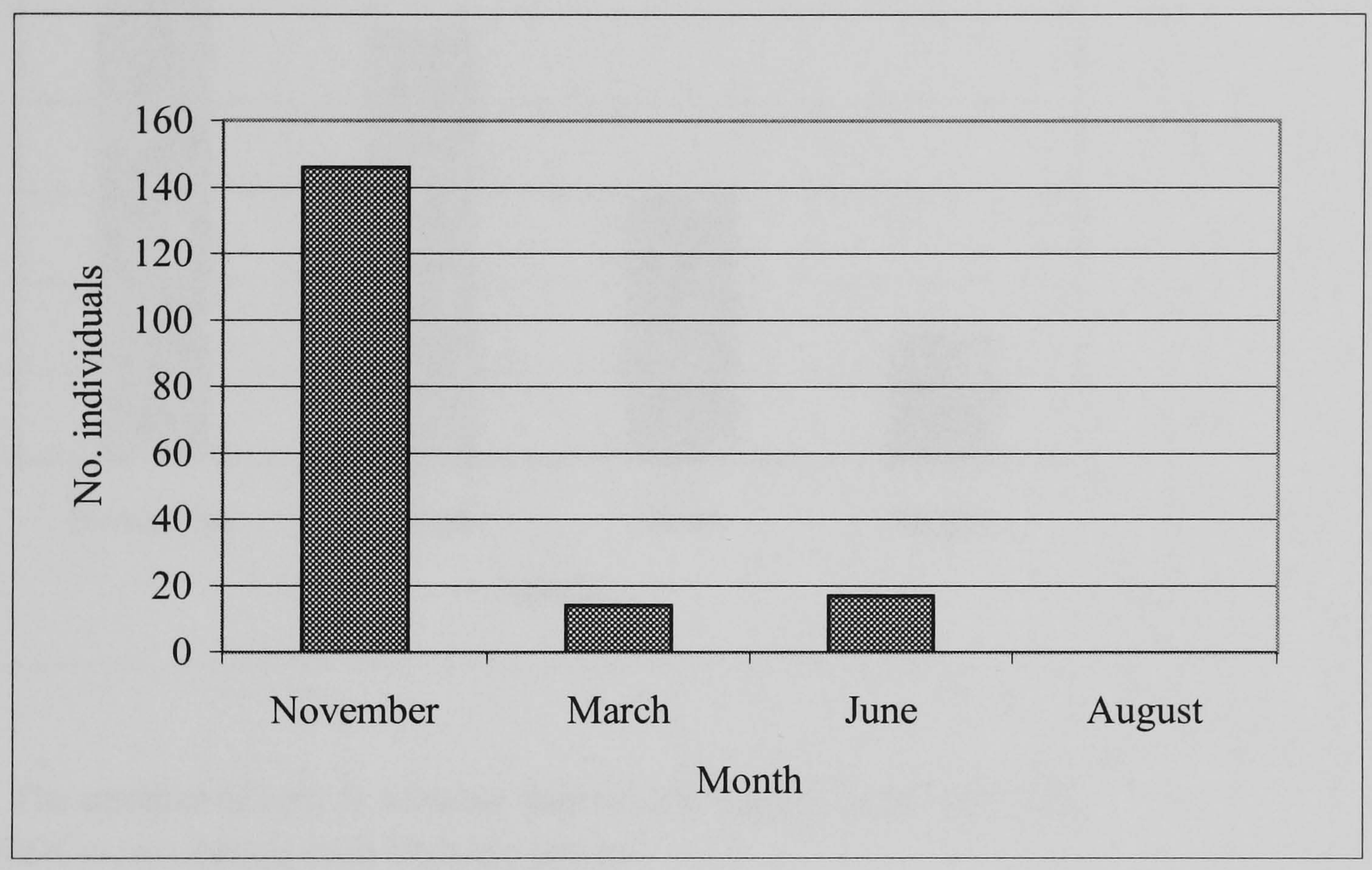


Figure 2.3. The number of new *S. araneus* individuals caught at the study site, Fulford Golf-Course, during each trapping period.

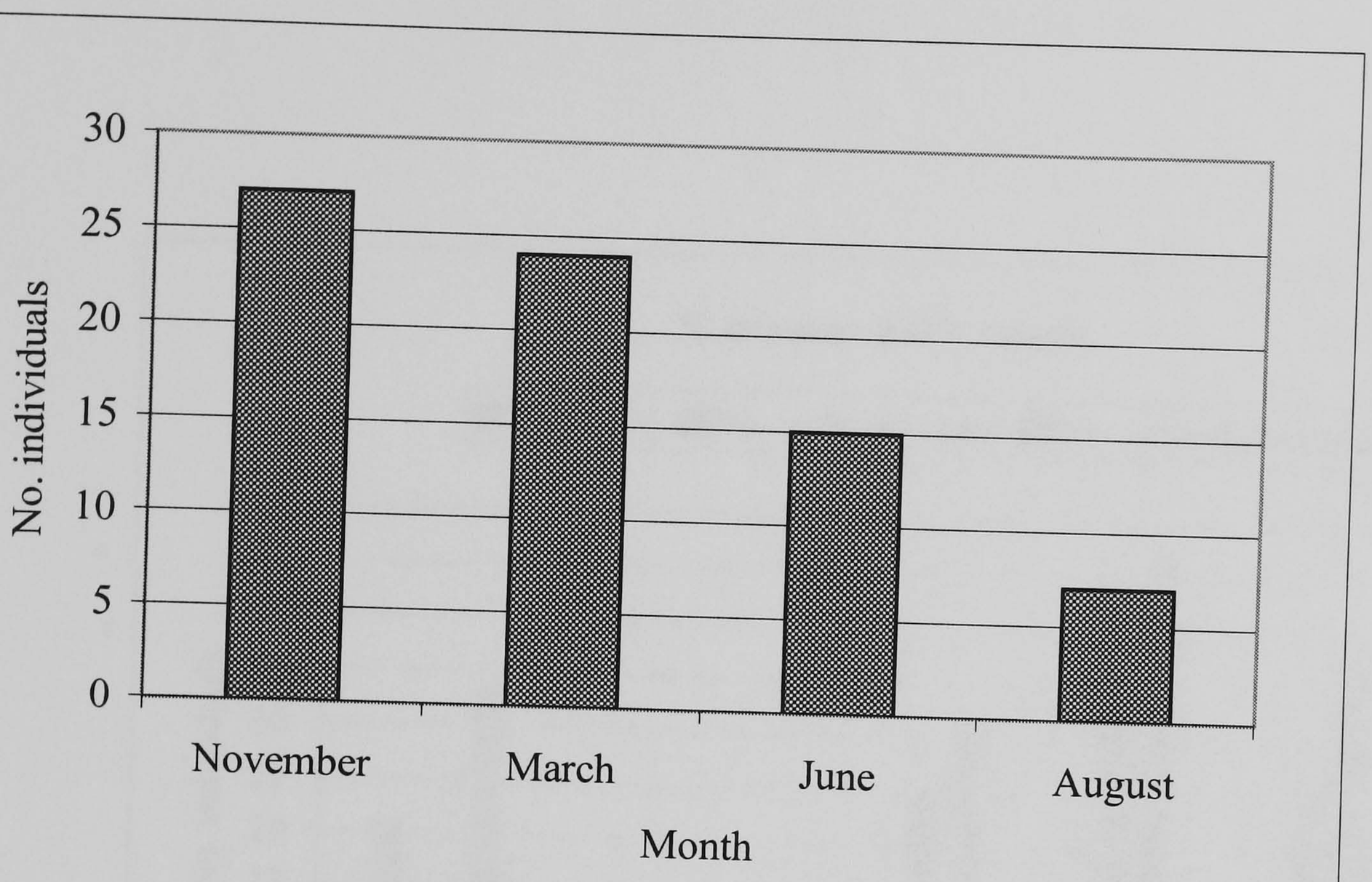


Figure 2.4. The number of new *S. minutus* individuals caught at the study site, Fulford Golf-Course, during each trapping period.

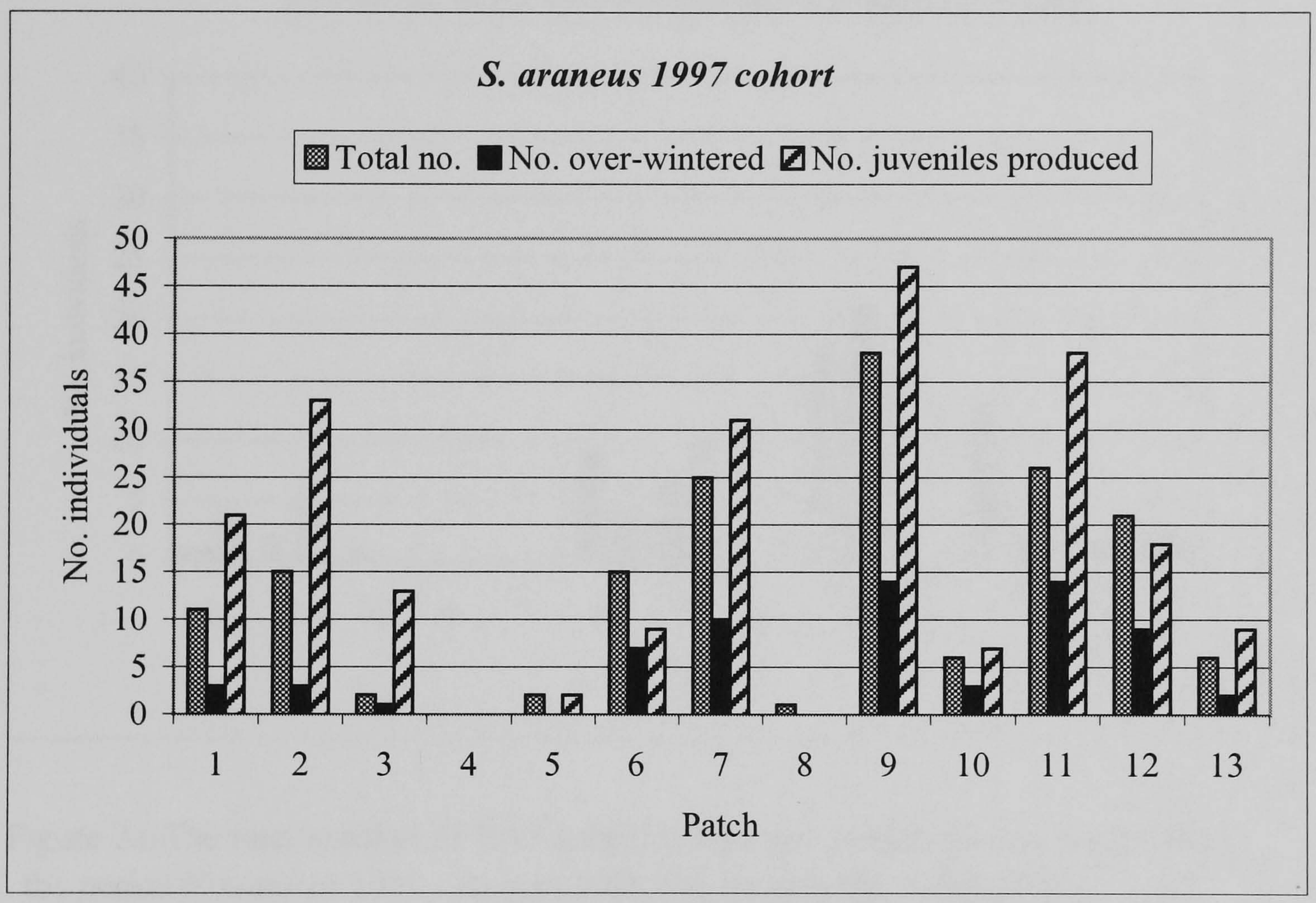


Figure 2.5 The number of 1997 cohort *S. araneus* caught in each patch during the period November 1997 - August 1998, the number that successfully over-wintered in each patch (i.e. were caught in November 1997 and then again in 1998), and the number of juveniles (offspring of the 1997 cohort) caught in each patch.

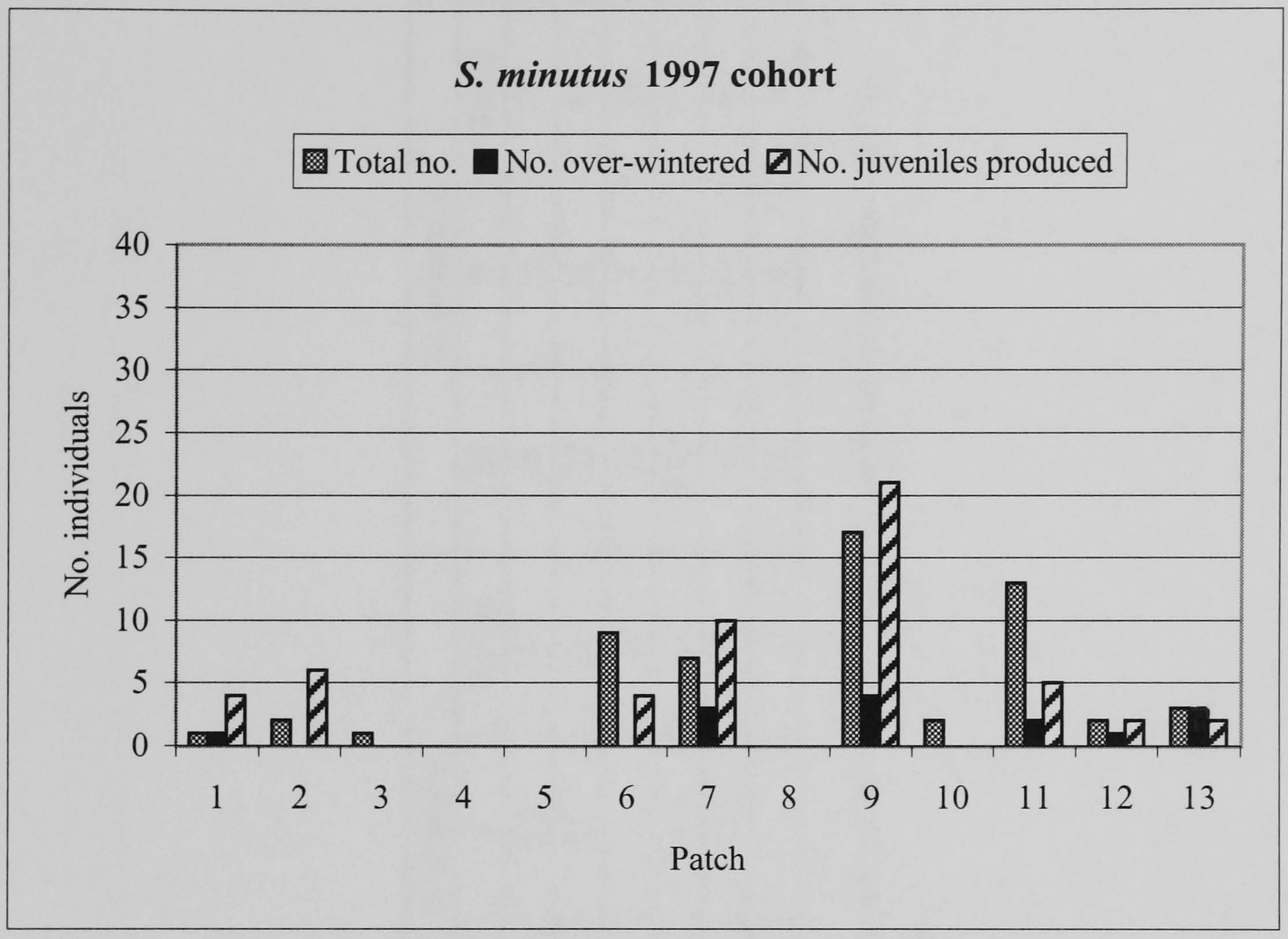


Figure 2.6 The total number of 1997 cohort *S. minutus* caught in each patch during the period November 1997 - August 1998, the number that successfully over-wintered in each patch (i.e. were caught in November 1997 and then again in 1998), and the number of juveniles (offspring of the 1997 cohort) caught in each patch.

	S. araneus			*S. minutus*		
	M	**F**	**Total**	**M**	**F**	**Total**
No. caught	92	85	177	38	35	73
No. caught >= twice (a)	57	57	114	22	21	43
No.indivs. that moved inter-patch	8	1	9	12	3	16
% indivs. that moved (of (a))	14	1.8	7.9	54.5	19	37.2
No. intra-patch movements	100	127	227	36	53	89
No. inter-patch movements	11	1	12	22	4	25

Table 2.1 Results of the live-trapping regime carried out at Fulford Golf-course from November 1997 to August 1998. M = males, F = females

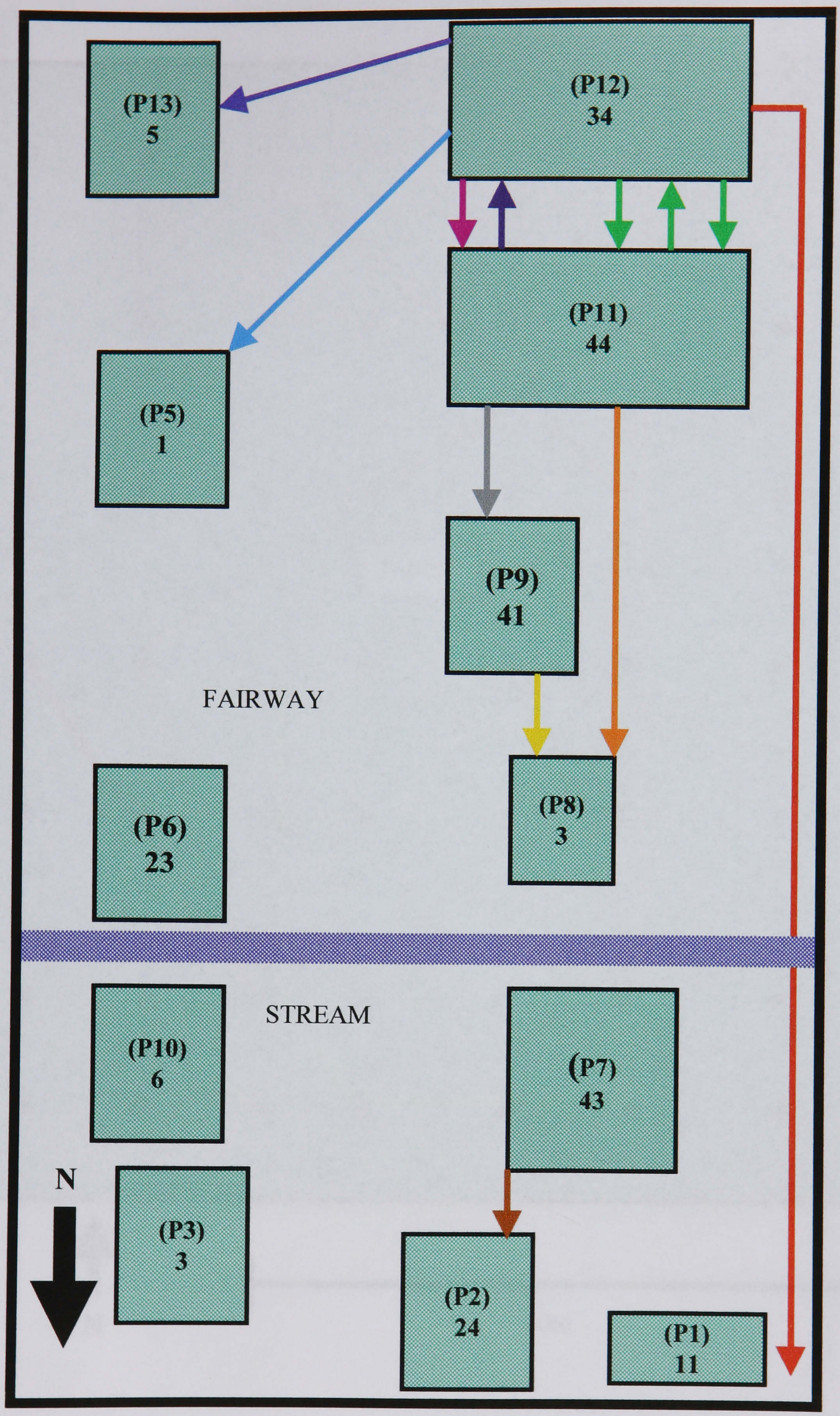


Figure 2.7 Diagrammatic map (not to scale) showing the inter-patch movements made by *S.araneus* (1997 cohort) recorded at Fulford Golf-Course, November 1997 until August 1998. The number of intra-patch movements recorded is shown in each patch and the patch reference number is denoted in brackets. Each colour represents a different individual.

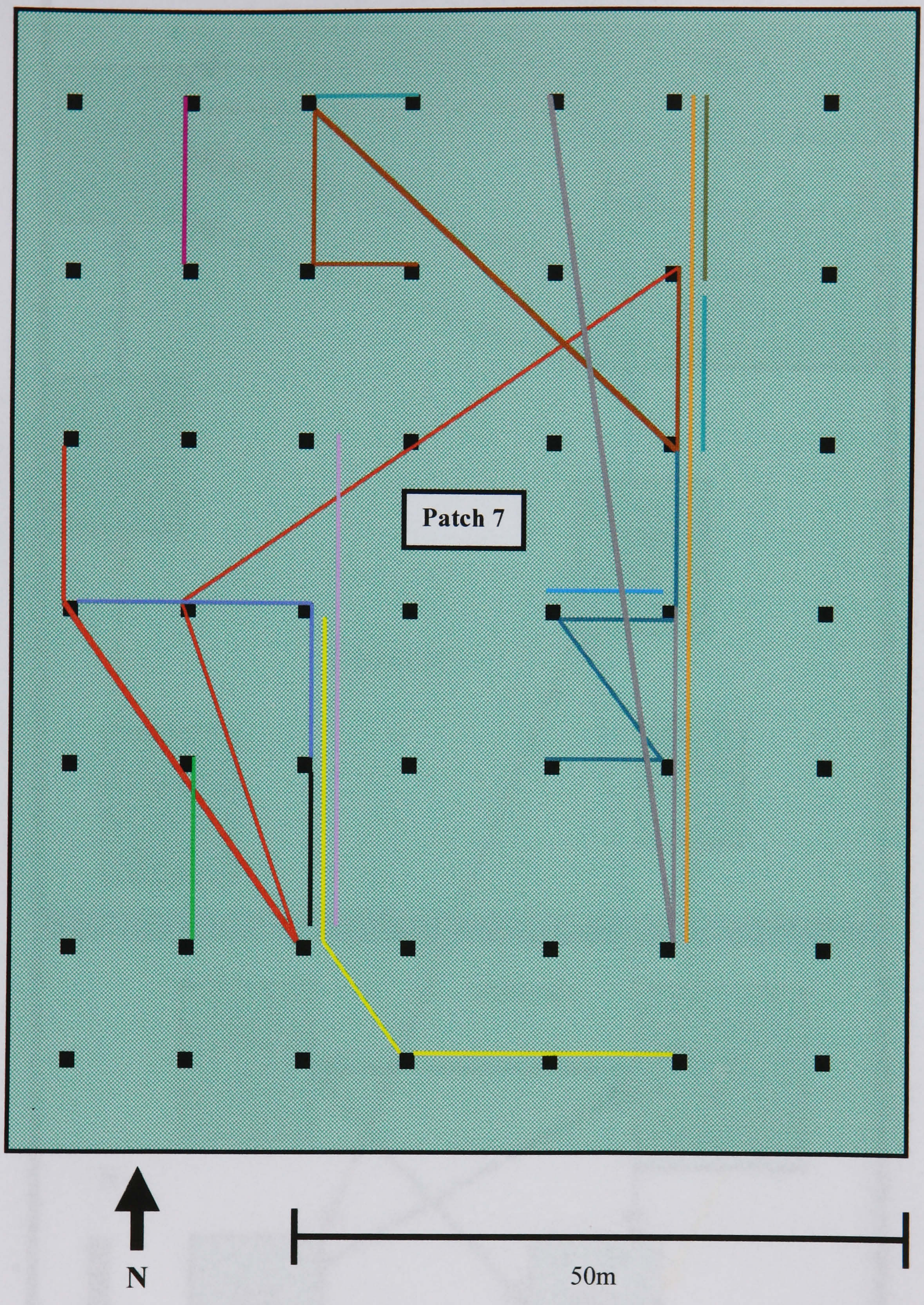


Figure 2.8. Diagrammatic map of Patch 7, Fulford Golf-course, showing all the movements recorded within it by *S. araneus*, from November 1997 until August 1998. Each colour represents a different individual.

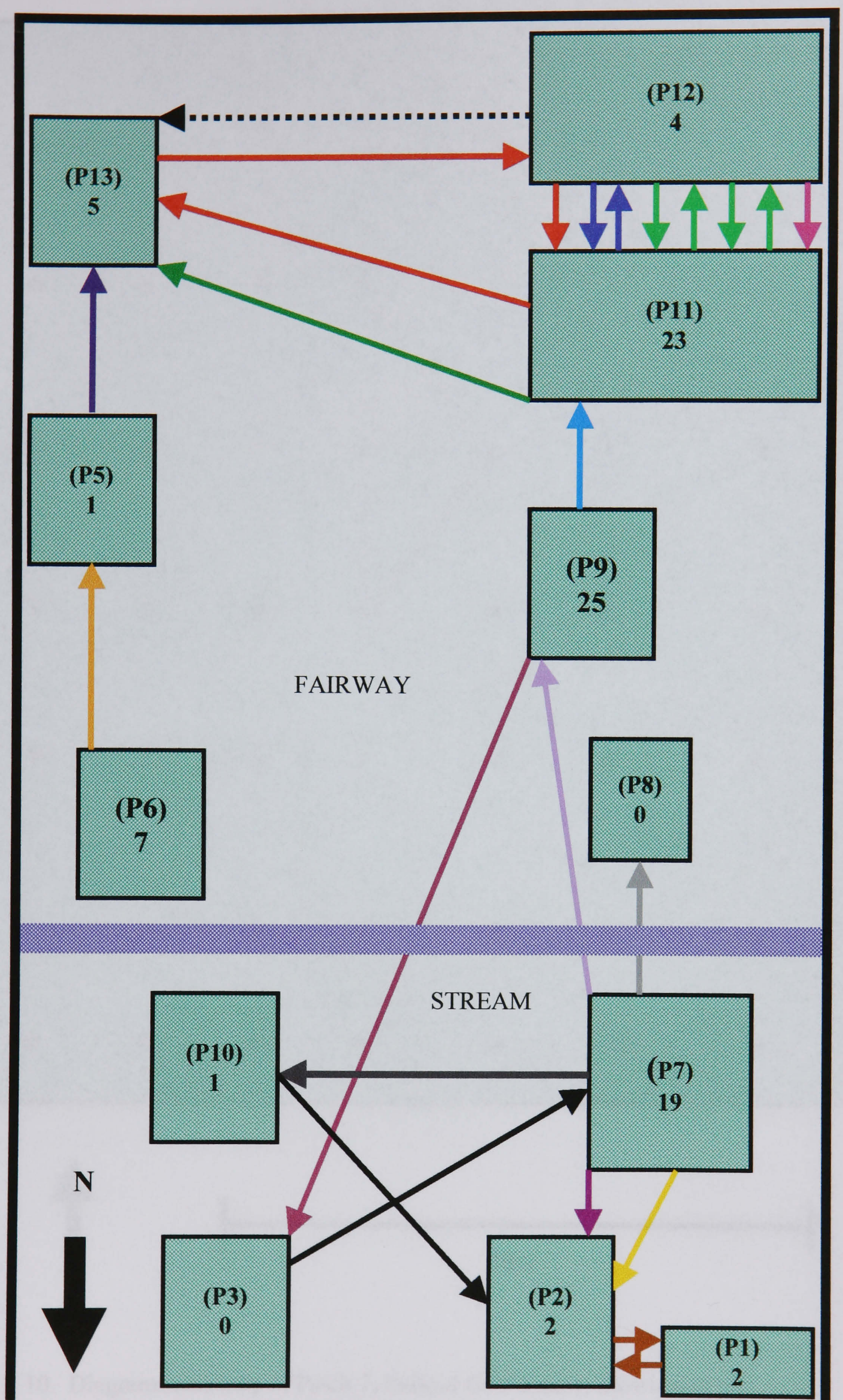


Figure 2.9 Diagrammatic map (not to scale) showing the inter-patch movements made by *S.minutus* (1997 cohort) recorded at Fulford Golf-Course, November 1997 until August 1998. The number of intra-patch movements recorded is shown in each patch and the patch reference number is denoted in brackets. Each colour represents a different individual.

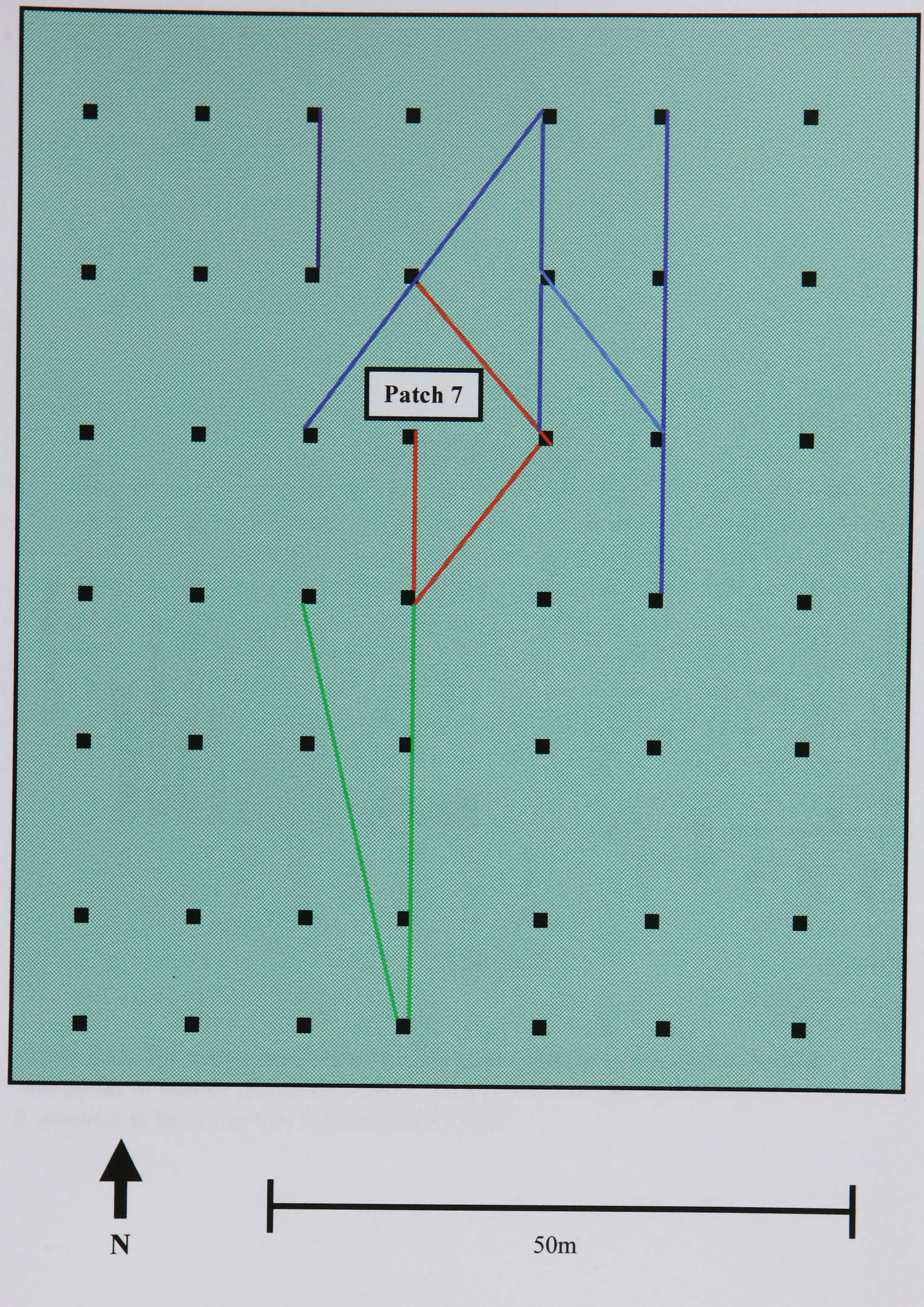


Figure 2.10. Diagrammatic map of Patch 7, Fulford Golf-course, showing all the movements recorded within it by *S. minutus*, from November 1997 until August 1998. Each colour represents a different individual.

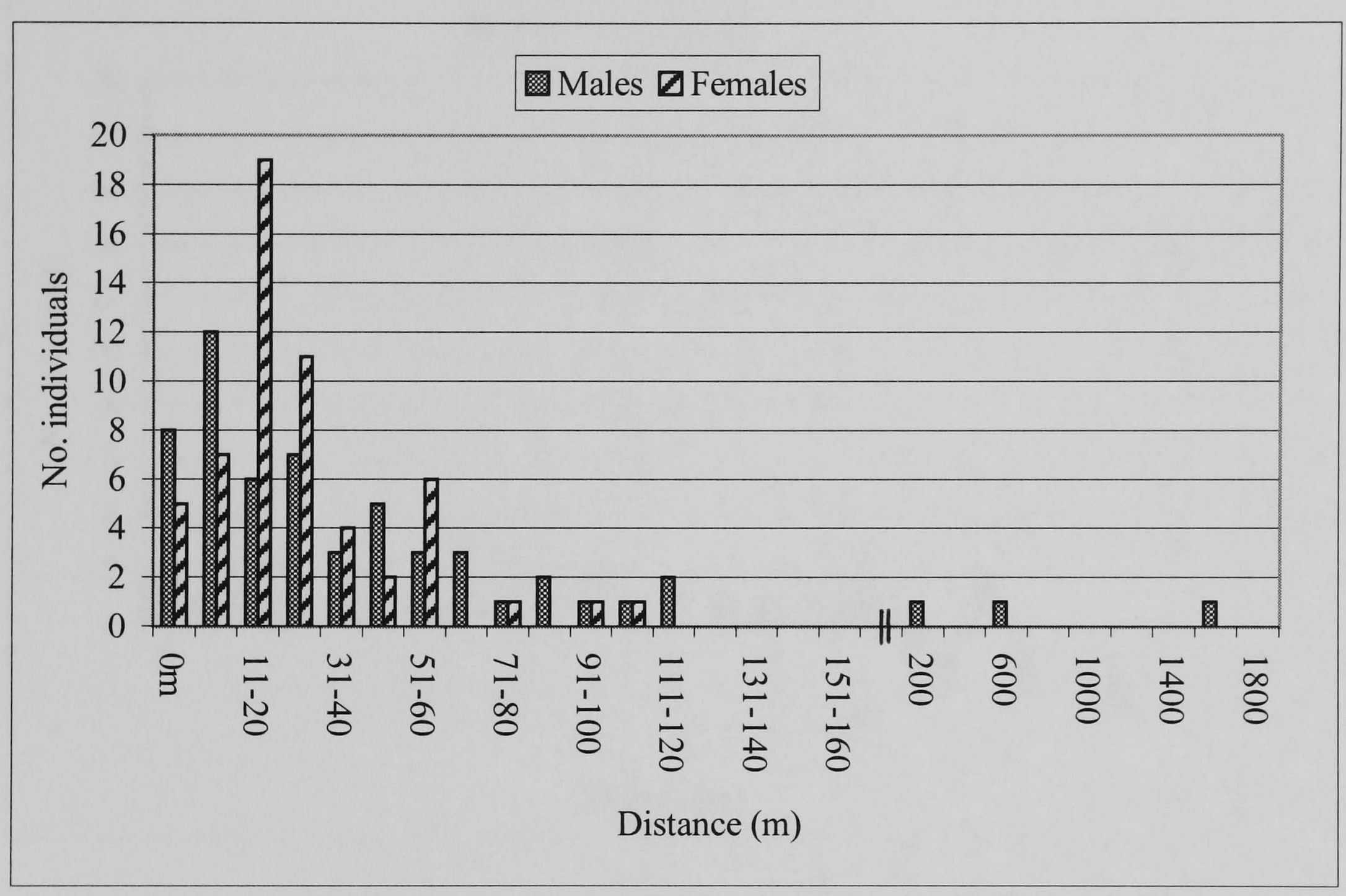


Figure 2.11. The maximum straight-line movement distances between the furthest two points of capture (November 1997 - August 1998) in male and female *S. araneus* at the study site, Fulford Golf-Course.

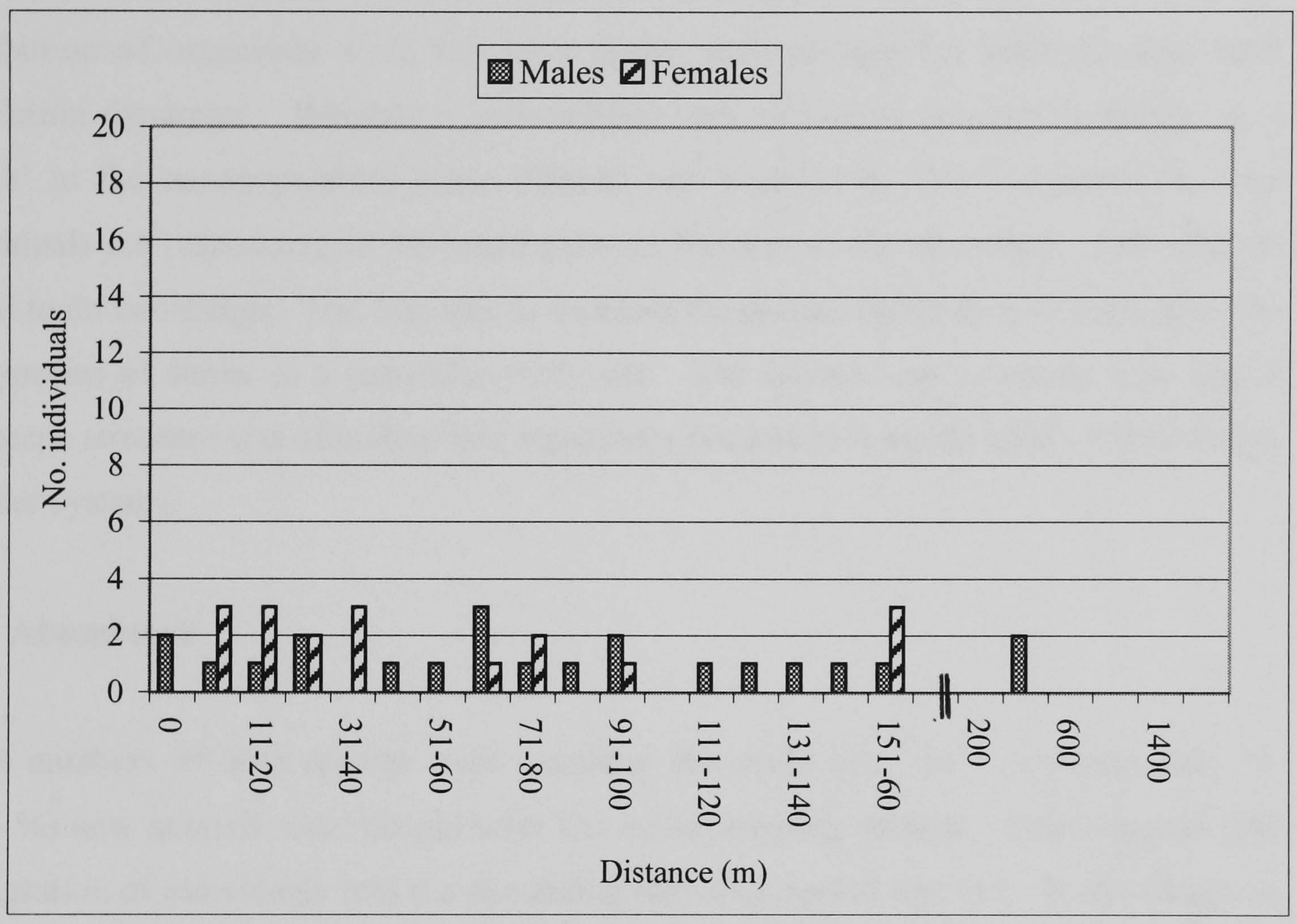


Figure 2.12. The maximum straight-line movement distances between the furthest two points of capture (November 1997 - August 1998) in male and female *S. minutus* at the study site, Fulford Golf-Course.

4 DISCUSSION

uman destruction of natural areas reduces the total amount of suitable habitat available r a species (Ims and Stenseth, 1989) and often leads to the creation of small, isolated d 'hard-edged' patches surrounded by a hostile matrix (Bjornstad *et al.*, 1998). It is portant to understand how the resulting landscape structure affects the spatial stribution of organisms as it will have direct consequences for understanding their opulation dynamics. Whether a well-defined area of habitat actually functions as a atch' in the metapopulation sense (Hanski and Simberloff, 1997) depends on how dividuals are responding to the heterogeneous features of the landscape. This chapter imed to do two things. The first was to examine the spatial distribution of individuals in wo species of shrew at a particular study site. The second was to assess how and if ndscape structure was affecting their movement because this would allow extrapolation other systems.

.4.1 Abundance

arge numbers of both species were caught at the study site. In *S. araneus*, only 31 17.5 %) new animals were caught after the initial trapping session. This suggests that mmigration of individuals into the site during the study period was low. It also suggests hat the trapping regime was intensive enough such that almost all the trappable animals vere caught. This is supported by the low number of individuals trapped in non-equential trapping sessions, but not in between. However, in *S. minutus*, 46 (63.0 %) ew animals were caught after the initial trapping session. This result may suggest that here was a greater amount of immigration into the site in this species than in *S. araneus*. Due to the long movement distances and response to landscape structure recorded in this pecies, this seems likely. However, it must also be borne in mind that this species is very light and may not always set a trap off despite it being set to a very high sensitivity (Shore *et al.*, 1995). No animals were caught in non-sequential trapping sessions and not n between. Although some of these animals were probably residents that were avoiding capture, the results suggest that immigration is higher in this species than in *S. araneus*.

4.2 Habitat suitability

evious work on both these species (e.g. Churchfield *et al.*, 1997) has shown that they e opportunistic in their habitat choice and their abundance is not affected by the ccessional stage of grassland habitat. On this basis, the habitat patches at the site have en defined as suitable habitat (see Chapter 3 for more supporting evidence). *S. araneus* as found in all patches at some point during the study period and *S. minutus* was found all patches at some time during the study period apart from patches 5 and 8. This pports that fact that the patches contain suitable habitat.

.4.3 Inter-patch movement

ıter-patch movement in *S. araneus* was shown to be very low. Only one female (1.2 % f the total number of caught) and eight males (8.7 % of the total number caught) moved etween patches. This strongly suggests that the individuals in each habitat patch do ıake up local populations which exchange migrants only rarely. The results also show hat more *S. araneus* males move between patches than *S. araneus* females. This is also pparent in terms of the number of intra- versus inter-patch movements made by the two exes. In *S. minutus* there is also a difference between the sexes. In females, four ndividuals (11.4 % of the total number caught) moved from one patch to another but in nales, twelve individuals (31.6 % of the total number caught) moved from one patch to ınother. However, in terms of inter- versus intra-patch movements, a difference between he species was found only in males. The results also show that there is a difference in he way the two species are responding to the patch structure. More *S. minutus* are noving between patches than *S. araneus*. These two species with apparently similar ıabitat requirements therefore seem to be utilising the habitat patches in different ways. Given the amount of movement between patches in *S. minutus*, it is not possible to classify the individuals in a habitat patch as making up a local population in the metapopulation sense. Territories in *S. minutus* have been found to be larger than those of *S. araneus* (Michielsen, 1966). The factors influencing this difference (which is thought to be prey-related (Michielsen, 1966)) may also be influencing the differences in response to landscape structure.

ıe results show that it is difficult to assign any general characteristics other than sex to ɜ group of individuals that moved between patches. There was no evidence that they ɜre all from a particular age class or that they were heavier than individuals that did not ɔve between patches. It would, therefore, be difficult to predict future inter-patch ɔvement events by particular individuals as a result of this study. Hanski *et al.* (1991) und that in years of low density *S. araneus* individuals that dispersed to islets in Lake ysma, Finland, were significantly smaller than residents. However, this was determined ;ing dry bone weight which is not possible to do in a live-trapping study such as this ıe.

.4.4 Patch dynamics

ı a metapopulation, patches can be occupied or empty (Levins, 1969). If they are mpty, determining why may help to understand how the system is operating. In . *araneus*, individuals were found to have over-wintered in all patches except for the mallest patch, patch 8 (1,000m^2). This may be due to it being too small to sustain ıdividuals over the winter when food becomes scarce. Hanski (1986) found that *S. raneus* was unable to over-winter on islands in a lake under 100 m^2, thus suggesting that ıere is a minimum 'island' size for over-wintering in this species. Patch 8 was destroyed fter March and therefore it was not possible to see whether or not it supported breeding dults. However, an area of this size will therefore only contain breeding individuals if it ɜ close to a larger patch ('source') and may be referred to as a 'sink' (a patch in which he growth rate is negative in the absence of migration (Hanski and Simberloff, 1997)). n all remaining patches breeding adults and juveniles (offspring of the 1997 cohort) were ɔresent during Summer 1998. This suggests these patches are able to sustain local ɔopulations of *S. araneus*.

n *S. minutus*, individuals were found to have over-wintered on only the largest six ɔatches at the site (although patch 13 is an anomaly in this case, where three individuals ɔver-wintered). This suggests that there is also a minimum patch size for this species

ring the winter. However, it is a larger than that required for *S. araneus*. This may so be due to the fact that *S. minutus* requires larger territories in order to obtain enough od (Michielsen, 1966). Breeding adults and juveniles were found on all patches except 5 and 10. Individuals must therefore have moved into patches 6 and 2 from ighbouring patches to breed. These could also be defined as 'sink' populations (Hanski d Simberloff, 1997).

ne above shows that snap-shot studies of habitat patches do not always provide enough formation to understand how a system is working. If a habitat patch is occupied it does ot necessarily mean that it can sustain a 'local population' (Hanski and Simberloff, 997).

.4.5 The influence of patch edges and areas of unfavourable habitat on movement

aving described the temporal and spatial distribution of the two species at the site, it is ow possible to determine whether their movement is restricted by the patch edges. This ill indicate how sensitive they are to habitat heterogeneity in general and therefore llow extrapolation to other landscapes. The results show that the study is being carried ut at the correct spatial scale. In *S. araneus*, the maximum straight-line distances in ales and females are greater than the nearest-neighbour inter-patch distances. This uggests that movement tendencies are not the reason for the lack of individuals moving om one patch to another. Data from previous studies also substantiate this. As well as n ability to swim long distances (Skaren, 1980, Hanski, 1986, Hanski and Kuitunen, 986), *S. araneus* has also been shown to have moved distances of several kilometres ver ice (Tegelström and Hansson, 1987). This, combined with the fact that there was ery low inter-patch movement in *S. araneus*, suggests that movement is being inhibited y landscape structure, in particular by the patch edges and the exposed habitat beyond it. n this species, this seems to be particularly so in females. This further substantiates revious studies that show that response to landscape structure can be sex-specific (Ims nd Rolstad, 1993).

ng-distance movements have been shown to be greater in *S. minutus* than in *S. ıneus*, and movement distances up to 355 metres have been recorded (Michielsen, 66). This, combined with the movement distances recorded at the site, also suggest ıt movement tendencies are not the reason why inter-patch movement is low in this ecies. There is less evidence to suggest that movement in *S. minutus* is being restricted the patch edges and exposed habitat. There is therefore a difference between these o species. This further substantiates previous studies which show that response to ıdscape structure can be species-specific (e.g. Verboom and van Apeldoorn, 1990; iens *et al.*, 1993).

a metapopulation, inter-patch movement is assumed to be substantially reduced ımpared with the amount of movements individuals undertake within their natal patch Lindvall, 1999). Studies looking at the effect of roads on movement have also ımpared the number of movements in the favourable habitat bordering the roads with e number that occurred across the road (e.g. Mader *et al.*, 1984; Merriam *et al.*, 1989). he intensive trapping regime used during the study period enabled this to be vestigated. The results show that lack of movement in *S. araneus* was not the reason ır this species not moving freely between patches. In females, 127 movements were corded during the study period. Of these, only one was between two different patches. ı males, 100 movements were recorded and eleven were between patches. Although ıere is a slight difference between the sexes, this shows that the animals are moving but ɔt between patches. This strongly suggests that they are reluctant to cross the patch dges.

ack of movement was also not evident in *S. minutus*. However, the contrast between ıter- and intra-patch movements in males was much less than for *S. araneus* of either ex. In females, 53 intra-patch movements were recorded compared with three inter-atch movements. This suggests that they are reluctant to cross patch edges. However, ı males, 36 intra-patch movements were recorded compared with 22 inter-patch ıovements. This is approximately a ratio of 2:1 and shows that movement restriction by atch edges is reduced in *S. minutus* males.

4.6 The spatial nature of movement

both species, the smallest inter-patch distance at the site was the only one to be crossed ore than once. This suggests that distance over exposed habitat may also influence ter-patch movement. It is possible that individuals will only move out of a patch if they e able to detect a target patch from their patch edge. More studies are required to certain whether this pattern is real. Shrew eyesight is said to be poor (Sharma, 1958; alls, 1942) but it is possible they have certain echolocatory abilities (Forsman and almquist, 1988). The smallest inter-patch distance was also the only one that was ossed more than once by the same individuals. This further suggests that if a target tch is within a certain distance, landscape structure may not present such a barrier. his could also be due to behavioural characteristics which are not influenced by any holocatory ability. An animal may move for a certain distance and/or a certain time ver exposed habitat before turning back. This would also explain why movements tween patches that are relatively close to each other are more common than between ose that are further away from each other. This result supports other studies (e.g. itzgibbon, 1997) that show that the amount of exposed habitat between favourable abitat patches also contributes to the barrier effect. Further studies are required to vestigate the influence of inter-patch distance on the barrier effect of patch edges.

n *S. araneus*, only one male and no females moved to more than one patch. In . *minutus*, only two males moved to more than one patch. However, one of these was ventually caught back in its original patch. This occurred over a period of several onths and it therefore seems unlikely that it was maintaining a territory over more than ne patch. This shows that movement beyond a single target patch is rare in both species. nter-patch movement to adjacent patches is also more common than movement to further atches in both species. Patches surrounded by more than one patch will therefore have a wer risk of extinction and a higher rate of gene flow than patches with only one eighbour. If neighbouring patches are within two metres, the study suggests that this vill further reduce the risk of extinction and increase the rate of gene flow.

4.7 Characteristics of the inter-patch movers

here is no detectable pattern in the ages of those individuals that moved between tches. Although in both species more males moved between patches than females, ere is no striking difference between the number of sub-adults and adults that did so. his is perhaps surprising as adult males of both species have been shown to move large stances. Long-distance movement has been recorded in adult male *S. minutus* Aichielsen, 1966) and in adult male *S. araneus* (Stockley *et al.*, 1994). Later maturing ales have been observed to make repeated long-distance forays in search of females Stockley *et al.*, 1994). However, this study shows no evidence of such movement ccurring between patches during the breeding season.

4.8 Comparisons with other studies

his study contributes to previous work that has looked at the effect of habitat eterogeneity on small mammal movement. Such studies are important due to the ontinual altering of natural habitat by humans. Due to the increasing number of roads eing built throughout the world (in Great Britain there are 365,000 kilometres of roads nd this figure is increasing every year, Dept. of Transport (1995); Richardson *et al.*, 1997)), many of these studies have looked at the extent to which roads inhibit small ammal movement. However, results from such studies have presented different ndings. Mader (1984), for example, showed in Germany that the bank vole, *Clethrionomys glareolus* and the wood mouse, *Apodemus sylvaticus* were highly mobile, et did not cross a six metre paved highway. However, Korn (1991) cleared a road island f animals every two months for 15 months and showed that these same two species rossed a 22 metre paved highway regularly. This latter study is the only one that ncludes *S. araneus* and *S. minutus*. Korn suggests that they behave similarly to rodents. His study did not look at individual movement detail, such as whether or not the same ndividuals moved back and forth between patches. However, he states that due to their

egular capture rate at the site, the results may have over-estimated movement across e highway in these species.

ıe results presented in this chapter suggest that movement over unfavourable habitat tween two patches will be rare in *S. araneus* males and females and in *S. minutus* males. As a result, both species can be said to be living as local populations in the bitat patches found at the site (Hanski and Simberloff, 1997). However, due to *S. inutus* males moving between patches at a higher frequency, this patch structure will be eater in *S. araneus* than *S. minutus*. More studies are required to determine if the sults found in this study are representative of other heterogeneous landscape systems.

CHAPTER 3

ABUNDANCE, SURVIVAL AND NATURE OF MOVEMENT FROM BIRTH TO BREEDING

3.1 INTRODUCTION

Landscapes are continually being fragmented and as a result, many populations occupy recently created heterogeneous areas. It is important to understand how individuals are moving within such systems due to the effect landscape features can have on their spatial distribution and as a result, their population dynamics.

The aim of this chapter is to examine the ecological characteristics and life-time movement of *S. araneus* and *S. minutus* in such a system. The study has been carried out at a large spatial scale relative to the mean home range size of both species. This was in order to minimise the number of animals lost through dispersal during the study and also to ensure that long-distance movements were detected.

A study of this nature also provides an opportunity to gain insight into ecological features of the two species. These findings will also be discussed.

3.2 METHODS

The live-trapping methodology is described in the previous chapter. Juvenile animals of both species were caught in June and August 1998 (Summer 1998). These animals will be hereafter referred to as the 'Summer 1998 Cohort'. It was assumed that their point of capture was close to their place of birth. Animals were re-captured in the first two weeks of April 1999. It was assumed that any movement from place of birth to place of breeding would have occurred by this time and that the distance moved by each individual was close to the maximum distance they would have moved during their life-time.

Trapping data from the previous year had shown that the first two weeks of April was just before the onset of the first oestrus at the site. In the previous year, the first young were caught at the end of May. Gestation and weaning can take up to five weeks (Crowcroft, 1957) and therefore from this, the first oestrus was deduced to have been in the last two weeks of April.

3.3 RESULTS

3.3.1 Trapping regime

Immatures were sexed using the technique of Searle (1985). The results were validated by comparing the sex recorded for each adult animal with that recorded for the immature animal. This showed that in *S. araneus*, only two females (2.1 %) had been sexed incorrectly. In *S. minutus*, one female was sexed incorrectly (6.7 %). The results were corrected prior to any analysis being carried out. Due to this low error rate, error in sexing the animals which were not subsequently recovered was assumed to be minimal. During the year, only one *S. araneus* individual lost an additional toe to those that had been clipped. However, its identity was still evident due to its sex. In *S. araneus*, 29 individuals were caught in June 1998 and April 1999. Six of these (20.7 %) were not caught in August 1998. In *S. minutus*, only two individuals were caught in June 1998 and April 1999. Neither of these were caught in August 1998. These measures give an indication of the consistency of trappability of all trappable individuals.

3.3.2 Abundance

The results of the trapping regime for both species can be seen in Table 3.1.

S. araneus

During Summer 1998, 235 *S. araneus* were caught and marked, 127 (54.0 %) females and 108 (46.0 %) males. In April 1999, 94 (40.0 %) of these were re-captured. Of these, 49 were female and 45 were male. Female survival was therefore 38.6 % and male survival 41.6 %. There were 141 (60.0 %) animals unaccounted for. None of the above sex ratios deviated from 50:50 (G-test, $p>0.05$). In April 1999, 35 new animals (14 females and 21 males - 12.9 % of the total number caught) were also caught. This sex ratio did not deviate from 50:50 (G-test, $p>0.05$).

S. minutus

During Summer 1998, 55 *S. minutus* were caught and marked, 29 (53.0 %) females and 26 (47.0 %) males. In April 1999, 15 (27.3 %) were re-captured. Of these, ten were female and five were male. Female survival was therefore 34.5 % and male survival 19.2 %. There were 40 animals (73.0 %) unaccounted for. None of the above sex ratios deviated from 50:50 (G-test, $p>0.05$). In April 1999, 43 new animals (22 females and 21 males – 43.9 % of the total number caught) were also caught. This sex ratio did not deviate from 50:50 (G-test, $p>0.05$).

3.3.3 Survival

Survival rates were based on the number of individuals caught during Summer 1998 and then again in April 1999. Animals that were not re-captured may have emigrated from the study area. However, as stated above, the large study site aimed to minimise individuals lost through dispersal. Despite this, survival must be defined as 'residency in the study area' (c.f. Churchfield, 1984). Table 3.2 and Figure 3.1 show annual survival rates and survival for the first two months of life (i.e. the number caught in June that were caught again in August 1998) that were calculated for both species on this basis. Figure 3.2 shows the number of new individuals of each species caught during the two trapping sessions. There was a significant difference in the number of male *S. araneus* and *S. minutus* that survived until April 1999 (Fisher's Exact Test $p<0.05$). There was no significant difference in annual female survival

between the two species (Fisher's Exact Test $p>0.05$). There was also no significant difference between male and female survival in either species (Fisher's Exact Test $p>0.05$ in both cases).

3.3.4 Density

Table 3.3 shows that population densities (calculated by combining the number of individuals caught in each patch in June and August 1998) in *S. araneus* and *S. minutus* varied greatly between patches (*S. araneus*, 12 – 130 individuals/ha; *S. minutus*, 5 – 36 individuals/ha). Figure 3.3 shows that there was a relationship between *S. araneus* density and *S. minutus* density in each patch (Linear regression, $F_{1,9} = 7.68$; $p = 0.02$). Figure 3.4 shows that there was no relationship between *S. araneus* patch density and annual survival for *S. araneus* (Linear regression, $F_{1,9} = 0.50$; $p = 0.496$) and Figure 3.5 shows that there was also no relationship between *S. araneus* density and *S. minutus* annual survival (Linear regression, $F_{1,4} = 0.13$; $p = 0.739$).

3.3.5 Landscape structure

The habitat at the study site was divided into two types: unfavourable habitat (the fairway) and favourable habitat (the rough patches). Both species are opportunistic in their habitat choice (e.g. Churchfield *et al.*, 1997) and given the nature of the grass/scrub patches, it was not felt necessary to include internal habitat structure in any analysis. Figures 3.6 and 3.7 show that *S. araneus* and *S. minutus* abundance were directly related to patch size which further supports this (Linear regression, *S. araneus*, $F_{1,9} = 25.50$; $p = 0.001$; *S. minutus* $F_{1,9} = 9.74$; $p = 0.012$).

3.3.6 'Expected' inter-patch movement

In order to assess the effect of landscape structure on movement in these two species, it was necessary to look at the amount of inter-patch movement that occurred.

However, for this to be relevant to how the two species perceive landscape structure, it is necessary to examine whether inter-patch movement is expected. The spatial scale at which the study is being carried out relative to the movement distances of the animals must therefore be examined. These distributions of movement distances must overlap or exceed the nearest-neighbour inter-patch distances for inter-patch movement to be expected.

Figures 3.8 – 3.11 show the maximum straight-line distances recorded for all individuals of both species that were caught in Summer 1998 and April 1999 and the nearest-neighbour inter-patch distances (which range from 2 – 25 metres, see Figure 1.1). There was a significant difference between the distances moved in *S. araneus* and *S. minutus* in both males and females (Mann-Whitney U-test, $p>0.05$ in both cases; *S. araneus* males, median 30 m, females, median 20 m; *S. minutus* males, 102 m, females, median 26 m). In both cases, *S. minutus* movement distances tended to be larger than those of *S. araneus*. Table 3.4 displays the details of the movement distances relative to the inter-patch distances. These show that the study was carried out at the correct spatial scale to assess the effect of landscape structure on movement in the two species.

3.3.7 'Observed' inter-patch movement

'Observed' inter-patch movement is defined as that which was recorded during the study. 'Effective' movement is a sub-set of this (see below).

S. araneus

Figures 3.12 and 3.13 show capture and movement details for males and females of this species. Of the 235 individuals that were caught, 224 were not subsequently caught in another patch. Eleven individuals out of a total of 235 (4.7 %) were found to have moved from one patch to another. Eight of these did so within the Summer 1998 trapping session. Of the 94 animals that were re-captured in the following year, six (6.4 %) had been found to have moved from one patch to another i.e. five of the

animals that had moved from one patch to another in Summer 1998 were not re-captured in April 1999 and an additional three animals had moved from one patch to another.

S. minutus

Figures 3.14 and 3.15 show capture and movement details for males and females of this species. Of the 55 individuals that were caught, 51 were not subsequently found in another patch. Four individuals out of the total of 56 (7.1 %) moved from one patch to another. One of these did so within the Summer 1998 trapping session. Of the 15 animals that were re-captured in the following year, three (20.0 %) had moved from one patch to another, i.e. the animal that had moved within the Summer 1998 trapping session was not re-captured in April 1999 and an additional three animals had moved from one patch to another.

3.3.8 'Effective' inter-patch movement

'Effective' inter-patch movement is defined as the number of animals that moved from one patch to another and survived until April 1999 i.e. survived until breeding (however, such a measure will also be subject to observational bias). In most cases this is expected to be lower than 'observed' inter-patch movement due to some inter-patch dispersers not surviving until breeding. It is equivalent to gene flow if the individuals reproduce successfully in their new patch and their offspring also successfully reproduce in that patch (Futuyma, 1986). It is important to separate it from 'observed' movement which could over-estimate the amount of gene flow occurring between patches. The difference between 'observed' and 'effective' inter-patch movement enables the survival rates of the dispersers to be calculated. These can be seen in Table 3.5.

a) i. ***S. araneus***

The number of 'effective' movers in this species is six, one female and five males. Of the 94 individuals that survived until April 1999, 6.3 % were effective movers. Of those that moved, 54.5 % were 'effective' movers.

a) ii. Survival of inter-patch dispersers

Of the eleven animals that moved from one patch to another, five were female and six were male. This result does not suggest any sex bias in inter-patch movement. However, of all the movers, only one female but five males were captured in April 1999. This suggests that despite there being no sex bias in inter-patch movement, there may be a difference in survival following inter-patch movement. Of the six males that moved, 83.0 % survived. Of the five females that moved, 20.0 % survived. There was no significant difference between the number of males that moved and survived and the number of females that moved and survived (Fisher's Exact Test $p>0.05$).

b) i. *S. minutus*

The number of 'effective' movers in this species is three, two females and one male. Of the 15 animals that survived until April 1999, 20.0 % were effective movers. Of those that moved, 75.0 % were 'effective' movers.

b) ii. Survival of inter-patch dispersers

Of the five animals that moved from one patch to another, two were female and three were male. The male that moved within the Summer 1998 trapping session was not re-caught. Of the two females that moved, 100.0 % survived. Of the two males that

moved, one survived. This sample size is too small to suggest sex-related patterns in inter-patch dispersal and survival.

3.3.9 Inter-patch movement detail

S. araneus

Inter-patch movement is shown graphically in Figure 3.16. Of the eleven animals that moved between patches, all moved to an adjacent patch in the first instance apart from one female. The five individuals that were not re-captured in the following year were not caught after this. Of the six animals that survived until summer 1999, two individuals, one male and one female then moved on to other patches and two males moved back and forth between two patches. The fifth male stayed in the patch adjacent to its natal patch. The only inter-patch distance that was crossed more than once was that between patches 11 and 12. The inter-patch distance involved is the smallest on the site, 2 metres. Figure 3.17 shows that there was no relationship between natal patch juvenile summer density and dispersal during the study period (Linear regression, $F_{1,9} = 0.977$, $p = 0.349$).

S. minutus

Inter-patch movement is shown graphically in Figure 3.18. Of the four animals that moved, three moved to an adjacent patch. The male that was not trapped in April 1998 was not found after this. The fourth animal, a female, was re-captured in April 1999 at some distance and several patches away from its initial point of capture. In this species, all movement was uni-directional (i.e. there was no movement back and forth between patches. Figure 3.19 shows that there was no relationship between *S. araneus* natal patch summer density and dispersal during the study period (Linear regression, $F_{1,9} = 0.810$, $p = 0.392$).

3.3.10 The influence of landscape structure on movement

S. araneus

Figure 3.20 shows that in males, a relationship was found between intra-patch movement distances and patch size (Linear regression, $F_{1,39} = 8.22$; $p = 0.007$). Figure 3.21 shows that there was no such relationship in females (Linear regression, $F_{1,45} = 0.52$; $p = 0.477$).

S. minutus

Figure 3.22 and 3.23 show that no relationship was found between intra-patch movement distances and patch size in either sex in this species (Linear regression, males, $F_{1,3} = 3.22$; $p = 0.171$; females, $F_{1,8} = 0.37$; $p = 0.560$).

	S. araneus		*S. minutus*	
	Summer 1998	**April 1999**	**Summer 1998**	**April 1999**
Females caught	127	49	29	10
Males caught	108	45	26	5
Total	235	94	55	15

Table 3.1 The number of *S. araneus* and *S. minutus* males and females that were trapped in Summer 1998 and April 1999.

	% survival	
	S. araneus	***S. minutus***
Total survival	40.0	27.3
Female survival	38.6	34.5
Males survival	41.6	19.2

Table 3.2 The proportion of male and female *S. araneus* and *S. minutus* that were trapped in Summer 1998 and re-trapped in April 1999.

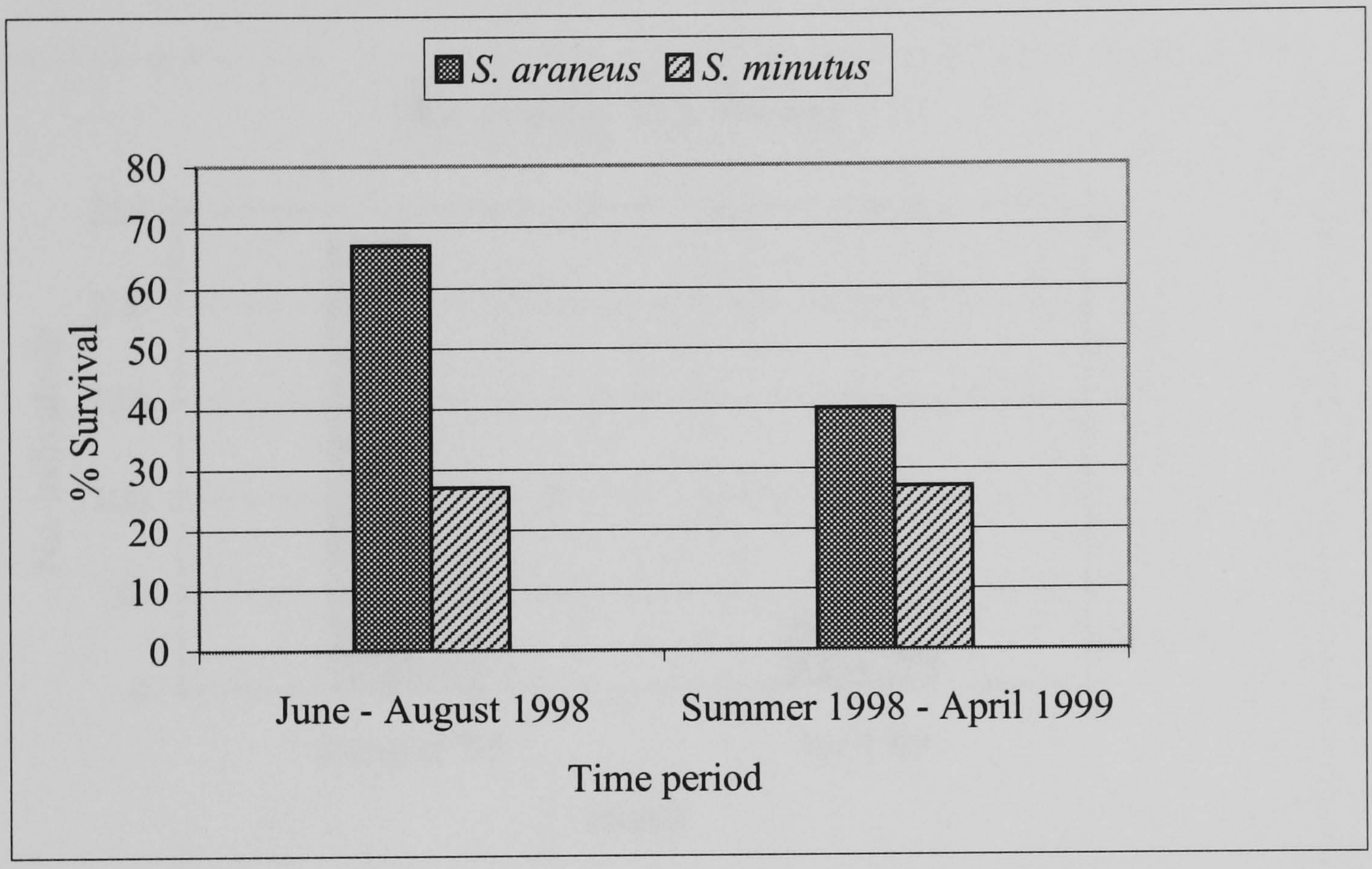


Figure 3.1 Survival of *S. araneus* and *S. minutus* over the summer of their birth (June - August 1998) and over a year (Summer 1998 - April 1999) at the study site, Fulford Golf-Course.

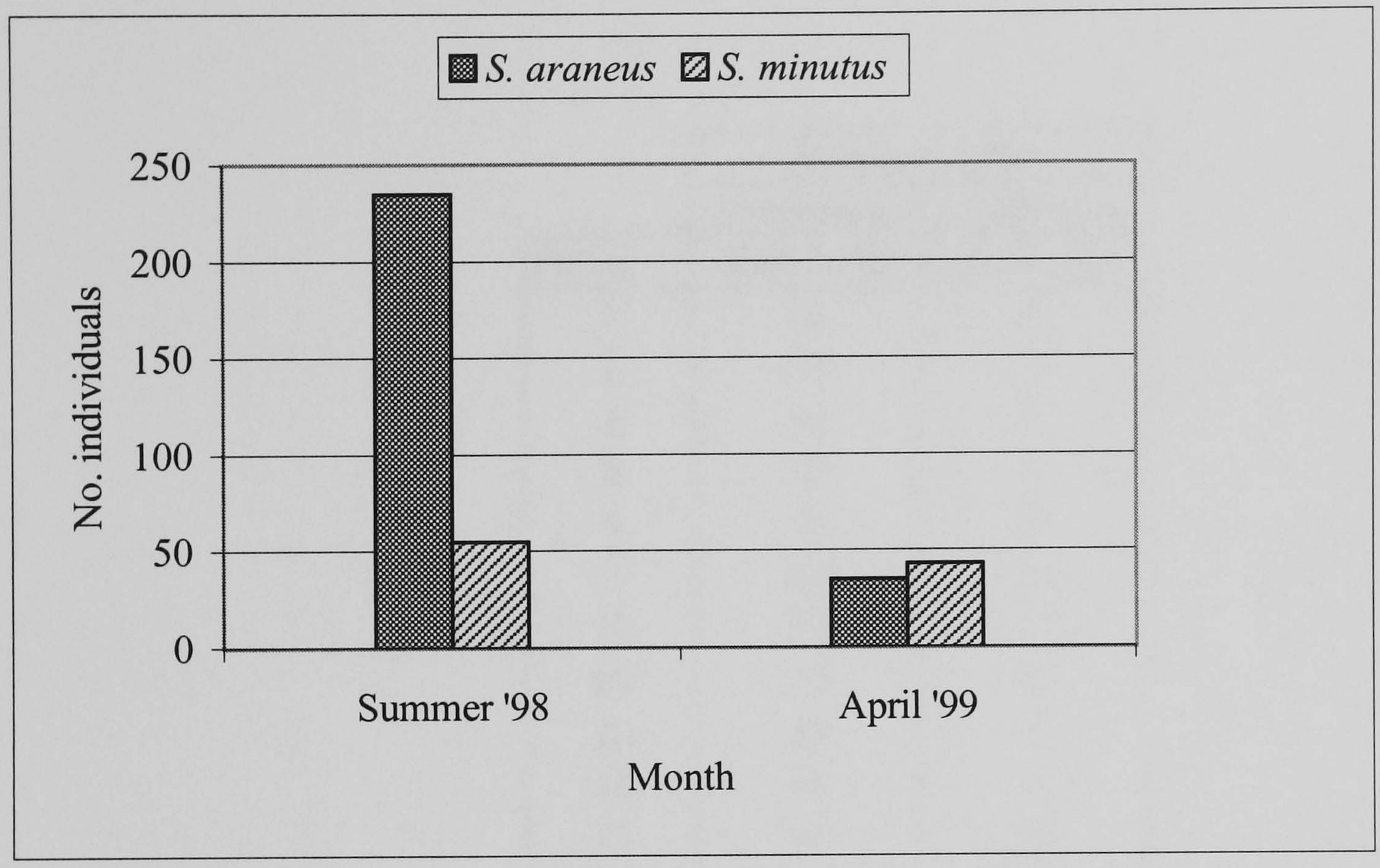


Figure 3.2. The number of new *S. araneus* and *S. minutus* caught during the two trapping sessions: Summer 1998 (June and August 1998) and April 1999, at the study site, Fulford Golf-Course.

	Summer 1998	
	S. araneus	*S. minutus*
Patch	**Indivs./ha**	**Indivs./ha**
1	63	13
2	130	27
3	44	0
5	12	0
6	42	19
7	107	36
9	59	27
10	70	0
11	58	7
12	49	5
13	46	13
Range	**12 - 130**	**5 - 36**

Table 3.3. The density of individuals per hectare found in each patch during Summer 1998

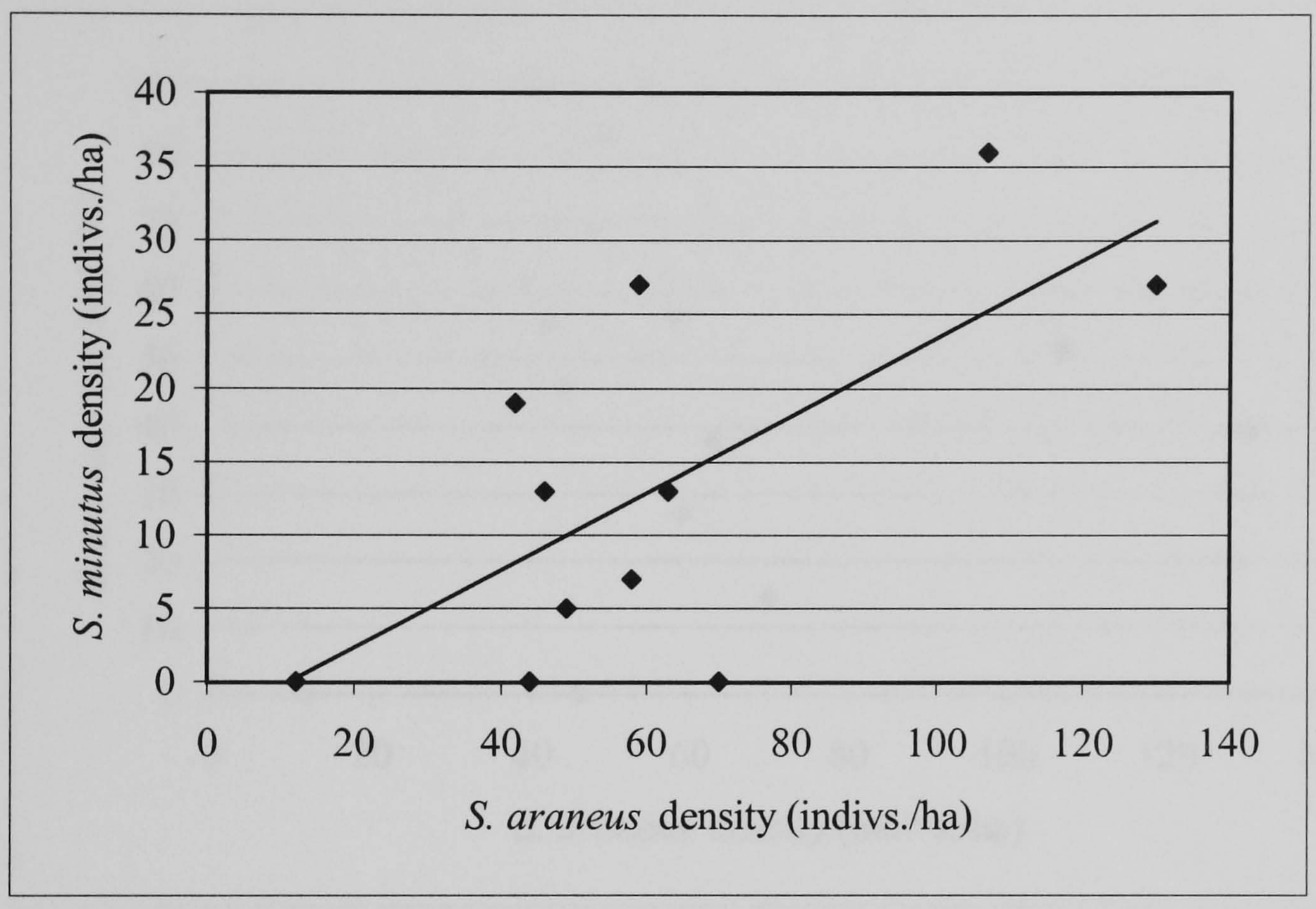


Figure 3.3 Scatter plot showing the relationship between *S. minutus* and *S. araneus* density in each patch during Summer 1998 at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 7.68$; $p = 0.022$).

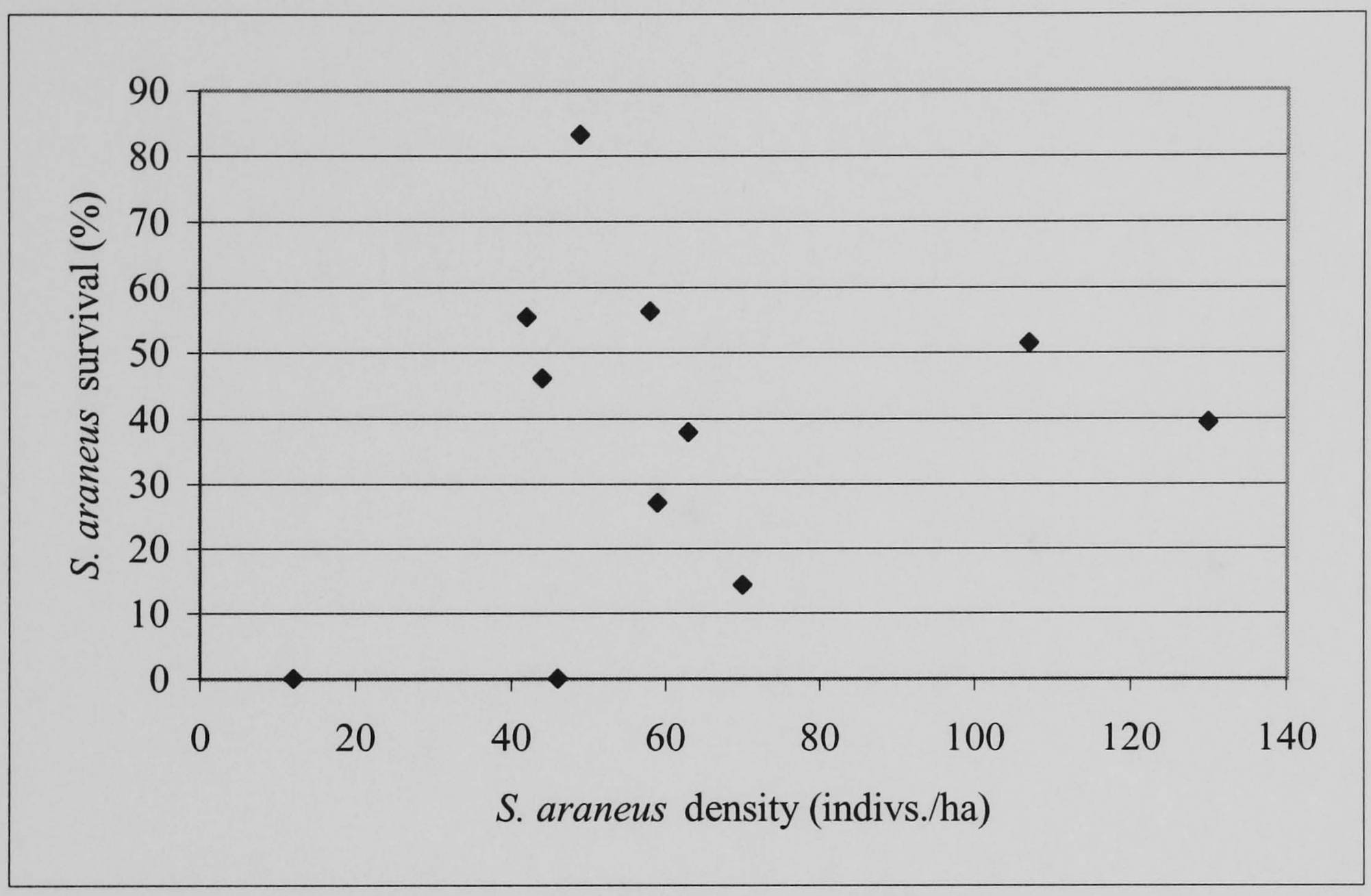


Figure 3.4 Scatter plot of *S. araneus* annual survival and *S. araneus* density in each patch during Summer 1998 at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 0.50$, $p = 0.496$).

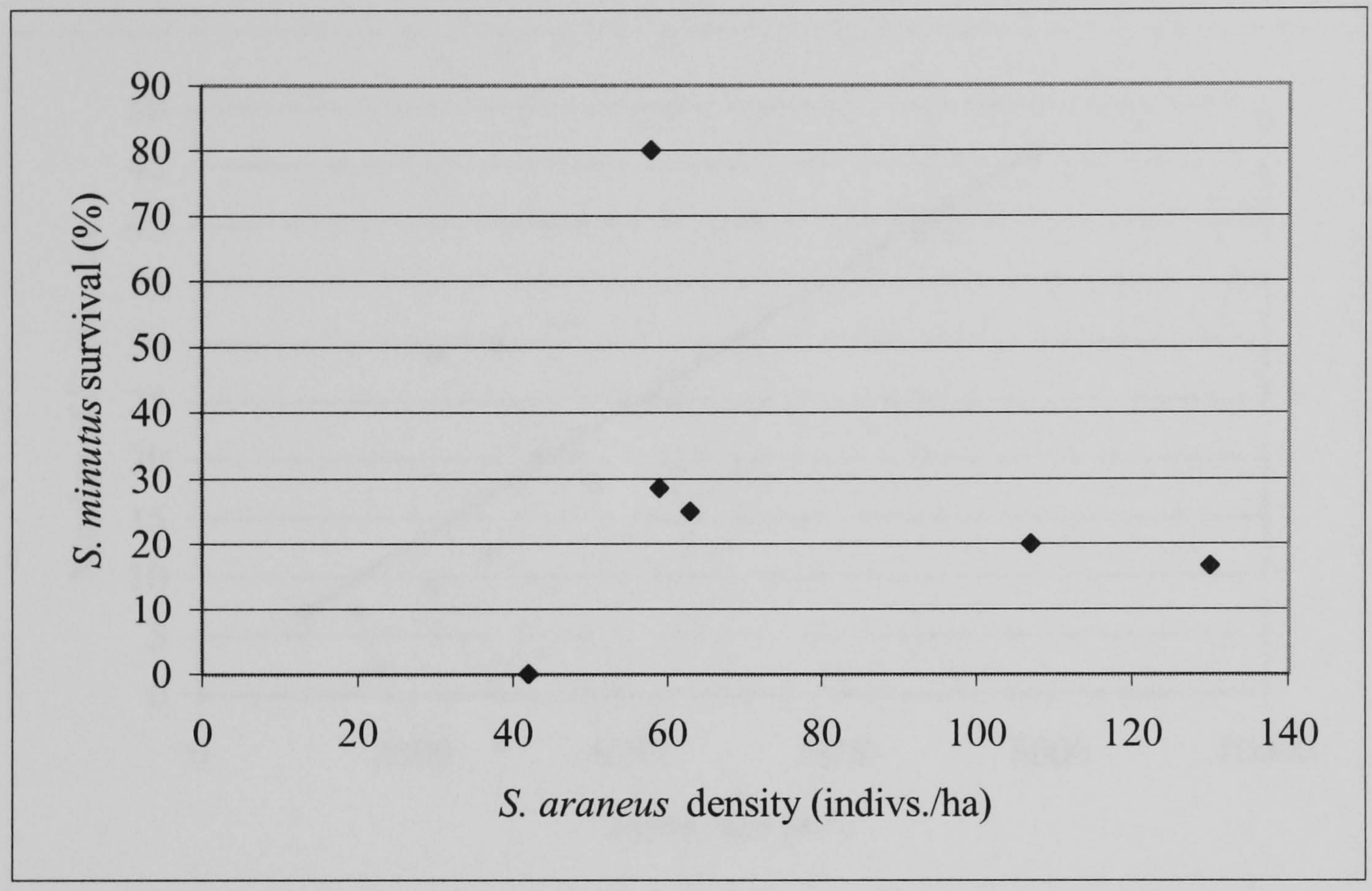


Figure 3.5 Scatter plot of *S. minutus* annual survival and *S. araneus* density in each patch during Summer 1998 at the study site, Fulford Golf-Course (Linear regression, $F_{1,4} = 0.13$, $p = 0.739$).

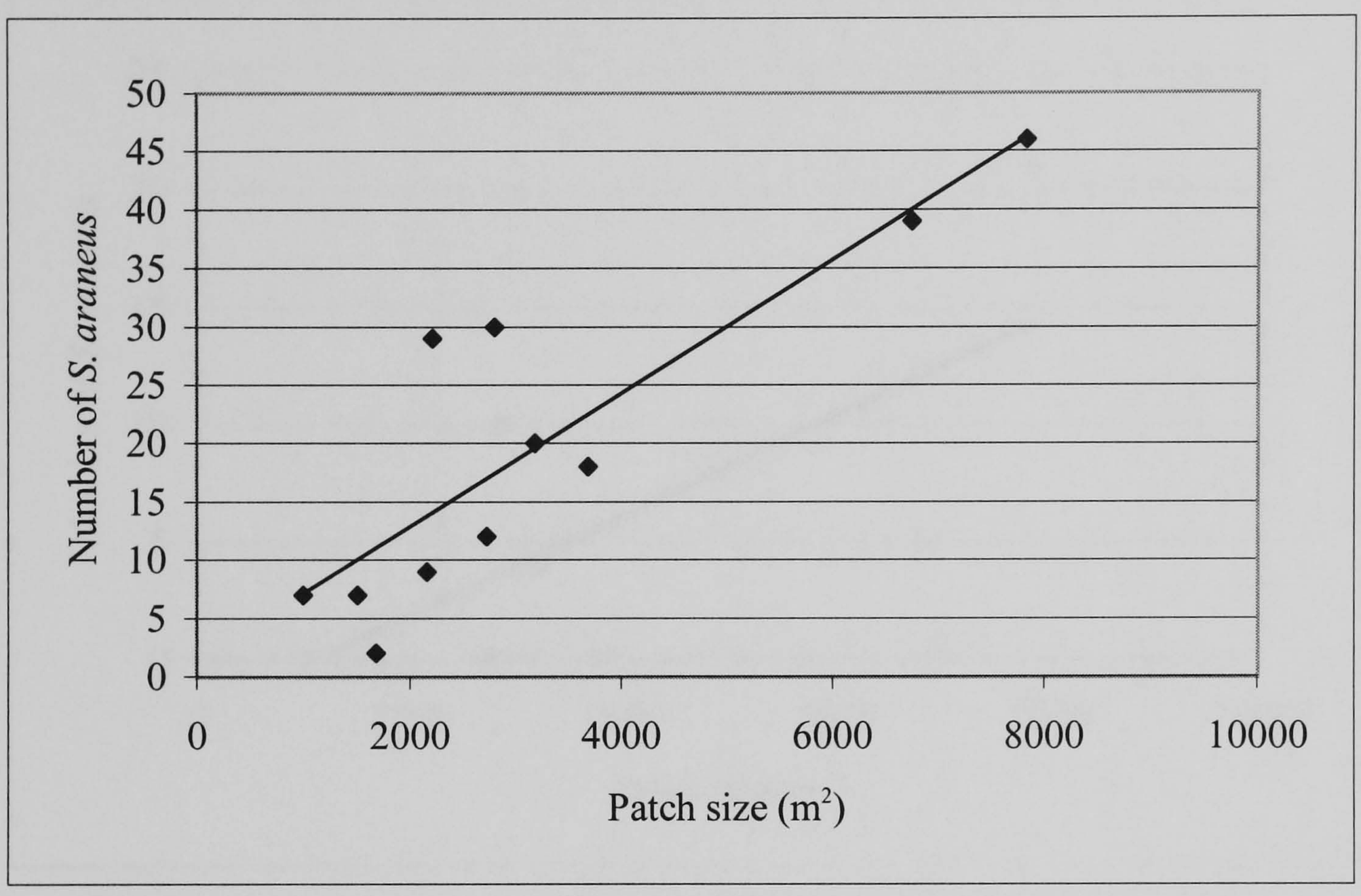


Figure 3.6 Scatter plot showing the relationship between the number of *S. araneus* and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 25.50$, $p = 0.001$)

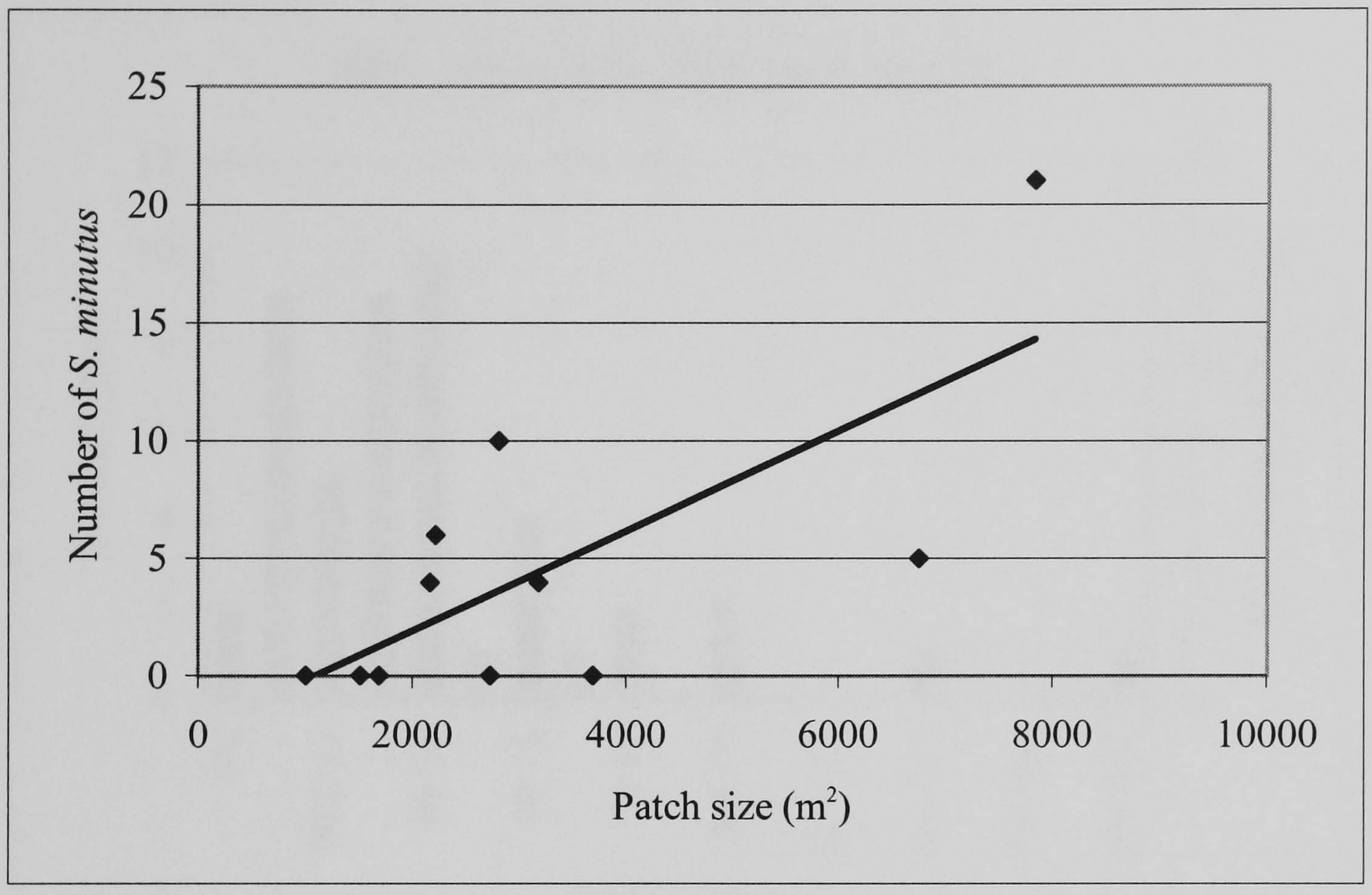


Figure 3.7 Scatter plot showing the relationship between the number of *S. minutus* and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 9.74$, $p = 0.012$)

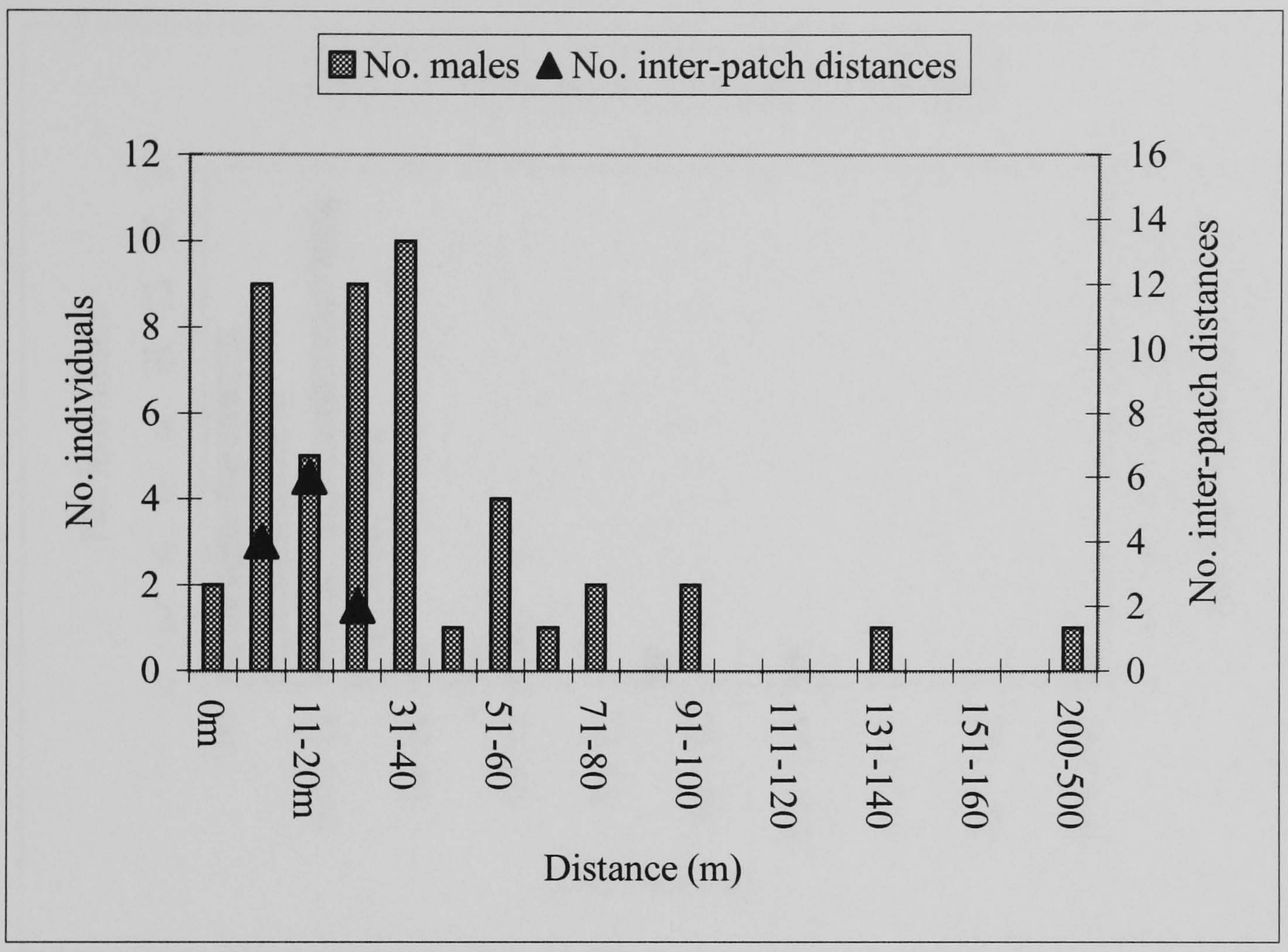


Figure 3.8 The maximum straight line distances moved by male *S. araneus* throughout the 1998-1999 study period relative to the nearest-neighbour inter-patch distances.

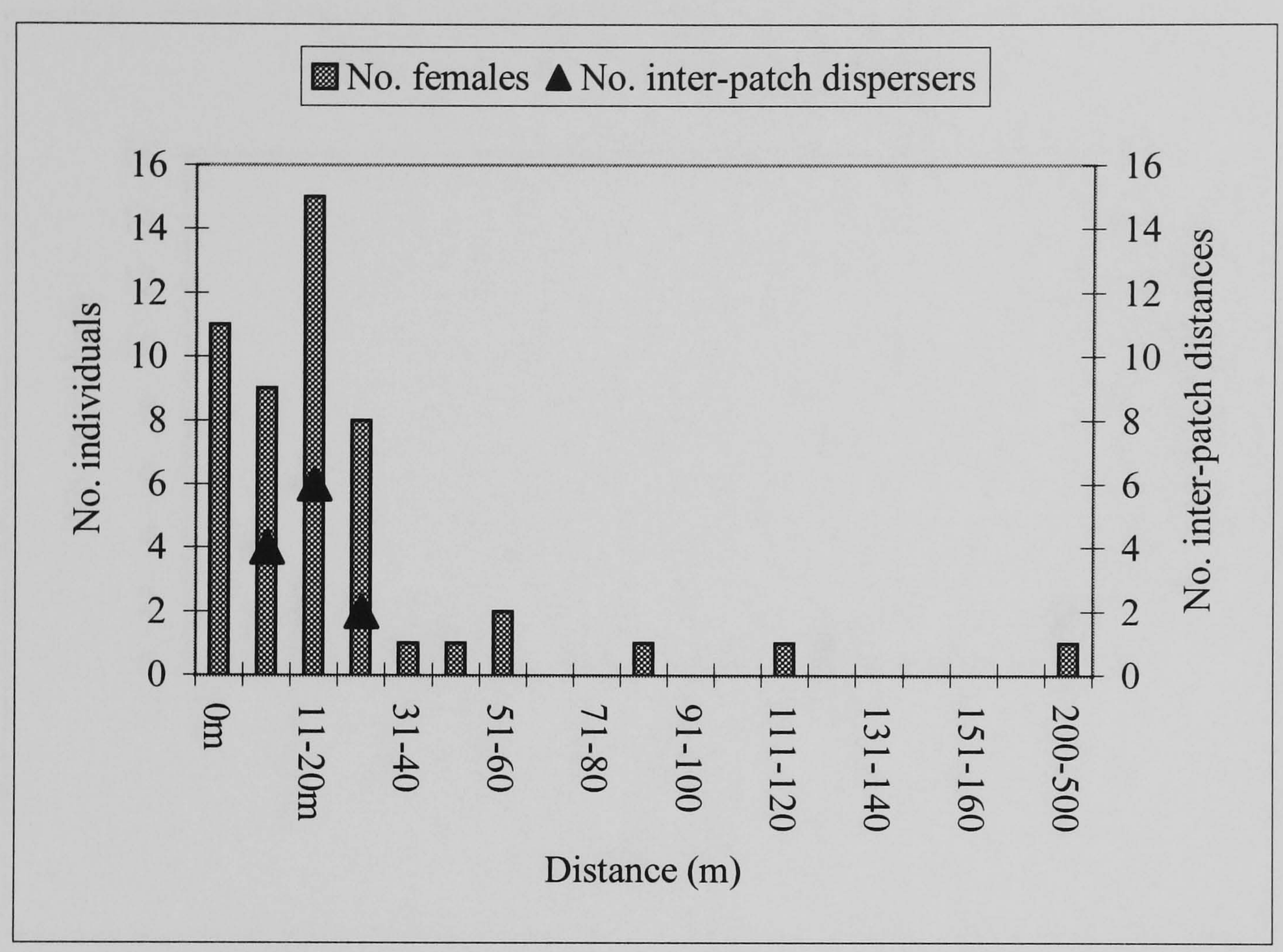


Figure 3.9 The maximum straight line distances moved by female *S. araneus* throughout the 1998-1999 study period relative to the nearest-neighbour inter-patch distances.

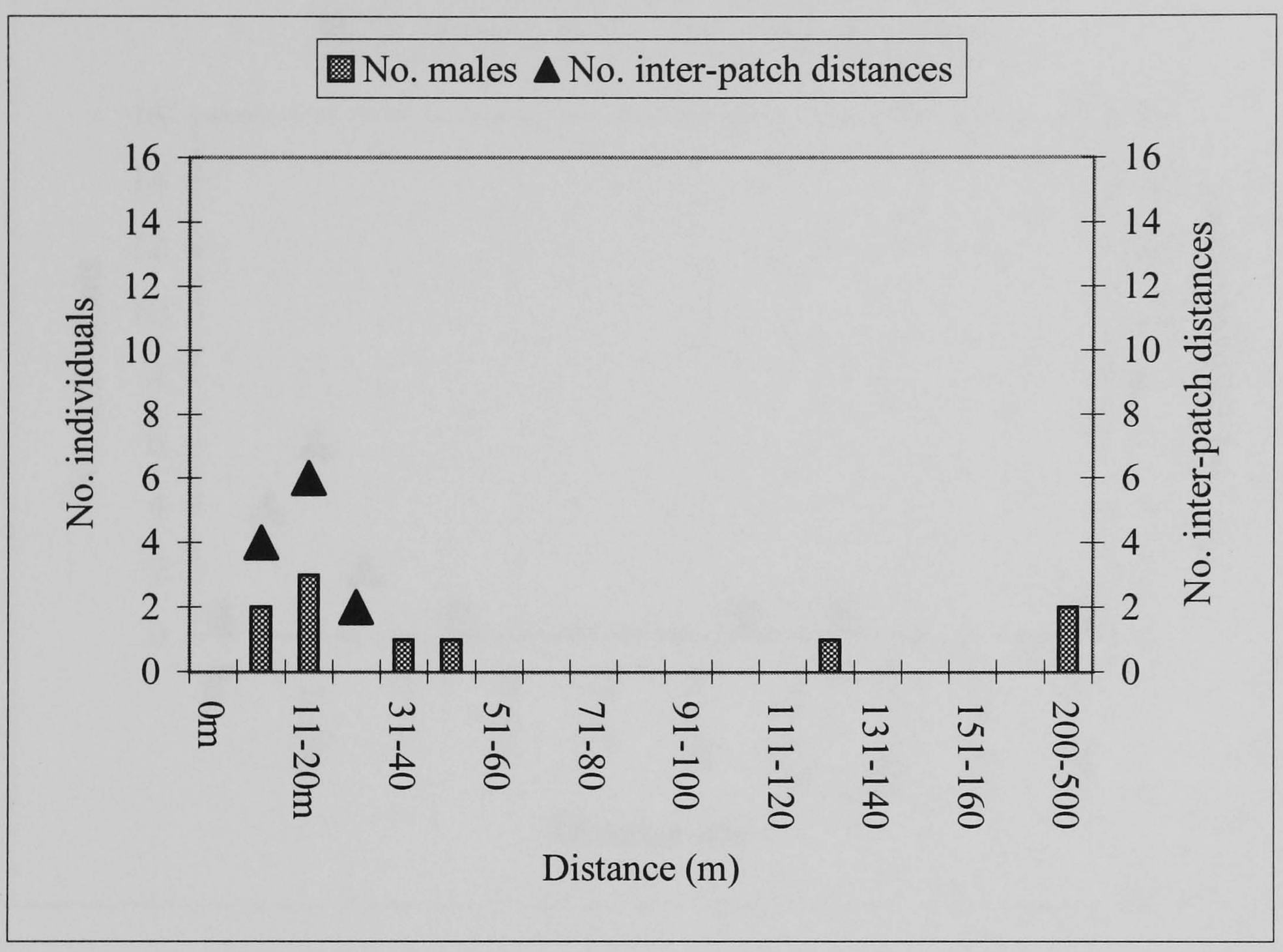


Figure 3.10 The maximum straight line distances moved by male *S. minutus* throughout the 1998-1999 study period relative to the nearest-neighbour inter-patch distances.

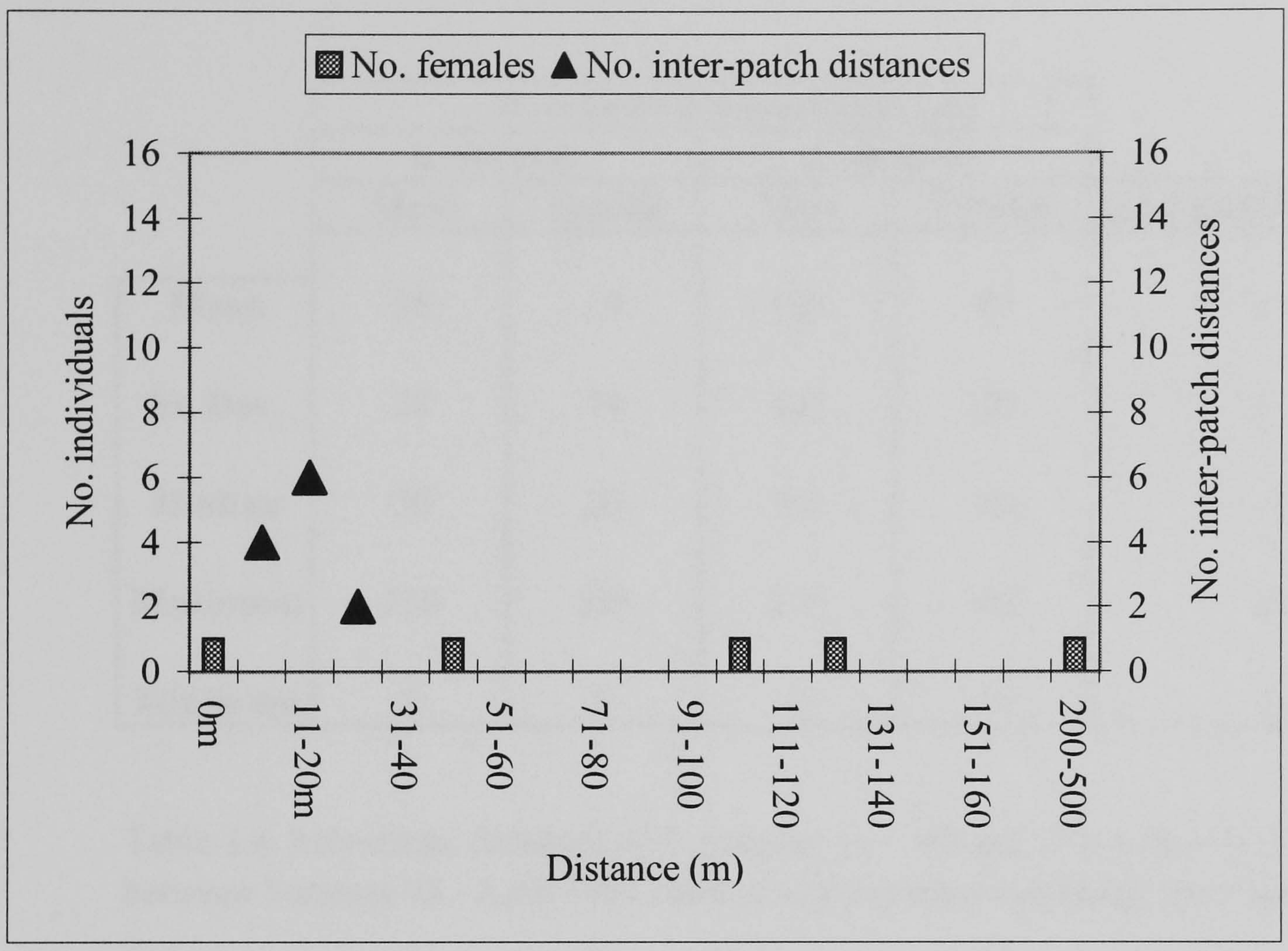


Figure 3.11 The maximum straight line distances moved by female *S. minutus* throughout the 1998-1999 study period relative to the nearest-neighbour inter-patch distances.

	Movement distances (metres)				
	S. araneus		*S. minutus*		
	Male	**Female**	**Male**	**Female**	**Inter-patch distance**
Mean	38	29	109	97	13
St. Dev.	38	74	102	137	8
Median	30	20	102	26	12
Maximum	220	513	270	352	25
Minimum	0	0	0	10	2

Table 3.4 Movement distances of *S. araneus* (n = 94) and *S. minutus* (n = 15) between Summer 98 - April 1999 relative to the nearest-neighbour inter-patch distanc

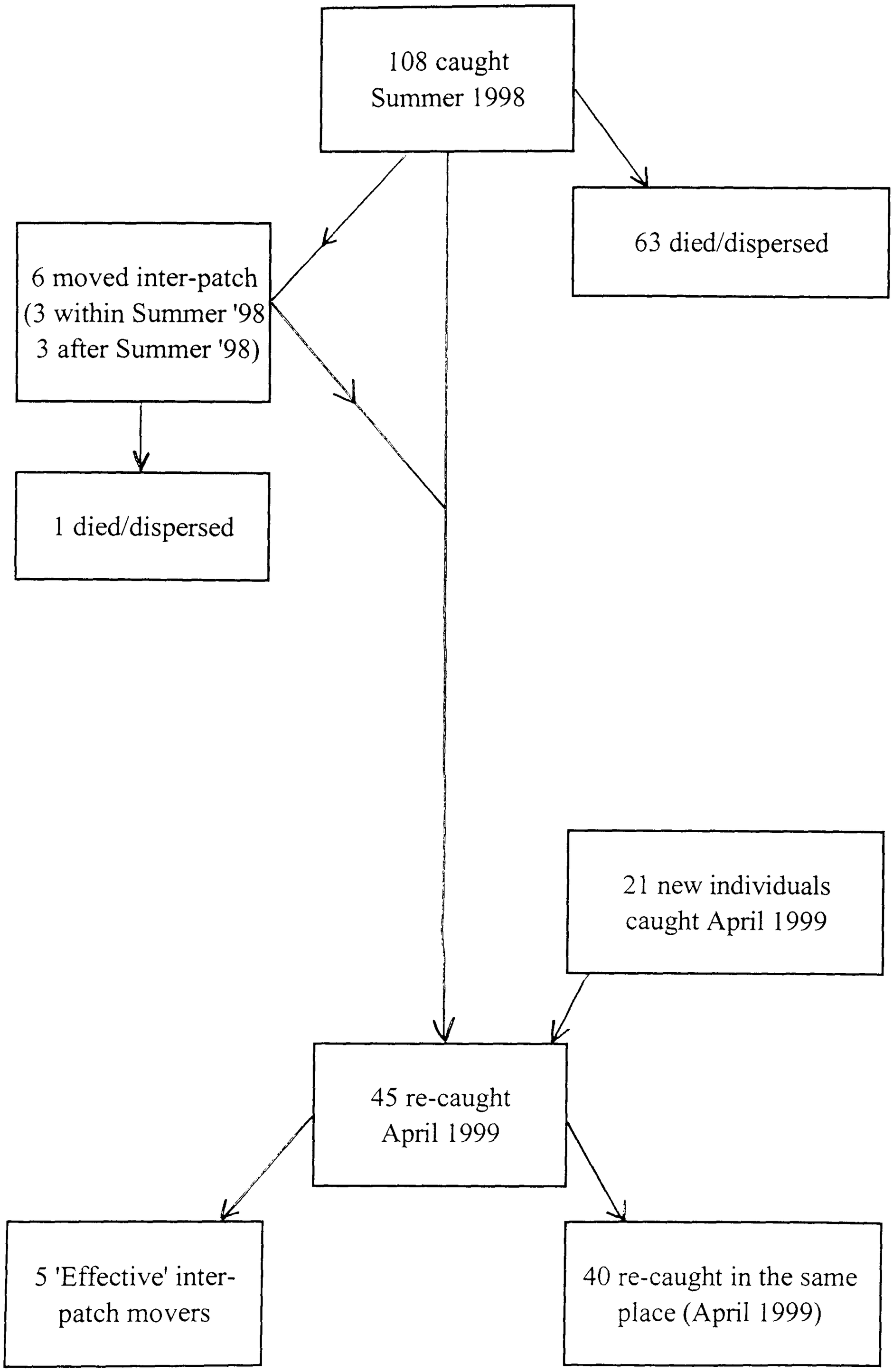


Figure 3.12 Summary of trapping data for male *S. araneus* from Summer 1998 at the field site, Fulford Golf-Course

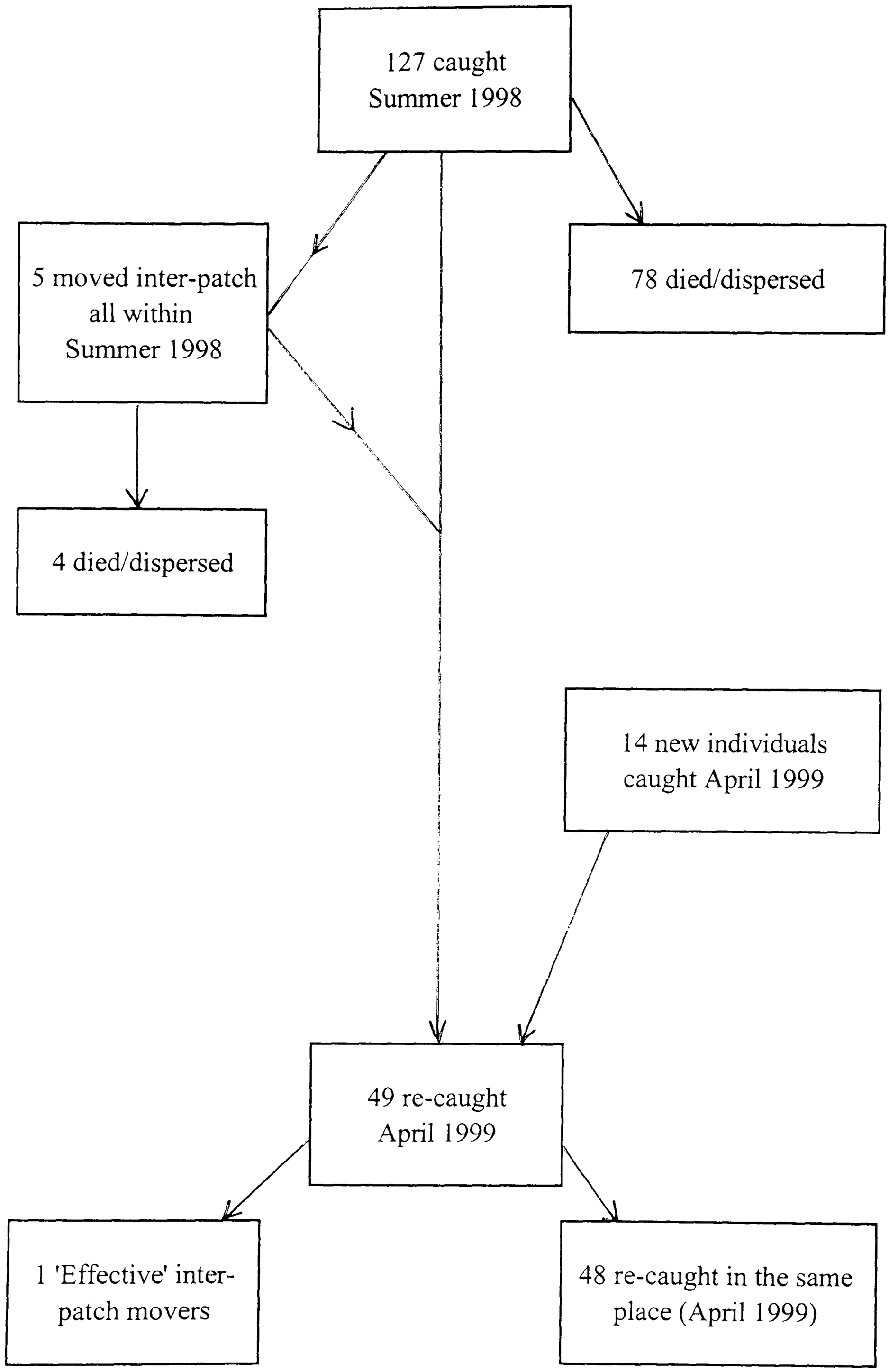


Figure 3.13 Summary of trapping data for female *S. araneus* from Summer 1998 at the field site, Fulford Golf-Course

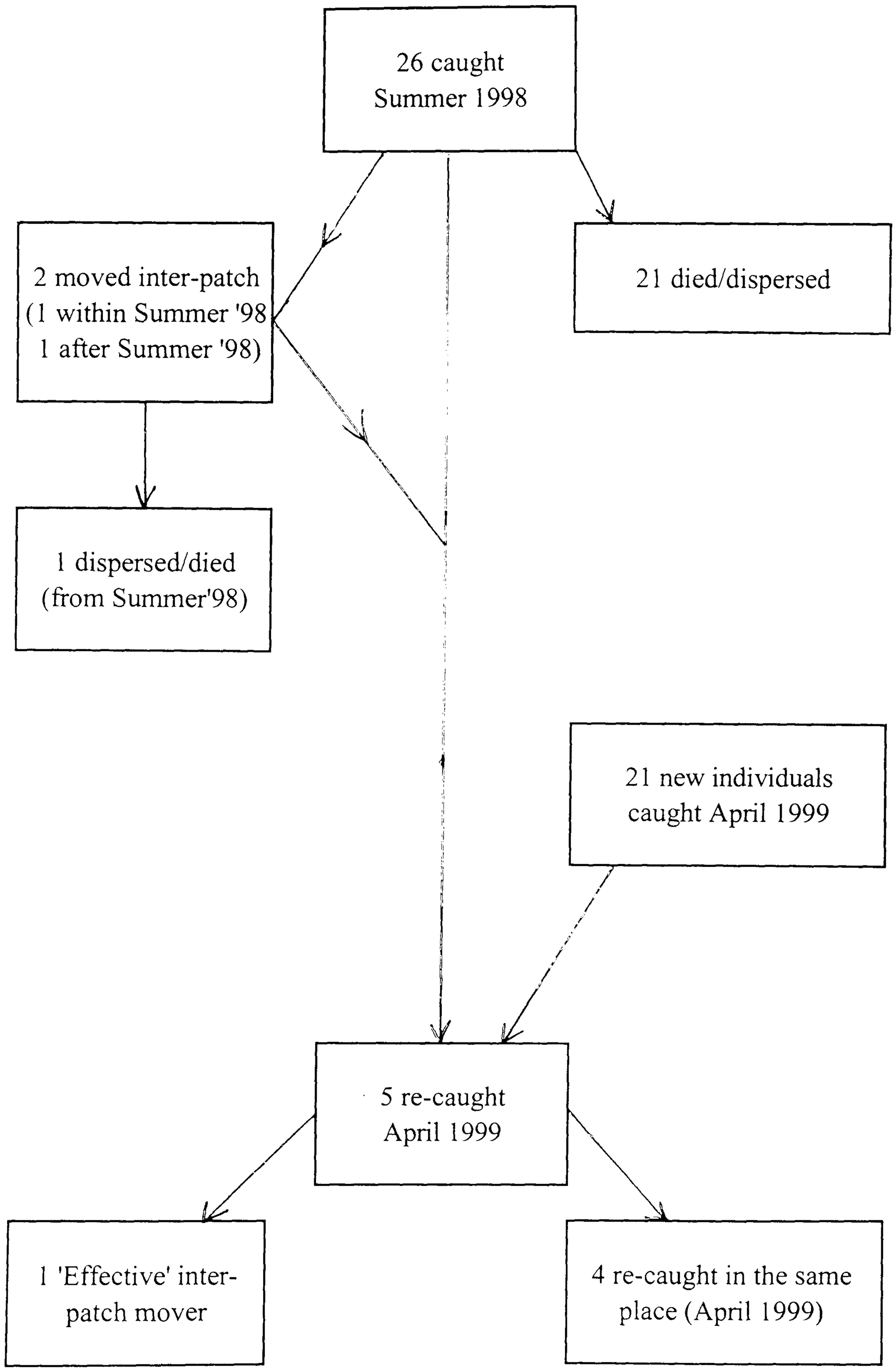


Figure 3.14 Summary of trapping data for male *S. minutus* from Summer 1998 at the field site, Fulford Golf-Course

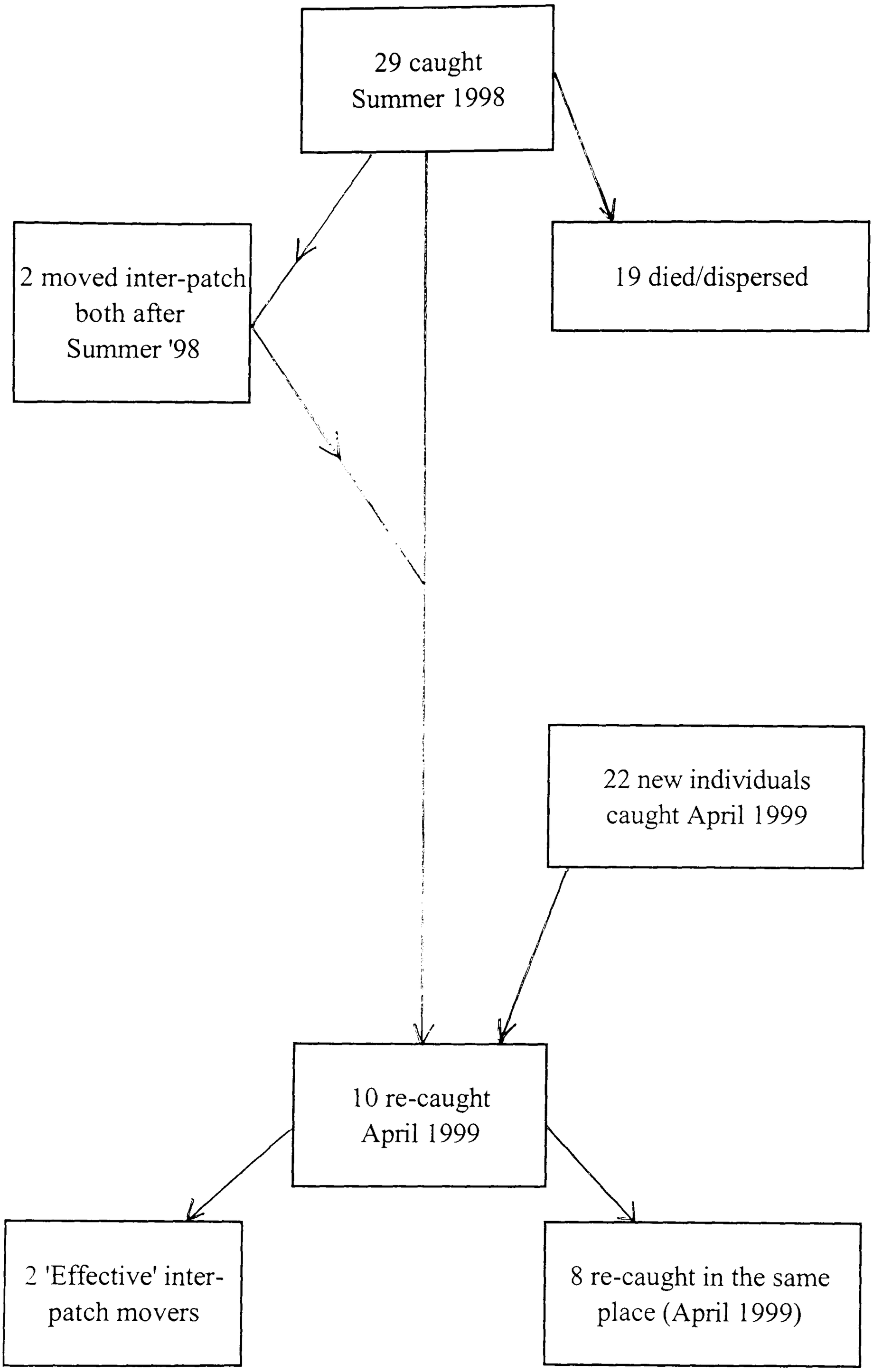


Figure 3.15 Summary of trapping data for female *S. minutus* from Summer 1998 at the field site, Fulford Golf-Course

	S. araneus			*S. minutus*		
	Males	**Females**	**Total**	**Males**	**Females**	**Total**
Total caught (Summer '98)	108	127	235	26	29	55
No. that moved ('Observed movement')	6	5	11	2	2	4
No. that moved+ survived ('Effective movement')	5	1	6	1	2	3
Survival of dipsersers (%)	**83.3**	**20.0**	**54.5**	**50.0**	**100.0**	**75.0**

Table 3.5 The survival rate of *S. araneus* and *S. minutus* following inter-patch movement

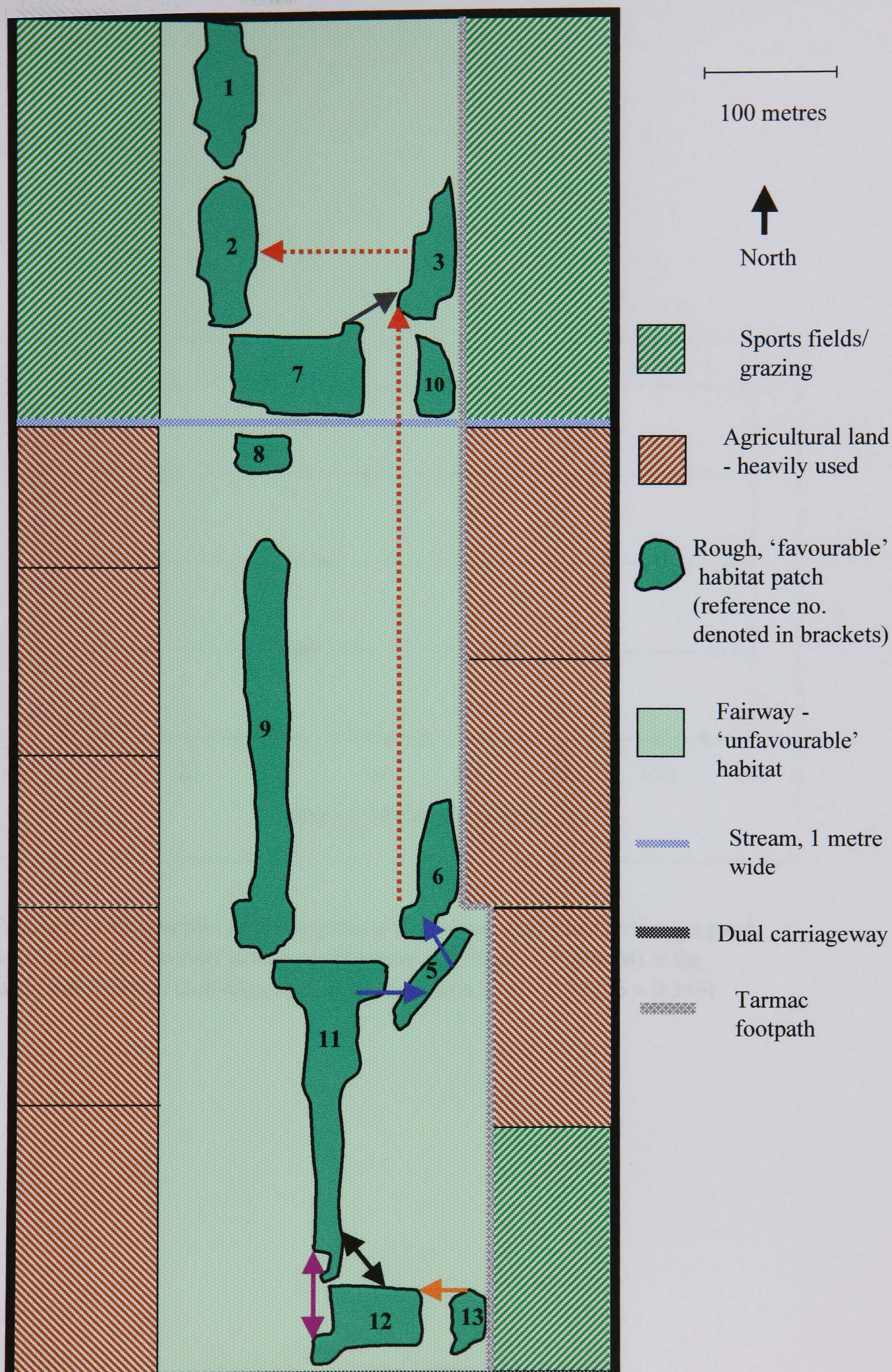


Figure 3.16 A map of the study site, Fulford Golf-Course, showing all 'observed' *S. araneus* movements between the patches of favourable habitat. Each individual is represented by a different colour. The dotted line represents the only female. All other lines represent males.

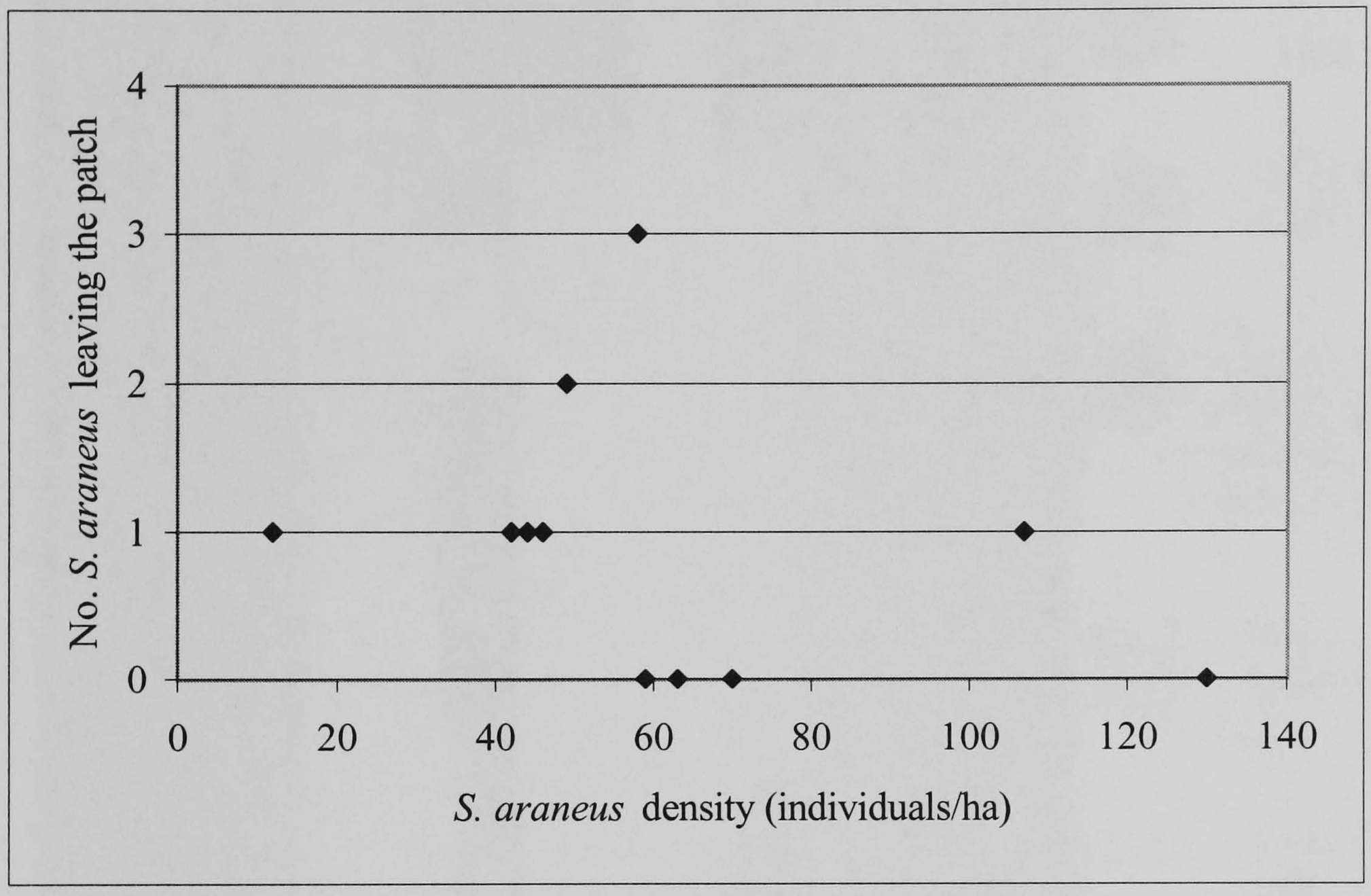


Figure 3.17 Scatter plot of the number of *S. araneus* individuals leaving a patch and *S. araneus* juvenile density during June and August (combined) at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 0.977$; $p = 0.349$).

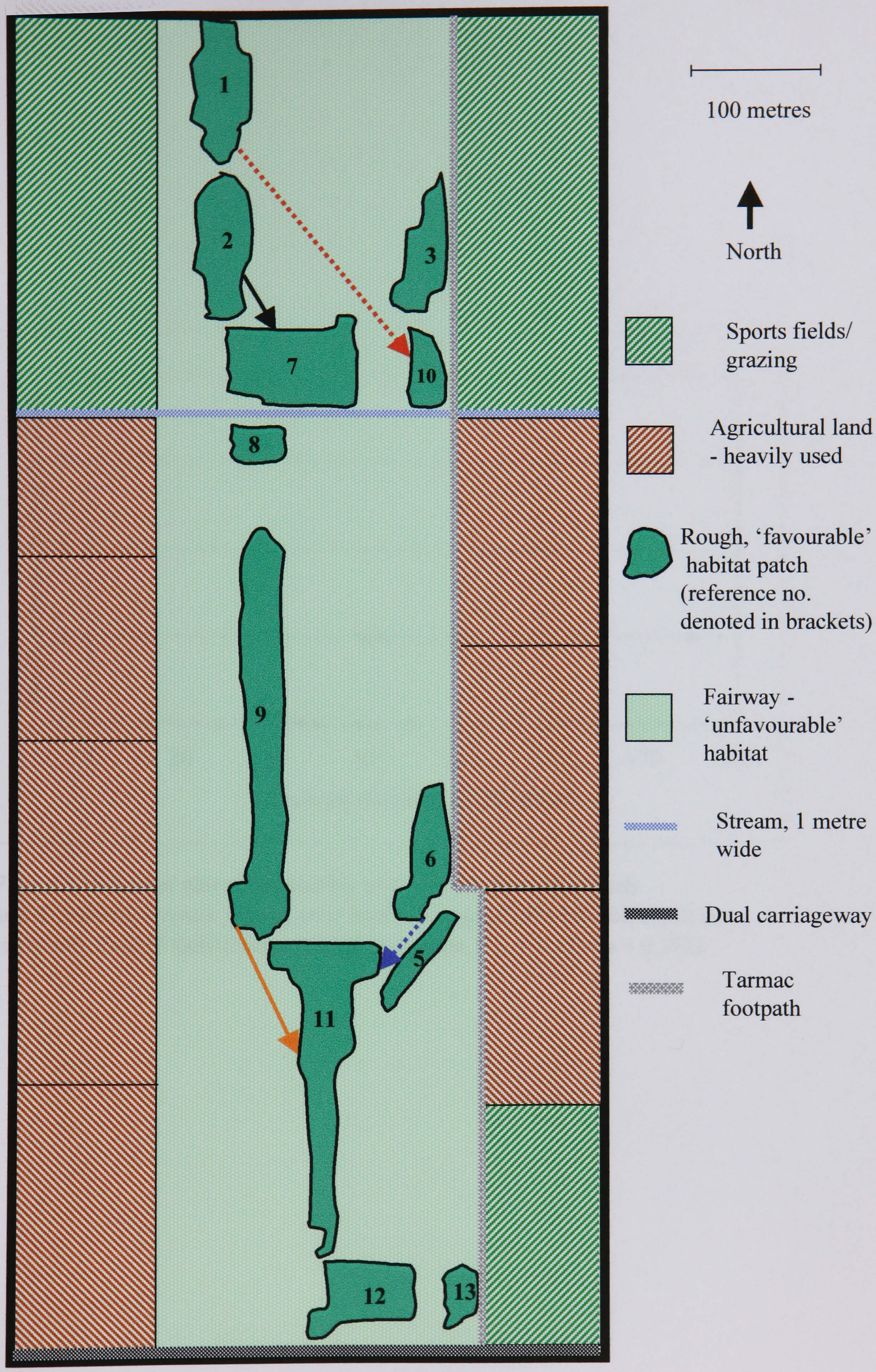


Figure 3.18 A map of the study site, Fulford Golf-Course, showing all 'observed' *S. minutus* movements between the patches of favourable habitat. Each individual is represented by a different colour. The dotted line represents the only female. All other lines represent males.

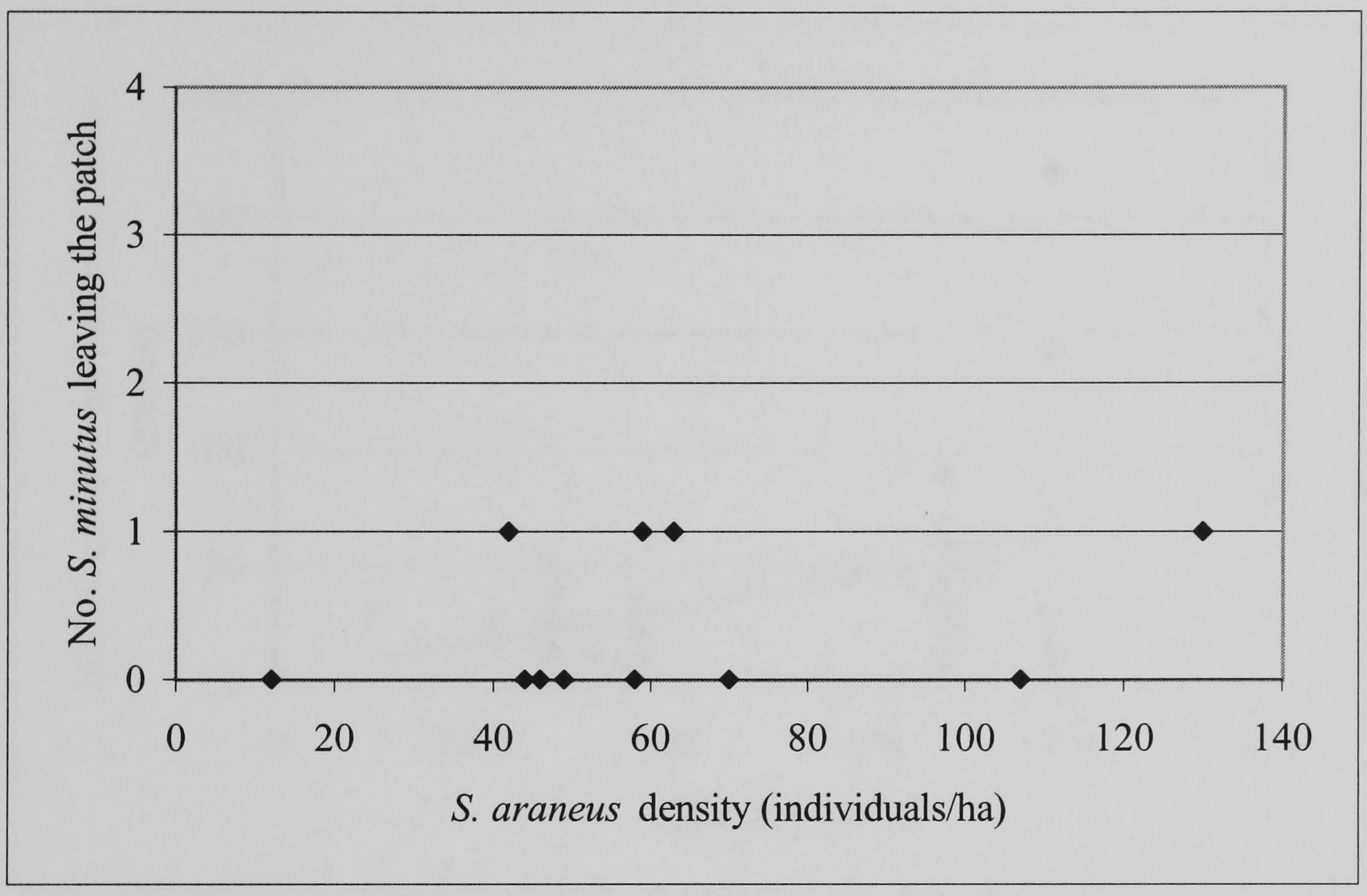


Figure 3.19 Scatter plot of the number of *S. minutus* leaving a patch and *S. araneus juvenile* density over June and August 1998 (combined) at the study site, Fulford Golf-Course (Linear regression, $F_{1,9} = 0.810$; $p = 0.392$).

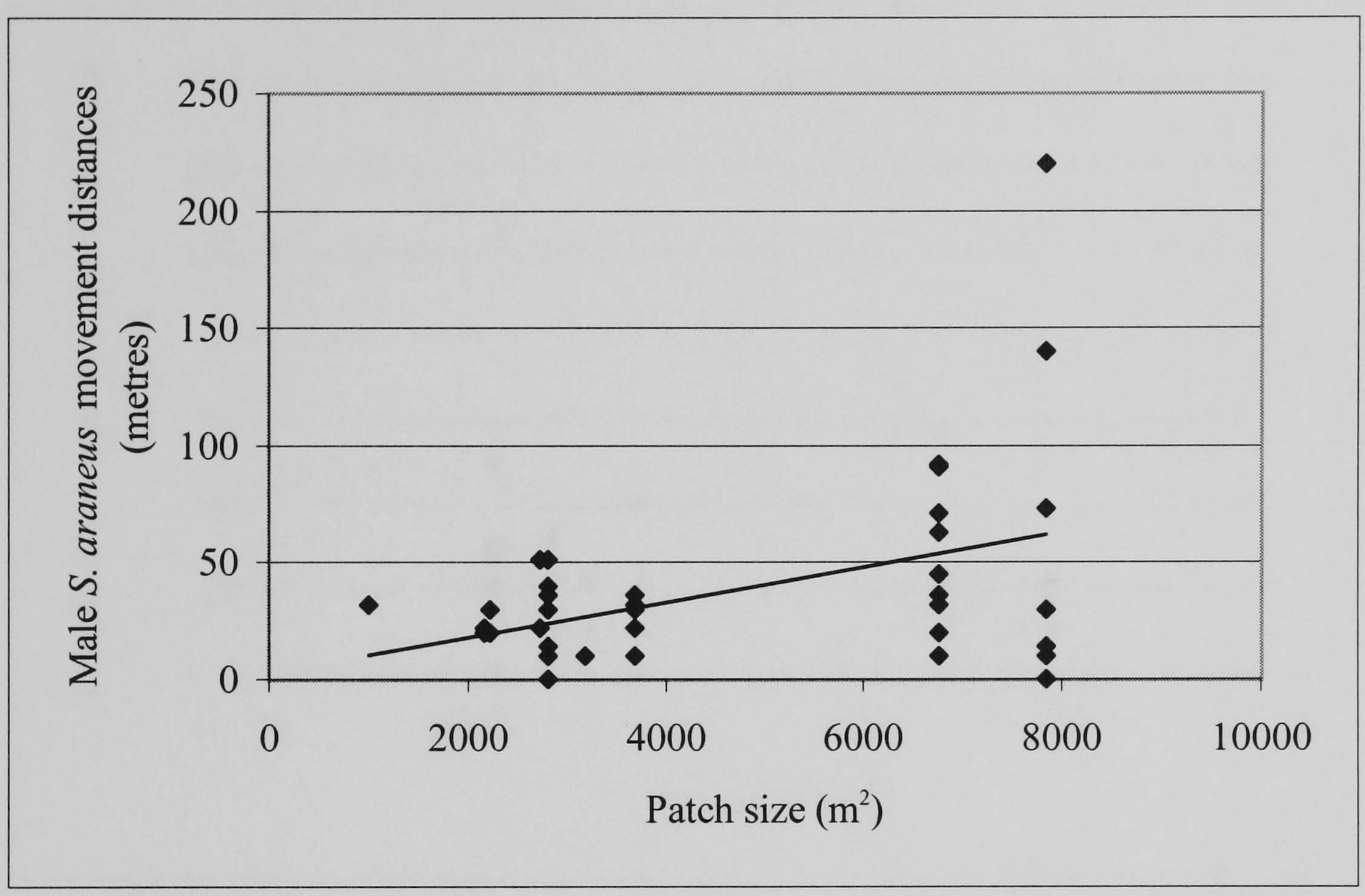


Figure 3.20 Scatter plot showing the relationship between *S. araneus* male movement distances (Summer 1998 - April 1999) and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,39} = 8.22$, $p = 0.007$).

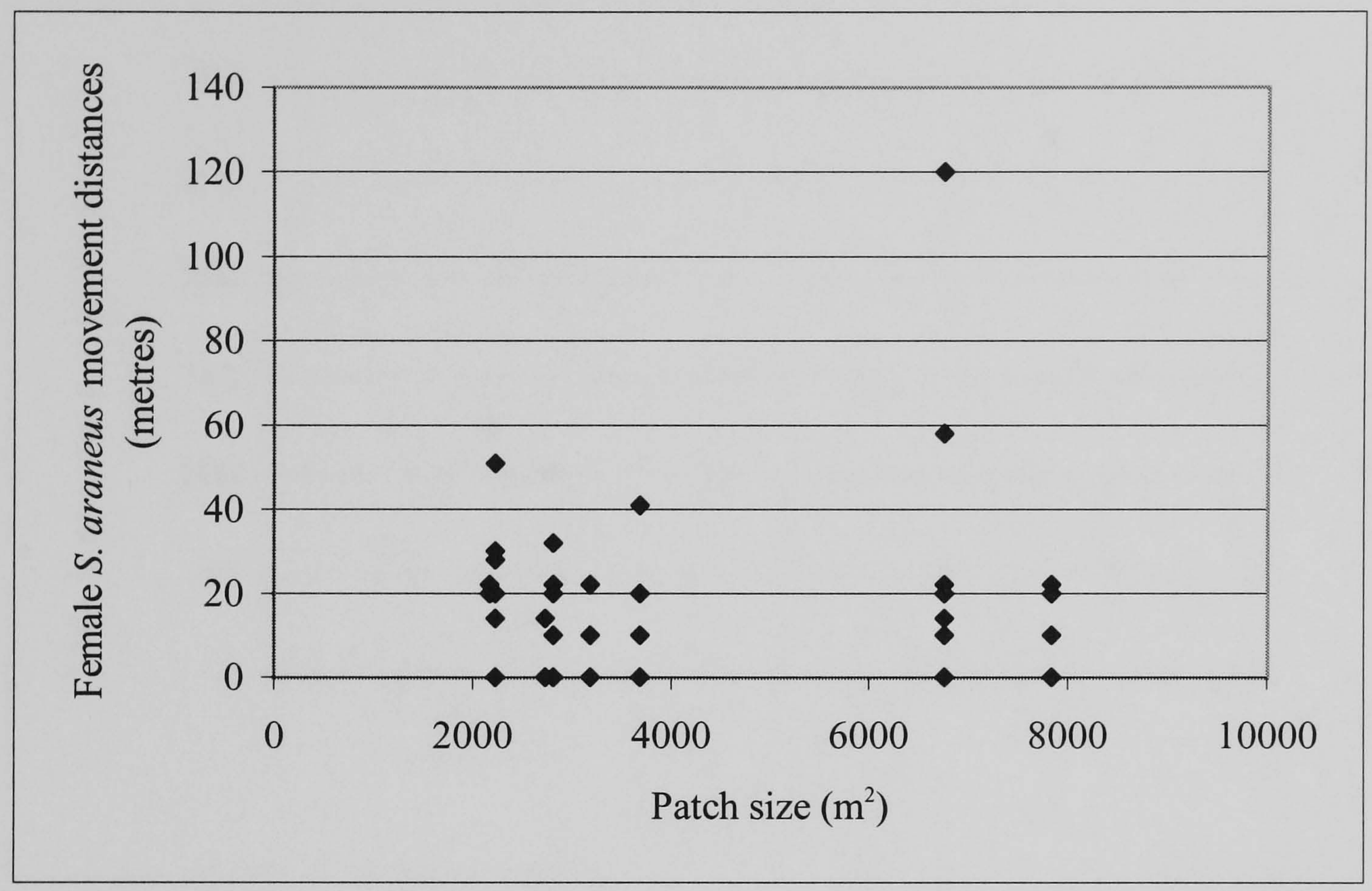


Figure 3.21 Scatter plot showing *S. araneus* female movement distances (Summer 1998 - April 1999) and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,45} = 0.52$, $p = 0.477$).

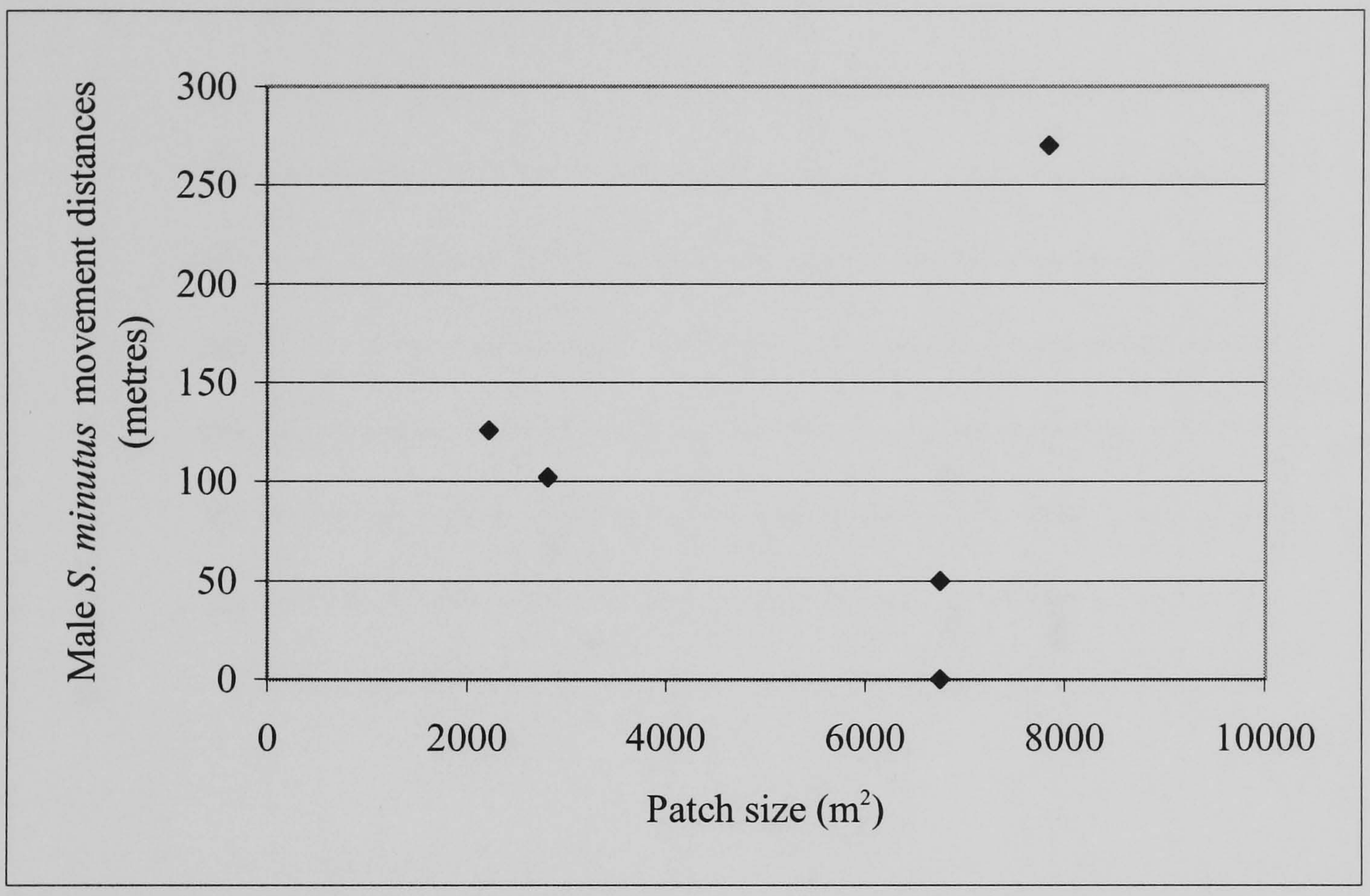


Figure 3.22 Scatter plot showing *S. minutus* male movement distances (Summer 1998 - April 1999) and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,3} = 3.221$, $p = 0.171$).

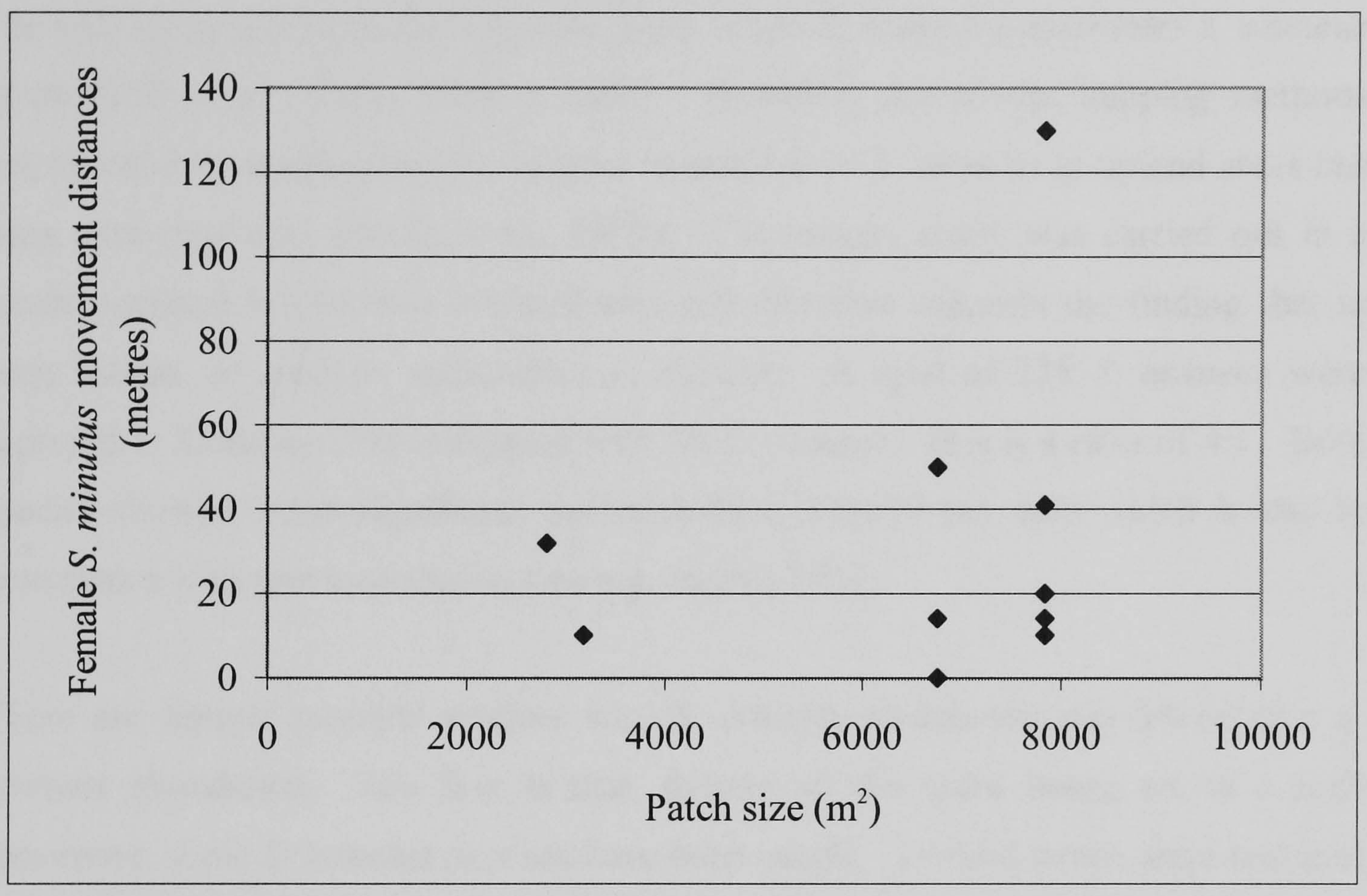


Figure 3.23 Scatter plot showing *S. minutus* female movement distances (Summer 1998 - April 1999) and patch size at the study site, Fulford Golf-Course (Linear regression, $F_{1,8} = 0.371$, $p = 0.560$).

3.4 DISCUSSION

3.4.1 Abundance and survival

Throughout most of Europe and into Asia, *S. araneus* and *S. minutus* occur sympatrically, with *S. araneus* occurring in greater numbers (e.g. Michielsen, 1966). The only exception to this is in upland areas where *S. minutus* outnumbers *S. araneus* (Butterfield *et al.*, 1981; Yalden, 1981). However, due to the trapping methods employed, it is possible that the relative abundance of *S. minutus* in upland areas has been over-estimated (Shore *et al.*, 1995). The present study was carried out in a scrub/grassland habitat in a lowland area and therefore supports the finding that in such habitat, *S. araneus* outnumbers *S. minutus*. A total of 235 *S. araneus* were captured in Summer 1998 compared with 56 *S. minutus*. This is a ratio of 4:1. Both species showed a non-significant deviation from a 50:50 sex ratio which is also in accordance with previous studies (see e.g. Searle, 1985).

There are several possible reasons why *S. minutus* abundance was lower than *S. araneus* abundance. The first is that, despite all the traps being set to a high sensitivity, some *S. minutus* may not have been caught. Treadle ramps were not used in this study and therefore it is possible that some individuals entered the trap under the treadle without setting it off. The second possible reason for this difference in numbers is that there was inter-specific competition occurring between *S. araneus* and *S. minutus*. However, the results show that as *S. araneus* density increases, so does *S. minutus* density. This shows that presence of *S. araneus* is not suppressing *S. minutus* numbers and that at these densities, inter-specific competition is not the reason for the low numbers of *S. minutus*. Both species seem to be responding to the habitat structure (patch size) rather than each other. The third possible reason for this difference in number is that *S. minutus* has been recorded as having larger home-ranges than *S. araneus* and being more mobile (Michielesen, 1966). This is substantiated by the results presented in this chapter and the previous one which show that *S. minutus* movement distances tend to be longer than those of *S. araneus*.

Densities of both species vary greatly between patches (*S. araneus* 12-130 indivs./ha, *S. minutus* 5-36 indivs./ha). The number of individuals of both species show a relationship with patch size, thus suggesting that internal patch structure is not of primary importance in determining the number of individuals present. However, this large range suggests that internal habitat structure may be of importance in determining the density of both species. Internal habitat structure should be included in a further study to determine why the densities vary so much between patches.

3.4.2 Survival

S. araneus

S. araneus and *S. minutus* are annual species. Individuals are born during the summer and remain sexually immature for their first calender year. They become sexually mature in the spring following their birth and die within the same year (e.g.Crowcroft, 1957; Grainger and Fairley, 1978). Previous studies in the south of Britain (Churchfield, 1980) found that survival in *S. araneus* was 50 % in the first two months of life. Social pressure was cited as the reason for the high mortality rate (i.e. competition for nest sites and food). After this, the fall-off was slower but only 20-30 % individuals survived to breed. The present study has found a similar pattern in survival. Survival of animals born in June in the first two months of life was 67 % and survival from birth to breeding (Summer 1998 - April 1999) was found to be 40 %.

There was no significant difference between overall male survival rate (41.6 %) and overall female survival rate (38.6 %) in *S. araneus*. Immature *S. araneus* have very similar behaviour (e.g. Stockley *et al.*, 1994). As this study was carried out prior to the onset of the breeding season, such a similarity in survival rates was expected. Churchfield (1980) did not record different survival rates for different sexes and it is therefore not possible to compare these results with her study.

S. minutus

The annual survival rate calculated for *S. minutus* in this study was 27.3 %. Of the 15 animals caught in June 1998, only two were re-captured in August. Two additional animals were caught in April 1999 (that avoided capture in August 1998). Survival in the first two months of life was therefore 26.6 % which is close to the overall survival rate. There was a significant difference in survival between male *S. minutus* and *S. araneus* (*S. araneus* 41.6 %, *S. minutus* 19.2 %). There are several possible reasons for this. *S. minutus* is smaller and therefore has a quicker starvation rate than *S. araneus* (Crowcroft, 1957). Some studies have shown that they live closer to the surface (e.g. Grainger and Fairley, 1978) and therefore they may also be more vulnerable to predation (See Appendix 2 for a list of potential predators observed at the site). However, these reasons do not explain why there is a difference between males but not females. The previous chapter has also shown that they undertake more inter-patch movements than *S. araneus*. This would make them increasingly vulnerable to predation and males undertake more of these inter-patch movements than females (see Chapter 2). However, it must be borne in mind that this result may also be due to irregular capture rates in this species and also the high mobility of the males which may move off the site.

3.4.3 Movement

This is the first entirely terrestrial study (as opposed to islands in lakes, e.g. Hanski, 1986) of either species to be carried out over such a large spatial scale with such a high density of traps. The results therefore provide the opportunity to look at both short and long-distance movement. The information gleaned is particularly useful with regards long-distance movement because to date, such movement has only been recorded as a result of chance observations (e.g. Tegelström and Hansson, 1987) rather than as a result of a consistent live-trapping regime.

The present study used the maximum distance between the furthest two points of capture as its measure of movement distance. This was because the main aim of the study was to look at movement distances relative to the scale of the landscape. The maximum recorded distance for a *S. araneus* female in the present study (513 metres) is greater than previously recorded for either sex using a live-trapping regime. A study by Tegelström and Hansson (1987) recorded individuals moving up to 3.5 kilometres over ice. However, they did not sex the animals. In males, movement was common in the region of 40 – 80 metres. Although it is difficult to compare these results with studies that looked at polygonal home-range areas, these distances are greater than the diameters of the home-ranges (30 metres) recorded in previous studies (e.g. Shillito, 1963; Stockley *et al.*, 1994). However, the general pattern which has previously been recorded for this species, that most individuals move a short distance from their place of birth but that there are a few long-distance dispersers (e.g. Shillito, 1963; Michielsen, 1966) is supported by this study. Although the general pattern is not disrupted by the patch structure found at the site, there will be relatively less movement between neighbouring areas of favourable habitat due to the tracts of unfavourable habitat in between them.

The results of this study also support those of a previous study which have shown that *S. minutus* is more mobile than *S. araneus* (Michielsen, 1966). For *S. minutus*, the maximum straight-line distance moved by individuals of this species varies from 0 metres to 300 metres. Although the maximum recorded distance moved by *S. minutus* is lower than that recorded for *S. araneus*, the number of individuals in each movement category is fairly evenly distributed along the continuum between the maximum and minimum distances moved. This is very different from the distribution for *S. araneus* where the majority of individuals move much smaller distances. There is therefore no evidence in *S. minutus* that more animals stay close to their place of birth than do not. This supports Michielsen (1966) and the results presented in Chapter 2 that in general, *S. minutus* moves greater distances than *S. araneus*.

3.4.4 'Observed' inter-patch movement

'Observed' inter-patch movement is defined as the total number of inter-patch movements recorded. It is important to distinguish it from 'effective' inter-patch movement as these latter values will usually be lower. 'Effective' inter-patch movement is a sub-set of 'observed' inter-patch movement and refers to those animals that move to another patch and survive to breed. If they breed successfully in their new patch, it is equivalent to gene flow. Restricted movement between patches of habitat will reduce gene flow and may result in inbreeding and its associated problems (Caughley, 1994). The number of individuals moving between habitats will only influence this if they survive in their new patch and breed successfully.

For *S. araneus*, the number of observed inter-patch movers is eleven, only 4.7 % of the total number of individuals caught. Although movement distances recorded in the present study are great relative to the inter-patch distances, the frequency of movement between patches separated by unfavourable habitat is low. Most of the movement across unfavourable habitat occurred during the summer, soon after the animals left the nest. This may be when exploratory movements were at their most frequent and inter-specific competition at its greatest. For *S. minutus*, 'observed' inter-patch movement is also low. Only four inter-patch movements were recorded. This is in contrast to the results presented in Chapter 2 where many more *S. minutus* moved between patches. This may be a consequence of the smaller number of trapping sessions undertaken throughout the year which, in combination with low survival, high mobility and unreliable 'trappability' resulted in the pattern obtained for the 1997 cohort being absent in the 1998 cohort. The low numbers also meant that this was not able to be tested statistically. However, a higher proportion (7.1 %) of the total number of individuals caught in this species moved between patches than in *S. araneus* (4.7 %). There is no indication that, like *S. araneus*, in *S. minutus* the majority of inter-patch movements occurred during the summer months soon after weaning. This supports the fact that in *S. araneus* such movements are undertaken in search of territories whereas in *S. minutus*, such movements are taken more regularly

and are due to larger home ranges and generally higher mobility. However, the small sample size involved prevents any real patterns being detected.

As predicted, 'effective' inter-patch movement is lower than 'observed' inter-patch movement in both species. This emphasizes the importance of distinguishing between the two. The difference between them enables the survival rate of inter-patch movers to be calculated.

3.4.5 Survival of inter-patch movers

In *S. araneus*, six out of eleven (54.5 %) inter-patch movers survived until April 1999. This is higher than the overall survival rate for the species and therefore does not suggest that inter-patch movements are risky. However, this survival rate may be due to the low number of inter-patch movers. In *S. araneus* there is minimal sex differences in the number of inter-patch movers: five females and six males moved from one patch to another. In addition, there was no significant difference between the survival rates of the inter-patch movers in each sex.

In *S. minutus*, three out of four (75 %) inter-patch movers survived until April 1999. This survival rate is also greater than the annual survival rate for the species. However, this may also be a result of sample size. In this species, the number of effective movers is closer to the number of observed movers than it is for *S. araneus*. Due to the low number of inter-patch movers, it is not possible to speculate on the differences between male and female dispersal rate and subsequent survival. The reasons for higher survival in inter-patch movers in both species may have been a result of those individuals being more vigorous than those that stayed in their natal patches. However, results from Chapter 2 show that inter-patch movers do not differ in weight from those that stay in their natal patch.

3.4.6 Inter-specific comparisons

The results highlight the ecological differences between males in the two species. This may influence the population structure of both species in a heterogeneous landscape. *S. minutus* males have a lower survival rate and move larger distances than *S. araneus* males.

3.4.7 Movement detail

S. araneus

It is important to look at the spatial nature of the inter-patch movement so as to predict the nature of the gene flow that may be occurring between patches. In *S. araneus*, nine out of eleven animals moved to patches adjacent to their natal patch. Only two individuals, one male and one female moved to patches beyond their adjacent patch. This predicts that most gene flow will occur between adjacent patches. It also predicts that patches with more than one neighbour will receive more gene flow than a patch with only one neighbour. The results presented in this chapter (the 1998 cohort) support those found in the previous chapter (the 1997 cohort) that the most frequently crossed inter-patch distance was also the smallest at the site. Two individuals, both males, crossed from Patch 11 into Patch 12 and then back into Patch 11. This suggests that gene flow will be more frequent between patches that are situated relatively close to each other.

S. minutus

The spatial nature of movement in *S. minutus* was similar to that found in *S. araneus*. Three out of the four individuals moved to patches adjacent to their natal patch. Only one animal, a female, moved to a patch further away than this. In this species, more gene flow is also predicted between adjacent patches than between those further away from each other. There was no movement back and forth between patches in this

species. All movement was uni-directional. There was no indication that inter-patch distance was affecting the frequency of inter-patch dispersal in this species.

3.4.8 The influence of landscape structure on movement

The results presented in this chapter describe the movement of *S. araneus* and *S. minutus* in a heterogeneous landscape. One striking feature in both species is that movement between patches over unfavourable habitat is rare and is undertaken by very few individuals. Given the spatial scale at which the study has been carried out and the distances moved by the individuals in the patches relative to the nearest-neighbour inter-patch distances, this is surprising. General movement characteristics of these species can only be gained from the results if possible reasons for this are identified.

One possible reason for this low rate of inter-patch dispersal is that individuals are reluctant to cross habitat borders between favourable and unfavourable habitat i.e. their movement is restricted by the habitat edges found at the site. This could be determined if an expected number of inter-patch movers were compared with the number of dispersers observed. However, calculating an expected value for this is difficult. A similar study of a continuous area of habitat in order to obtain such a value is is unrealistic firstly, because finding such an area would be very difficult and secondly, because of the number of traps involved and the number of field-work hours required would be very large. An alternative approach to determining whether or not habitat edges are restricting movement is to look at movement distances within the patches. If movement is restricted by habitat edges, then it would be expected that movement in smaller patches would be over smaller distances than movement in larger patches.

S. araneus

The results show that in male *S. araneus*, movement distances within patches are directly related to patch size, thus strongly suggesting that their movement is restricted by habitat edges. No such relationship was found in females. However, the fact that so few females moved from one patch to another suggests that their movement is also restricted by habitat edges, despite no relationship being found.

S. minutus

No relationship was found between patch size and movement distances in either sex. In males, this may be because their movement is not restricted by patch edges which would support the results found in the previous chapter. In order to obtain more information on this species and its response to landscape structure, a more temporally intensive trapping regime is required such as the one described in Chapter 2. A greater proportion of *S. minutus* than *S. araneus* did move from one patch to another. It therefore seems that, as found in the previous chapter, *S. minutus* is less sensitive to landscape structure than *S. araneus*.

CHAPTER 4

DOES TIMING OF BIRTH AND WEANING AFFECT PHYSICAL AND BEHAVIOURAL CHARACTERISTICS IN *SOREX ARANEUS* OFFSPRING?

4.1 INTRODUCTION

Female *S. araneus* can produce up to five litters during the breeding season but more generally they produce between two and three (Crowcroft, 1957; Stockley, 1996). The time of the first oestrus tends to be synchronous within a site and results in the pregnancy of essentially all the females (Stockley, 1996). Females have a gestation period of approximately 20 days and a lactation period of up to 24 days (Crowcroft, 1957). The first post-partum oestrus can occur while the female is still lactating (Crowcroft, 1957) and a second litter may therefore be born within approximately 24 days of the first.

Young shrews must establish a territory in order to survive the winter (Churchfield, 1980). Those which establish home-ranges early in the summer may have competitive advantages over those which do not (Moraleva, 1989). Churchfield *et al.* (1995), for example, showed that survivorship was higher in early-born cohorts than late-born cohorts. At the site used in the present study, the first young of the year were trapped in late May. The aim of this study was to see if any differences in physical and behavioural characteristics existed between these individuals and those born later in the year.

Work of this nature in vertebrates has primarily been carried out in birds where fledging dates and nest sites are easy to pin-point (e.g. Perrins, 1965). In many cases, differences have been found between individuals born at different times of the year. A number of studies report a decline in post-fledging survival with hatching date (e.g. Perrins, 1965; Grand and Flint, 1996). However, it is not always possible to elucidate the reasons for this. Survival probability may be causally linked to differences in

fledging date (i.e. timing) or it may be due to other characteristics such as body weight which has also been shown to be lower in later fledged individuals (Perrins, 1965; Magrath, 1991; Smith, 1993). In mammals, difficulty in observation and smaller number of species with sequential litters has resulted in fewer studies of this nature.

It is not possible to observe *S. araneus* nests directly and time the birth and dispersal of litters exactly. However, in this study, juveniles caught for the first time in June 1998 were assumed to be from earlier litters than those caught for the first time in August 1998. Work described in previous chapters shows that trap density and trapping intensity were such that the individuals caught during each trapping period were representative of those present at the site at the time. Although some error is inevitable (i.e. some individuals born in June will not be caught until August), the assumption made regarding timing of birth was felt to be justified.

4.2 METHODS

4.2.1 Live-trapping

The live-trapping regime is described in full in Chapter 1 (section 1.1). During June and August 1998, traps were set at 7.30 am and checked 3 hours later (so as to prevent lactating females being retained overnight). During April 1999, traps were set at dusk and checked at dawn.

4.2.2 Measurements taken

In April, various measurements were taken from each individual that had previously been caught and marked in June and August, 1998. Two indicators of body size were measured, weight and hind-foot length. Individuals were weighed using a Pesola spring balance accurate to 0.1g. This was always done on the first capture as shrews can put on large amounts of fat and therefore weight when being artificially fed (J. B.

Searle, pers. comm.). The left hind-foot length of every individual was also measured. Hanski *et al.* (1991) found that in years of low density, there were differences in the left hind-foot length between those individuals that dispersed and those that established home-ranges close to their place of birth. In addition, the extent of tail scarring was also scored (using categories, where 0 = none, 1 = minor, 2 = moderate and 3 = severe). Tails are often targeted in intra-specific fights, particularly in males but also in females (Crowcroft, 1957).

From the results of the trapping regime, cohort survival was calculated. This was using Churchfield's (1980; 1995) definition of survival as 'residency in the study area'. In addition, two different dispersal characteristics were measured. The straight-line distance moved between an individual's first point of capture in June/August 1998 and their first point of capture in April 1999 was measured. It was felt important to use the first point of capture in each case so that the results across cohorts were comparable and there was as little bias as possible resulting from trap-induced behaviour. The two cohort's response to landscape structure (i.e. amount of movement to other patches) was also quantified.

Various sexual characteristics were also assessed. In males, the left lateral gland was measured (using a ruler accurate to 1mm). Male shrews have a lateral gland on either side of their body, midway between their front and hind limbs. The exact function of these glands is unknown, but they are thought to be involved in reproduction as they are visible only in adult, breeding individuals (due to becoming enlarged). Testes were also assessed by their visual appearance (using subjective categories where 1 = just visible, 2 = medium and 3 = ready to breed). In females the presence or absence of nipples/nipple patches was scored. They were said to be present if they were visible without the sexing method of Searle (1985). Whether an individual was moulting or not was also recorded.

4.3 RESULTS

4.3.1 Cohort size

The number of individuals of each sex caught in each month can be seen in Figure 4.1. In June 1998, 88 *S. araneus* juveniles were caught. Of these, 50 were female and 38 were male. This sex ratio shows no deviation from a 50:50 sex ratio (G-test, $p>0.05$). In August 1998, 137 *S. araneus* juveniles were caught for the first time (i.e. had not previously been caught in June). Of these, 72 were female and 65 were male. This sex ratio also shows no deviation from a 50:50 sex ratio (G-test, $p>0.05$).

4.3.2 Survival

Figure 4.1 also shows the number of individuals from each cohort that were re-captured in April, 1999. From the previous year, 95 *S. araneus* were re-captured as adults in April 1999. Twenty-nine individuals were re-captured from the June cohort. Of these, 15 were female and 14 were male. Sixty-six individuals were re-captured from the August cohort. Of these, 32 were female and 34 were male. Neither cohort showed a deviation from a 50:50 sex ratio (G-test, $p>0.05$).

Survival is shown in Figure 4.2. It refers to the percentage survival of the June cohort over ten months (until April 1999) and to the percentage survival of the August cohort over eight months. If survival is defined as residency in the study area (c.f. Churchfield 1980; 1995) the June cohort had a survival of 32.9 % (females, 30% and males 36.8%) and the August cohort a survival of 44.9 % (females, 44.4% and males 52.3%). There was no significant difference found between female survival between the August and June cohorts or male survival between the August and June cohorts (Fisher's Exact Test, $p>0.05$). However, when the sexes were combined, a significant difference was found between survival in the two cohorts (Fisher's Exact Test, $p<0.05$).

4.3.3 Juvenile weight

Figure 4.3 shows the distributions in weight of the females in both cohorts at first capture. There was a significant difference in weight between females born in June (median 8.0g) and those born in August (median 7.5g) (Mann Whitney U-test, t_s = 2.489; $p<0.05$). Figure 4.4 shows the weight distributions of the males in both cohorts at first capture. No difference was found between males born in June (median 7.5g) and August (median 7.5g) (Mann Whitney U-test, t_s = 0.35; $p>0.05$).

4.3.4 Adult weight

Figure 4.5 shows the adult female weight distributions in each cohort. In females, there was a significant difference between the two (Mann-Whitney U-test, t_s = 1.96, $p<0.05$). The June cohort tended to be heavier than those from the August cohort (June median 8.8g; August median 8.1g). Figure 4.6 shows the adult male weight distributions in each cohort. In males, a significant difference between the two cohorts was also found (Mann-Whitney U-test, t_s = 3.01, $p<0.01$). Males from the June cohort tended to be lighter than those from the August cohort (June median 9.3g; August median 10.3g).

4.3.5 Dispersal distance

Dispersal distances of both sexes of both cohorts can be seen in Figures 4.7 and 4.8. A significant difference between the cohorts was found between these distances in both males and females (Mann-Whitney U-test, females, t_s = 2.135, $p < 0.05$; males, t_s = 231, $p < 0.05$). From the figures it can be seen that males and females from June tend to move further than those from August. One individual from June (female) moved 513 metres and one individual from August (male) moved 220 metres. These two were removed from the analysis as they were both outliers and would have biased the analysis.

4.3.6 Left hind foot length

The distributions of measurements for left hind foot length for both sexes of both cohorts are shown in Figures 4.9 for females (June mean 1.2cm; August mean 1.2cm) and 4.10 for males (June mean 1.3cm; August mean 1.3cm). No difference was found in either sex between the two cohorts (t-test, females, $t = 0.91$, $p > 0.05$; males, $t = 0$).

4.3.7 Inter-patch movement

Six individuals of the June cohort moved from one patch to another and six individuals of the August cohort moved from one patch to another. There was therefore no difference in the actual number of individuals from each cohort that moved between patches.

4.3.8 Tail scarring

The proportion of individual in each tail scarring category is shown in Figure 4.11 for females and Figure 4.12 for males. In order to test for differences between the cohorts, the first two categories were combined and compared with the latter two categories (which were also combined). In males, tail scarring was similar between the cohorts and no significant difference was found (Fisher's Exact Test, $p>0.05$). However, in females, no individuals from the June cohort were present in the most severe tail scarring categories and a significant difference was found between the two cohorts (Fisher's Exact Test, $p<0.01$).

4.3.9 Sexual characteristics

Figure 4.13 shows that in males, the length of lateral glands was similar between different cohorts (Mann Whitney U-test, $t_s = 0.6$; $p>0.05$). The proportion of individuals from each cohort in each testes score category are shown in Figure 4.14.

In order to test for differences between the cohorts, categories one and two were combined and compared with category three. In addition, category one was compared with categories two and three combined. No significant differences were found (Fisher's Exact Test, $p>0.05$ in both cases).

Figure 4.15 shows that there was no difference between cohorts in terms of the number of individuals with visible nipples/nipple patches in females (Fisher's Exact Test, $p>0.05$).

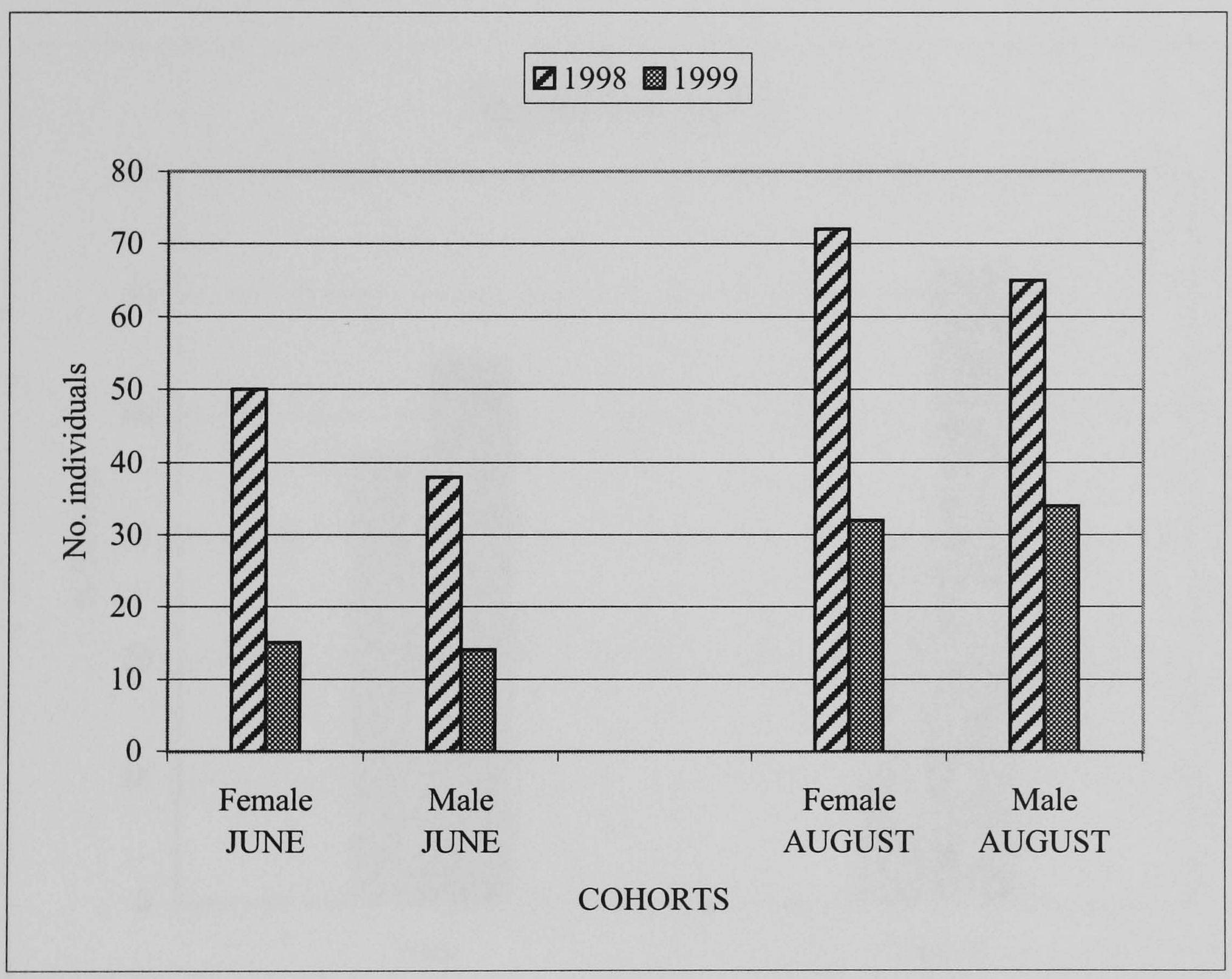


Figure 4.1 The number of male and female *S. araneus* in the June cohort and the August cohort and the number of these individuals that were re-caught in April 1999

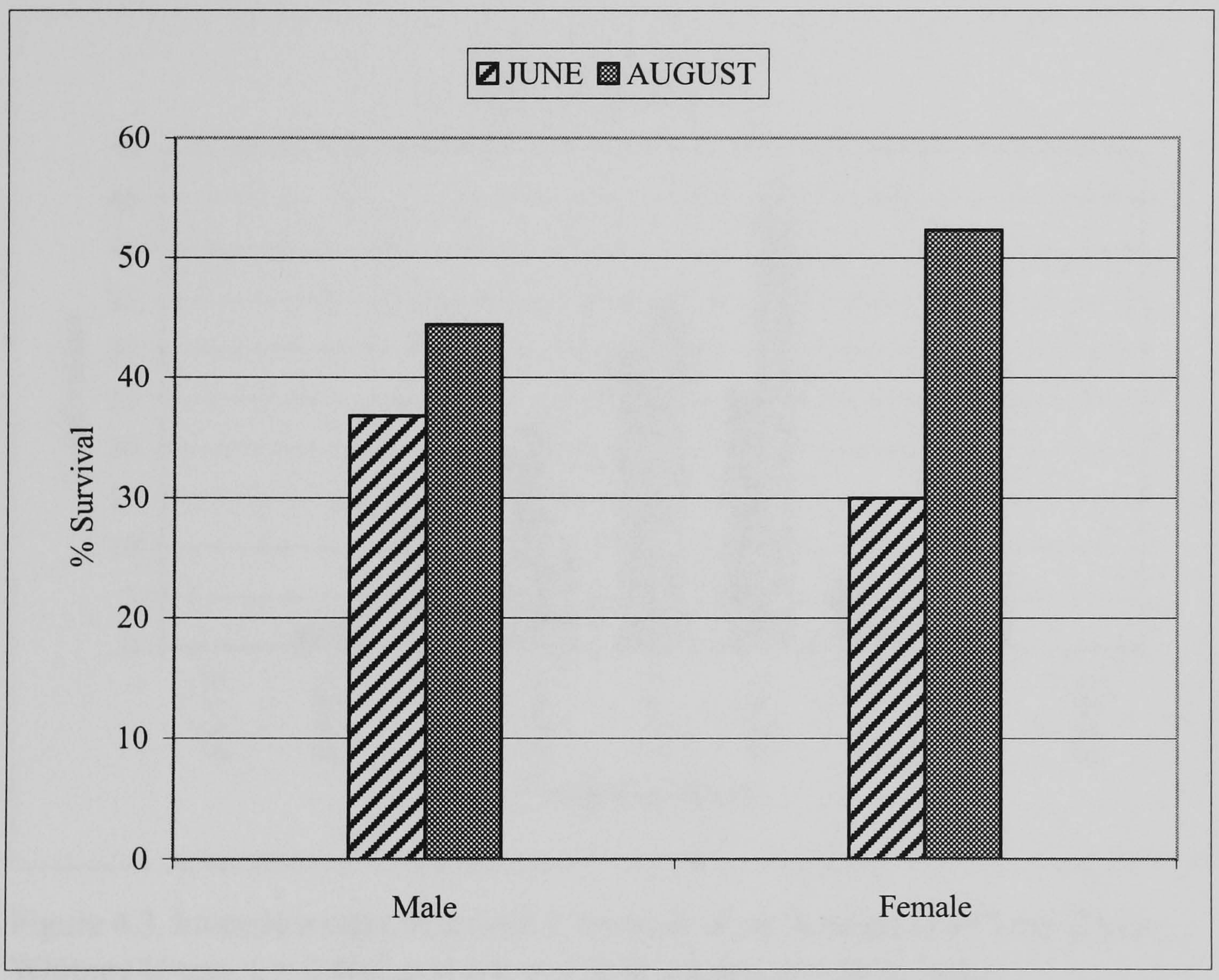


Figure 4.2 Annual survival of male and female *S. araneus* from each cohort.

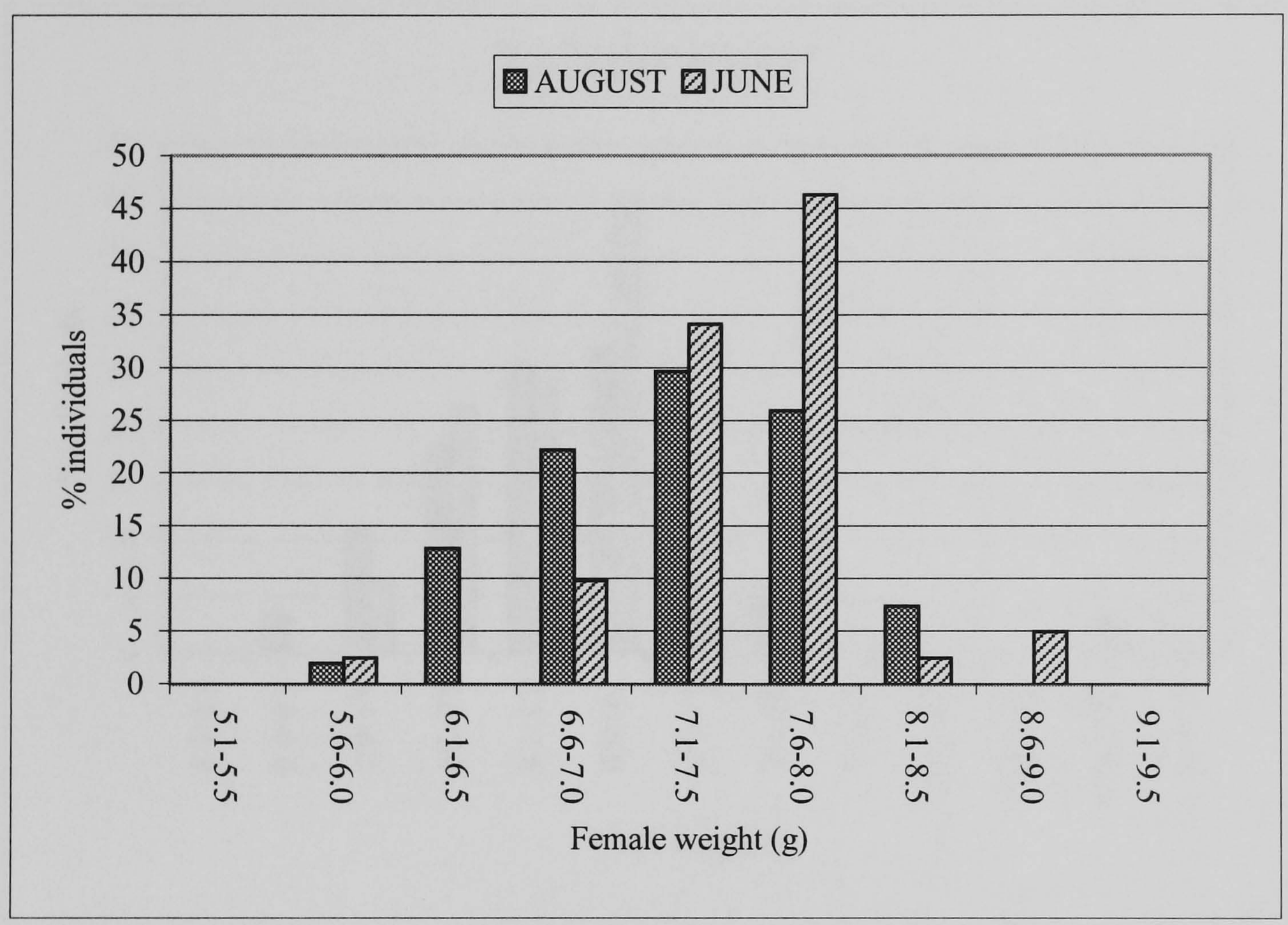


Figure 4.3. Juvenile weight of female *S. araneus* born in August and June (Mann-Whitney U-test, $t_s = 2.489$; $p<0.05$; n = 72 in August, n = 50 in June).
Each individual was weighed at first capture

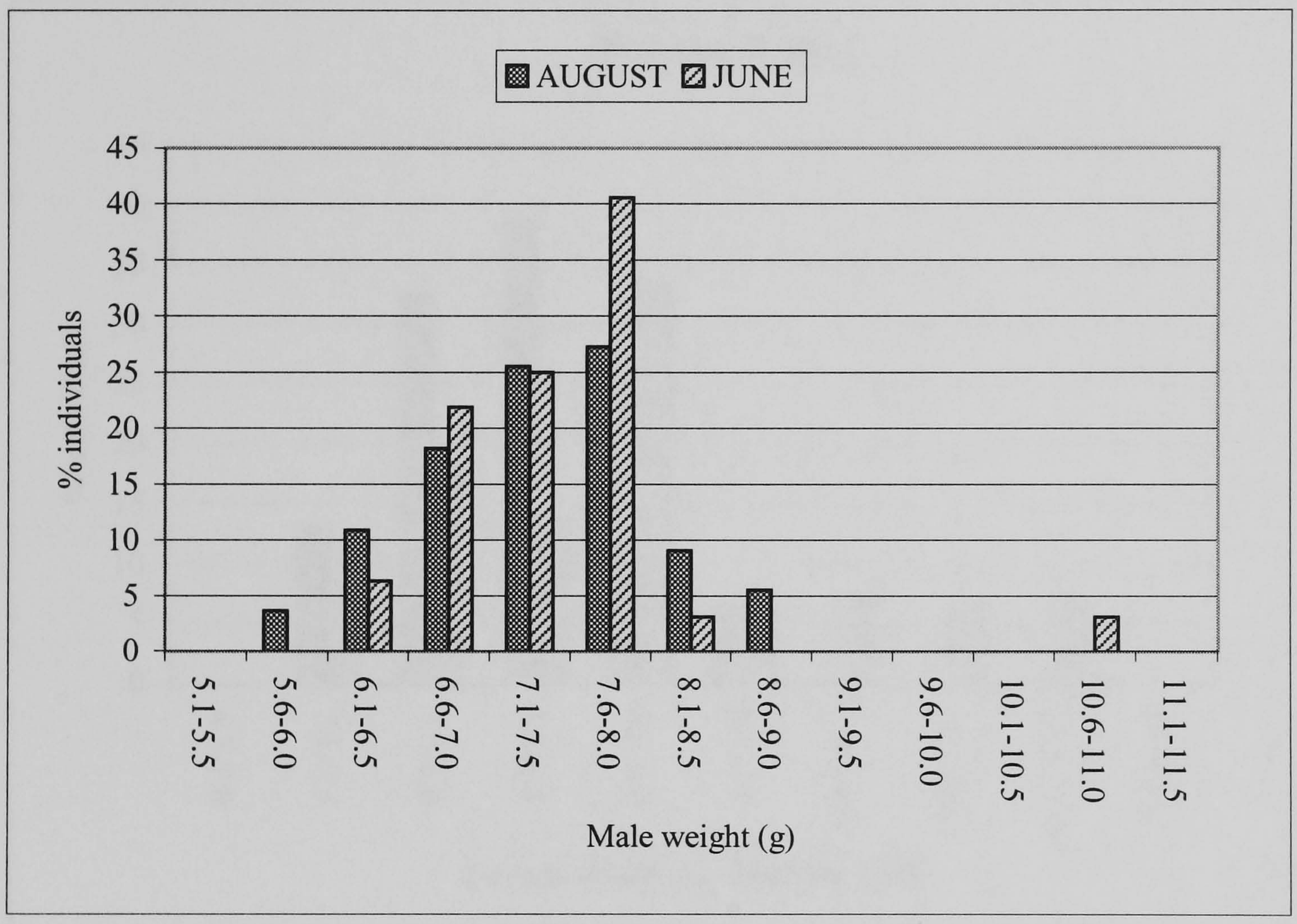


Figure 4.4 Juvenile weight of male *S. araneus* born in August and June (Mann Whitney U-test, $t_s = 0.35$; $p>0.05$; n = 65 in August, n = 38 in June).
Each individual was weighed at first capture

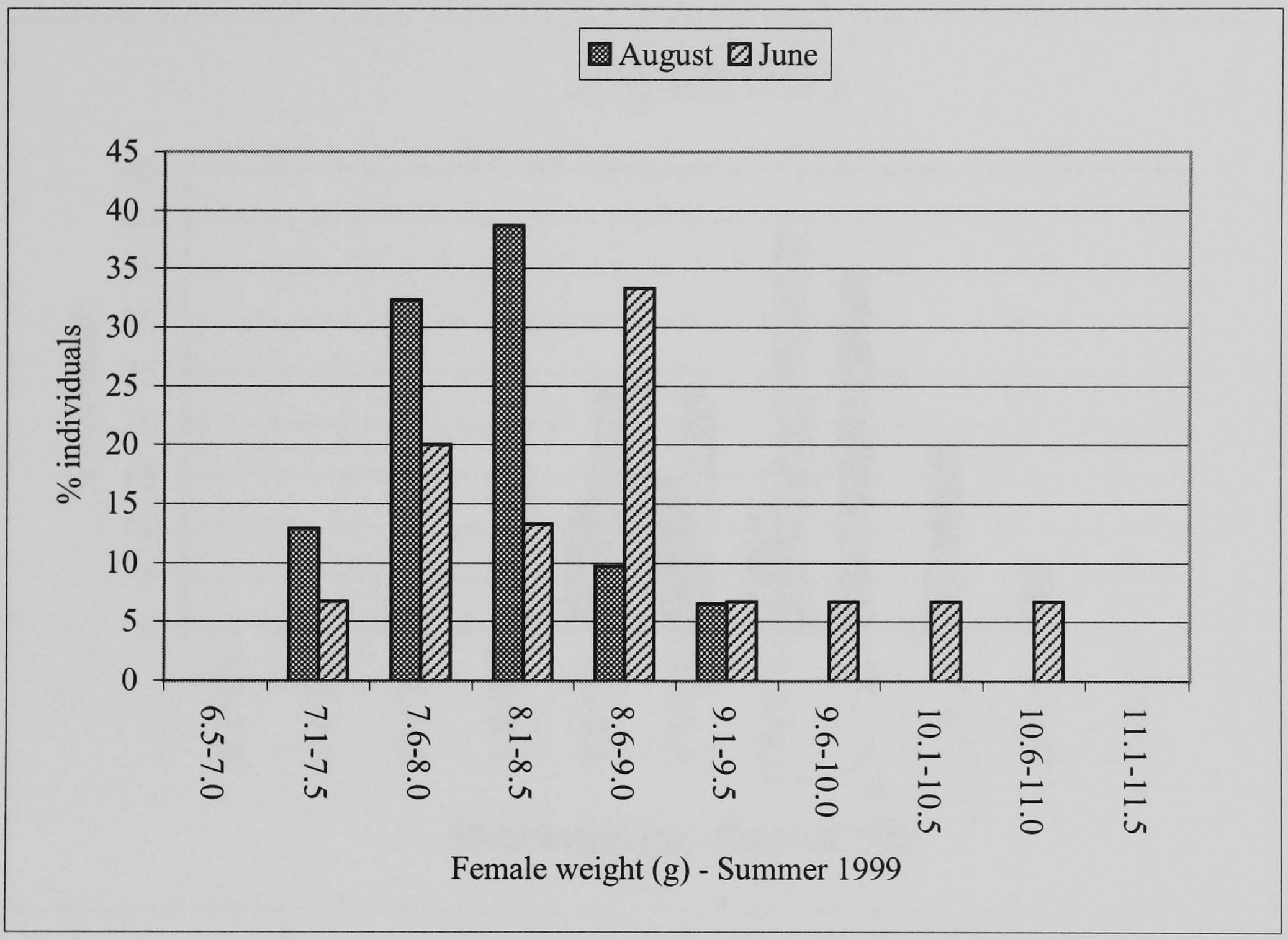


Figure 4.5. Adult weight of female *S. araneus* born in August and June (Mann Whitney U-test, $t_s = 1.96$; $p<0.05$; n = 32 in August, n = 15 in June).
Each individual was weighed at first capture during April 1999.

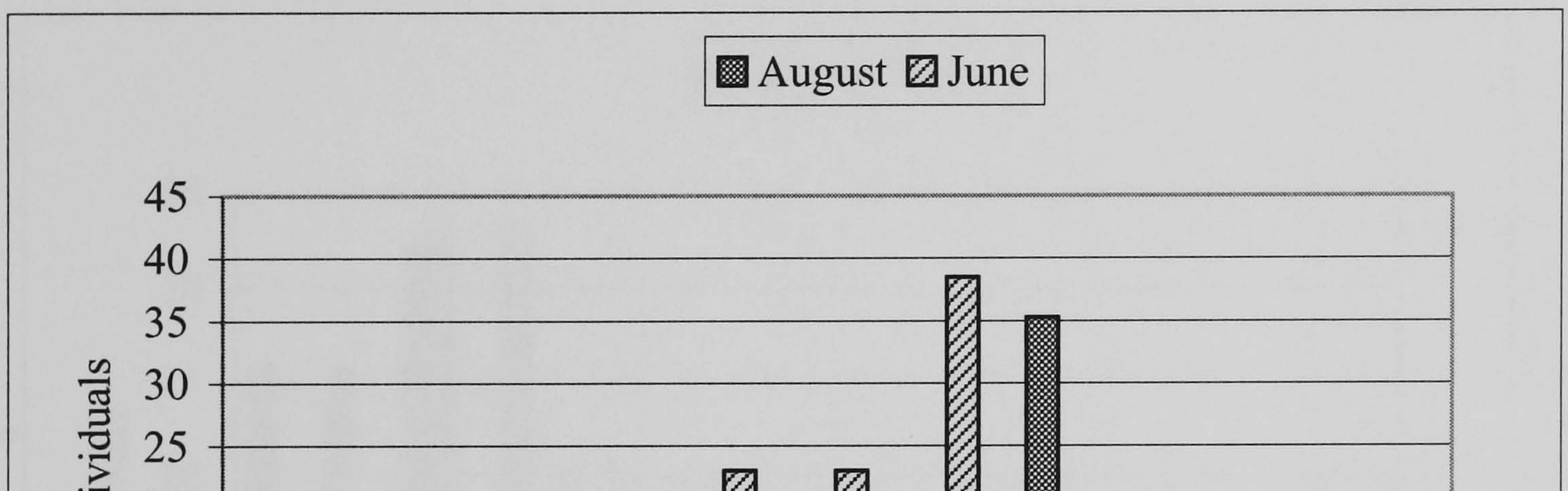


Figure 4.6 Adult weight of male *S. araneus* born in August and June (Mann Whitney U-test, $t_s = 3.01$; $p<0.01$; n = 34 in August, n = 14 in June). Each individual was weighed at first capture during April 1999.

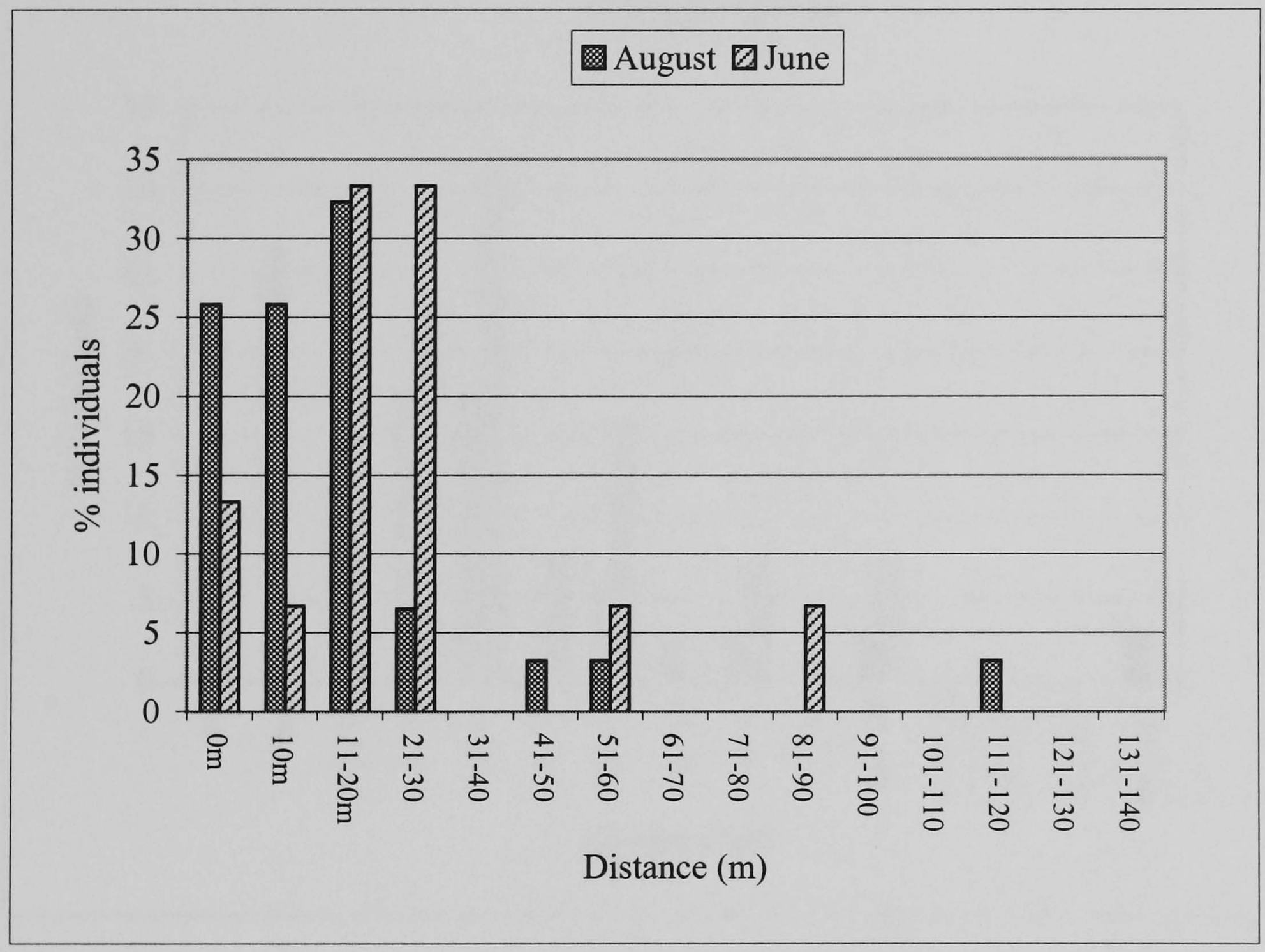


Figure 4.7 Distances moved by female *S. araneus* from both cohorts between their first point of capture in 1998 and 1999 (Mann Whitney U-test, $t_s = 2.135$; $p<0.05$; n = 32 in August and n = 15 in June).

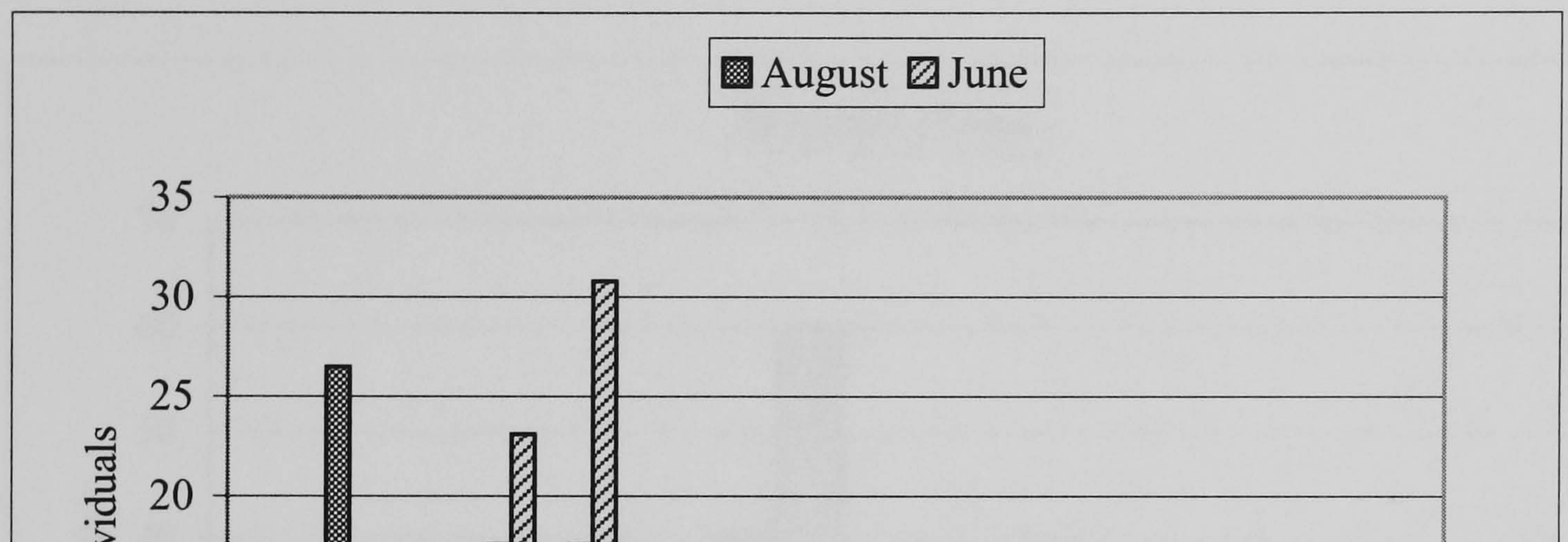


Figure 4.8 Distances moved by male *S. araneus* from both cohorts between their first point of capture in 1998 and 1999 (Mann Whitney U-test, $t_s = 2.31$; $p<0.05$; n = 34 in August and n = 14 in June).

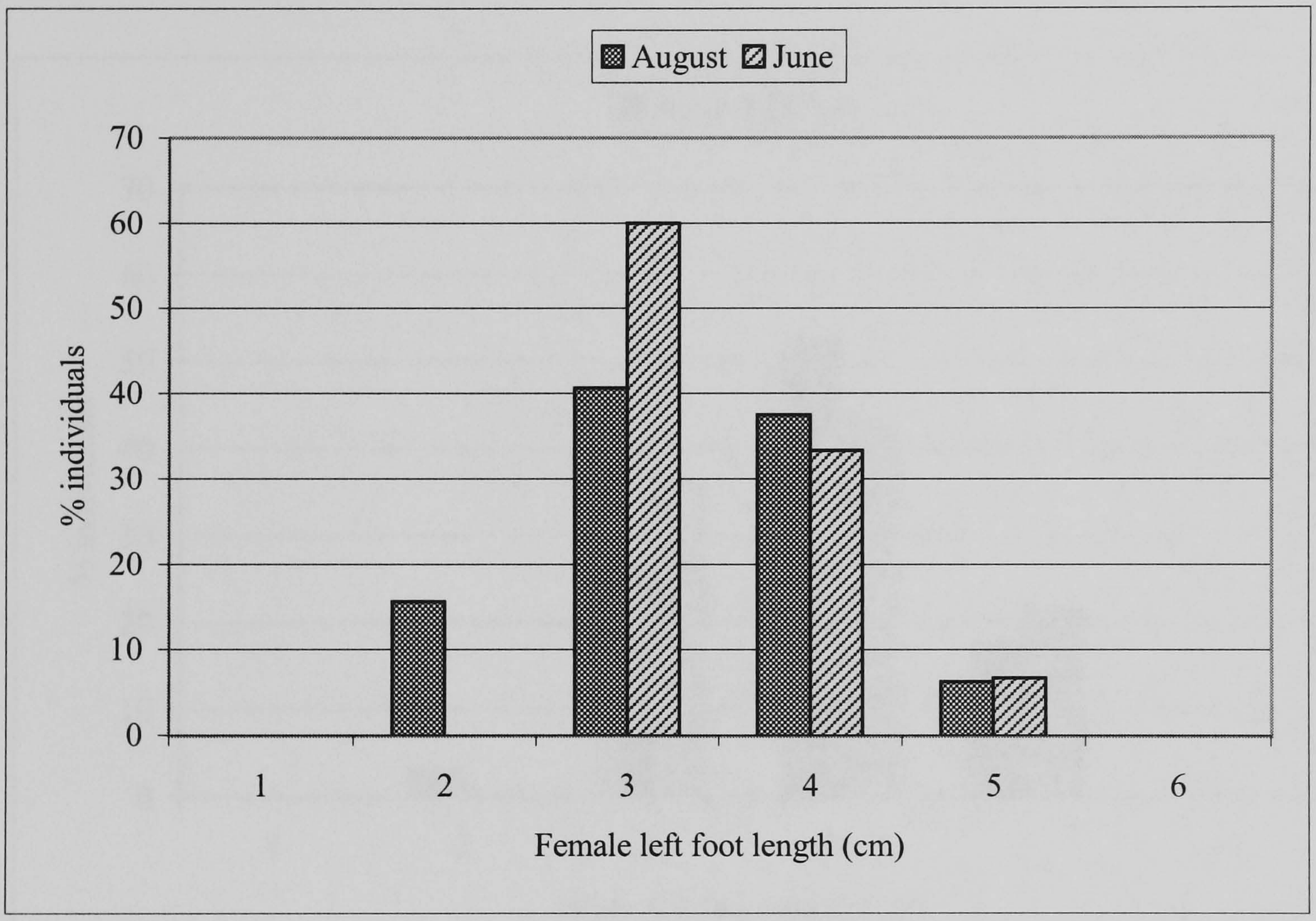


Figure 4.9 Left hind foot lengths of female *S. araneus* from each cohort measured in April 1999. (t-test, t = 0.91; df = 45; n = 32 August, n = 15 June).

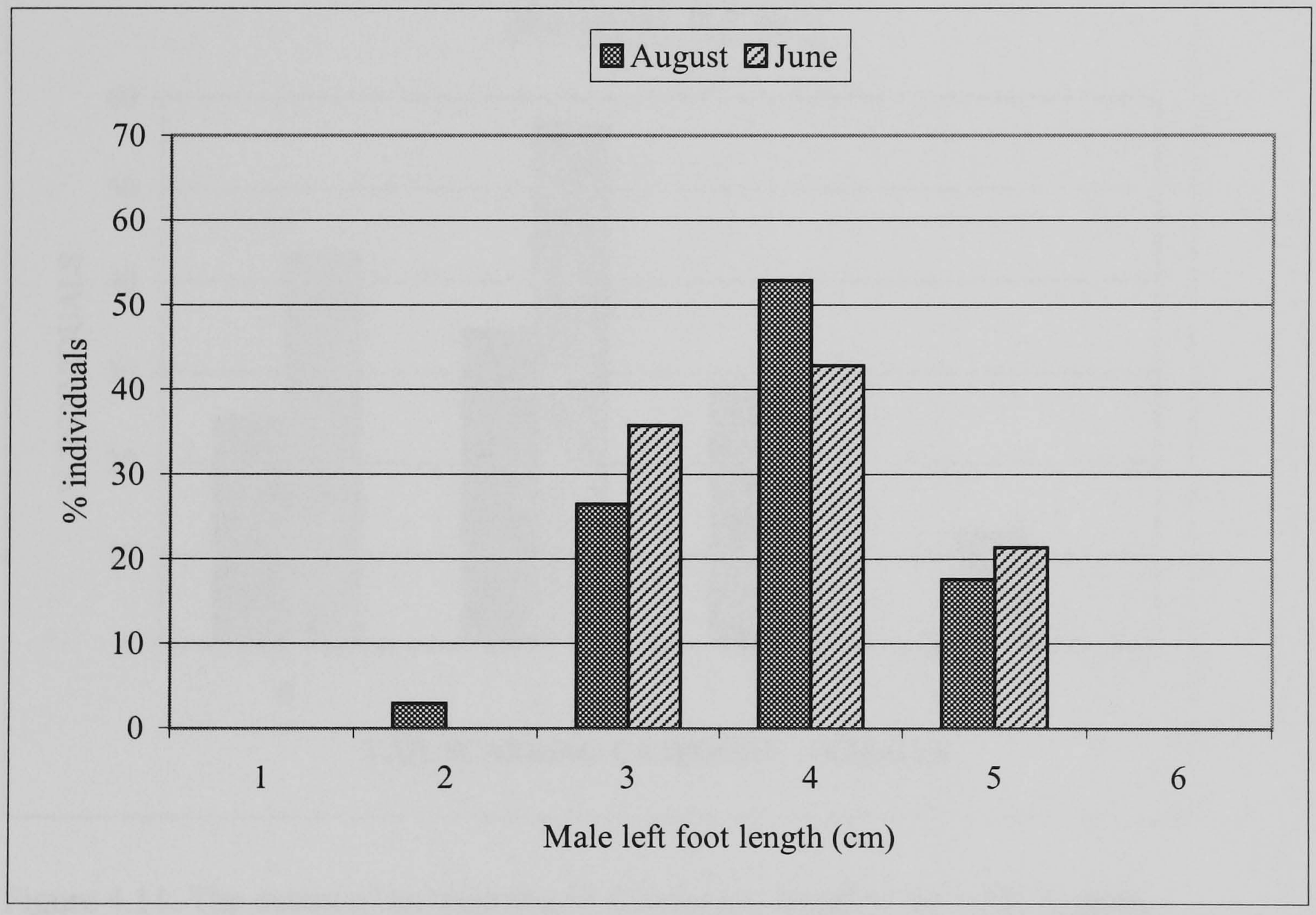


Figure 4.10 Left hind foot lengths of male *S. araneus* from each cohort measured in April 1999. (t-test, t = 0; n = 34 August, n = 14 June).

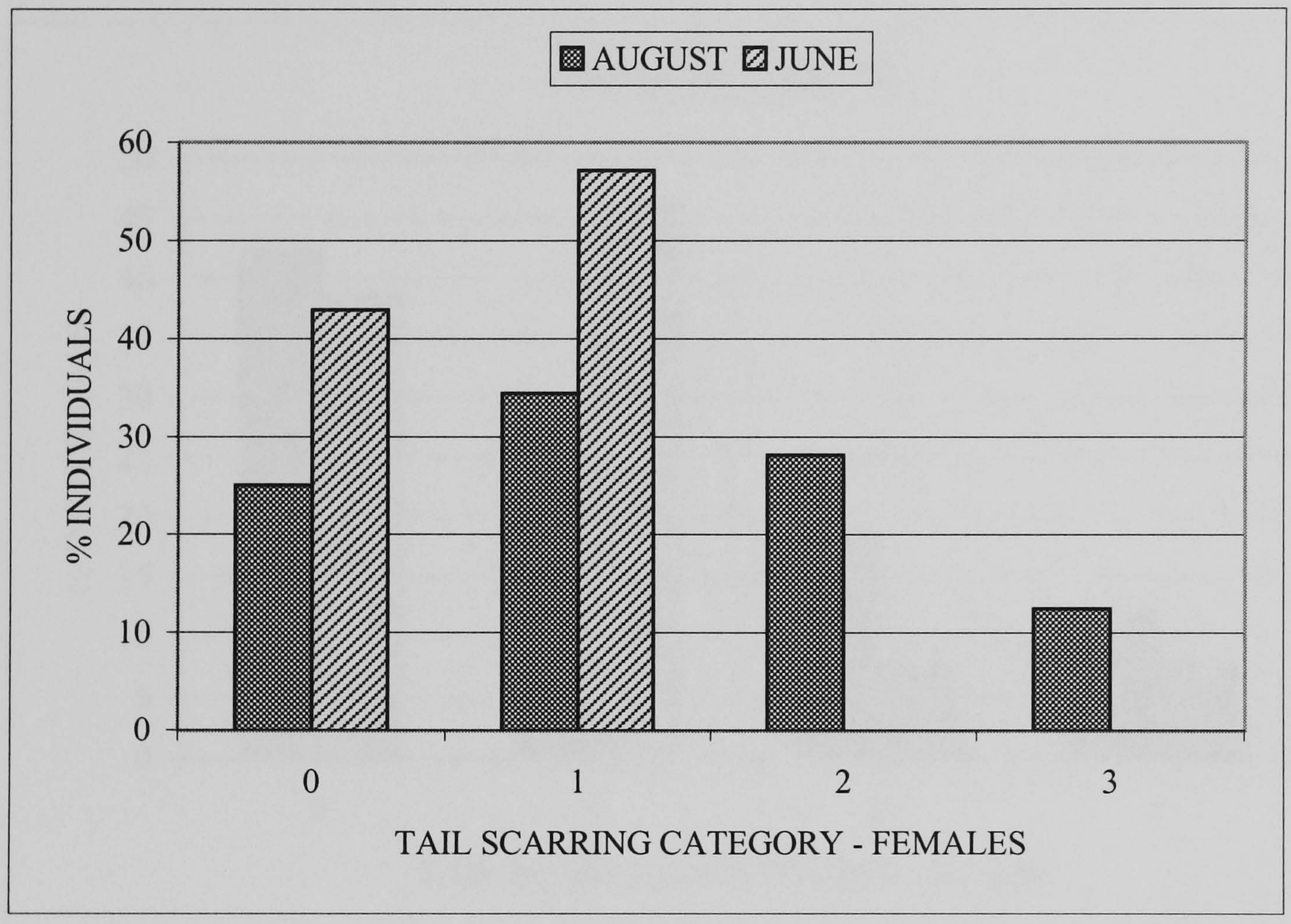


Figure 4.11. The extent of tail scarring in *S. araneus* females. (n = 32, August, n = 15, June). (Fisher's Exact Test $p<0.01$ when categories zero and one are combined and compared with categories two and three (also combined)).

Figure 4.12 The extent of tail scarring in *S. araneus* males. (n = 32, August, n = 15, June) (Fisher's Exact Test $p>0.05$ when categories zero and one are combined and compared with categories two and three (also combined)).

Figure 4.13 Length of lateral glands of male *S. araneus* from the June and August cohorts. Mann Whitney U-test, $t_s = 0.6$; $p>0.05$; n = 34 August, n = 14 June).

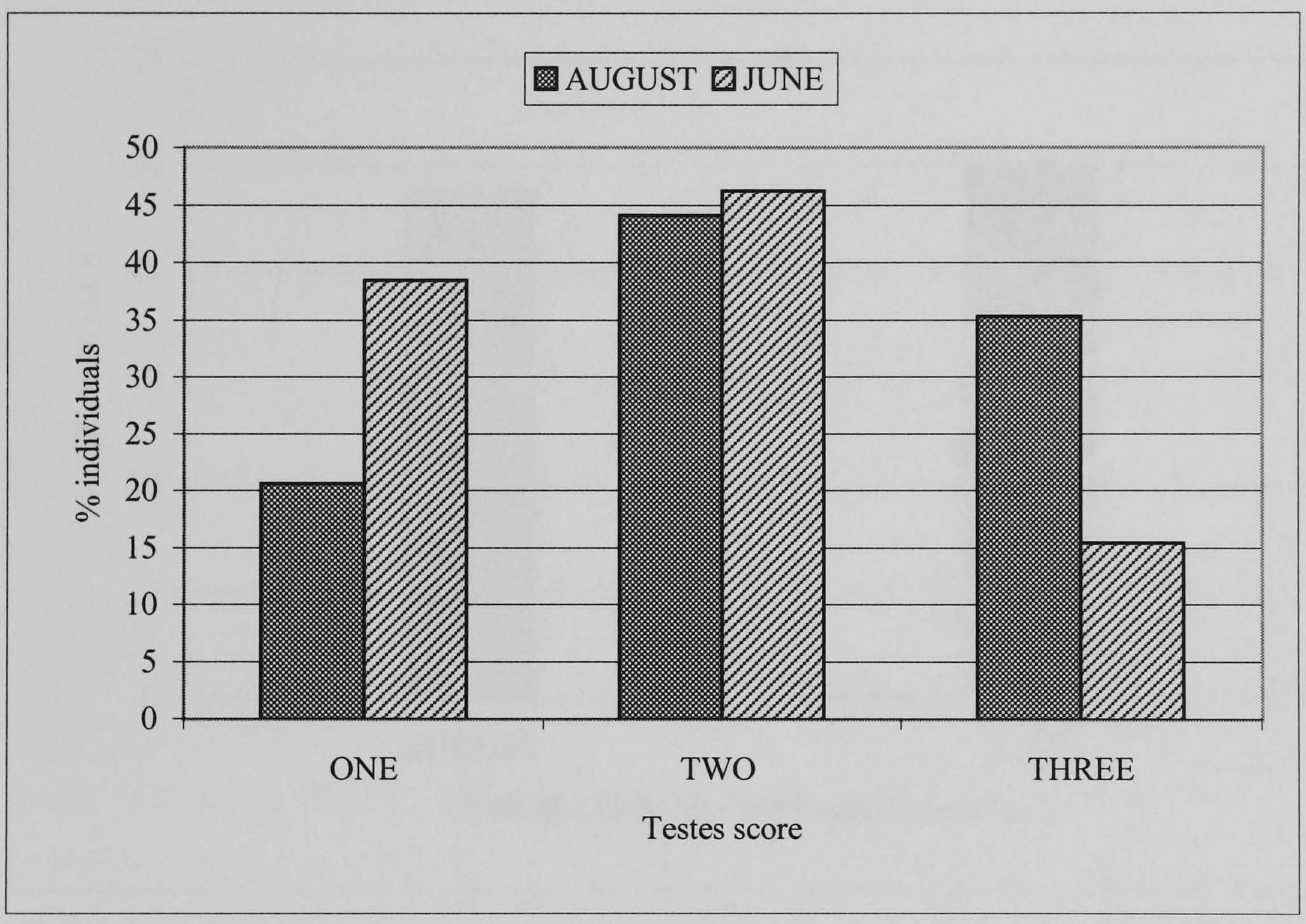


Figure 4.14 Testes score of *S. araneus* males from the August and June cohorts. (n = 34 August, n = 14 June). (Fisher's Exact Test $p>0.05$ when categories one and two are combined and compared with category three; Fisher's Exact Test $p>0.05$ when categories two and three are combined and compared with one).

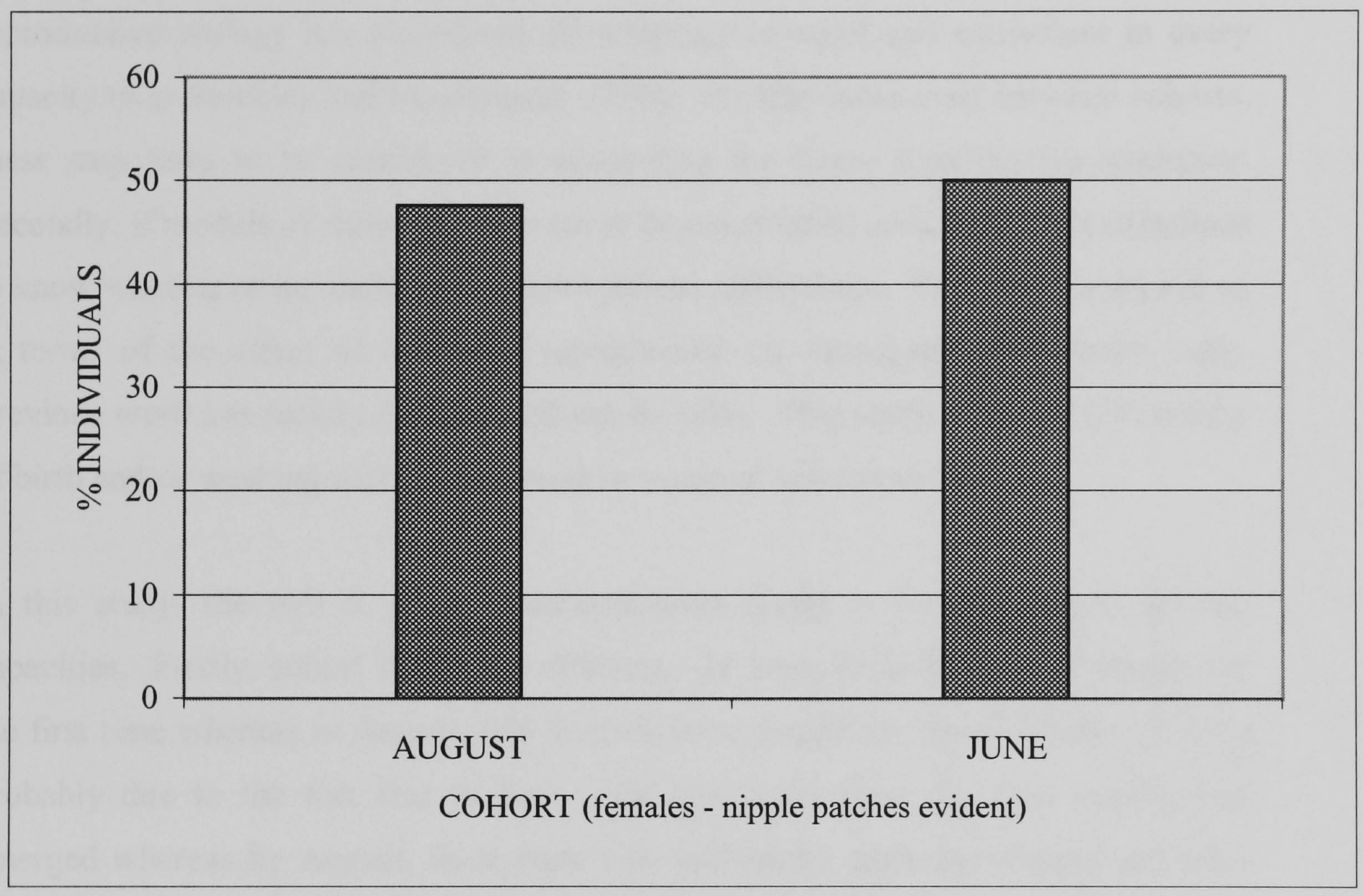


Figure 4.15 The proportion of female *S. araneus* with prominent nipple patches in both cohorts.(n = 32 August, n = 15 June). (Fisher's Exact Test $p>0.05$).

4.4 DISCUSSION

Competition between juvenile animals for territories is expected to occur in *S. araneus* (Stockley and MacDonald, 1998). If some individuals are born up to two months earlier than others, differences in physical characteristics and behaviour may occur between those born earlier and those born later. It is important to identify any differences that may exist for several reasons. Firstly, previous work on shrew reproductive biology has considered all offspring as equal and equivalent in every capacity (e.g. Stockley and MacDonald, 1998). If differences exist between cohorts, these may have to be considered in accounting for shrew reproductive strategies. Secondly, if models of shrew ecology are to be constructed accurately, it is important to know whether or not differences exist between individuals. Thirdly, it is important in terms of the effect of timing of reproduction on subsequent life-history traits. Previous work has mainly been carried out in birds. This study suggests that timing of birth and/or weaning may be important in mammal species as well.

In this study, the two *S. araneus* cohorts were found to be different in several capacities. Firstly, cohort sizes were different. In June, 88 animals were caught for the first time whereas in August, 146 animals were caught for the first time. This is probably due to the fact that in June, only the litters from the first oestrus had emerged whereas by August, there were also individuals from the second and third oestruses present. Individuals born in June would have emerged from the nest to completely different conditions (i.e. different densities and therefore access to resources) from those born later in the summer. More adults would have still been alive in June, but the competition from other juveniles for territory space would have been very much less than it would have been later in the summer. Despite the differences in cohort size, within each cohort there was no significant deviation from a 50:50 sex ratio. The sex ratio of offspring therefore remains constant over the breeding season. Although this has never been compared across cohorts before, such a ratio is expected for this species (see e.g. Searle, 1985).

A significant difference in survival was found between the two cohorts when the sexes were combined. The combined male and female survival rate for the August cohort was 48 % whereas that for the June cohort was 33 %. Although a significant difference was not found when the sexes were treated separately, they showed the same trend. Both males and females in the August cohort showed higher survival than those from the June cohorts. In the present study, although the June cohort was born earlier and therefore under conditions of less intensive inter-specific competition from other juveniles, it seems that it may have been advantageous being born later in the summer. By August, many of the adults from the previous year will have died or at least lost their capacity to maintain and defend their territory against younger animals. Emerging from the nest at this time of year may mean missing out on several weeks of territorial battles and therefore a higher proportion of survivors. Churchfield *et al.* (1995) showed that in a high-density population of *S. araneus* in grassland, early-born cohorts had a higher proportion of survivors than late-born cohorts at all stages of their life-cycle. Although their results cannot be directly compared with those of this study, future studies at the study site would shed light on whether this pattern was consistent and also whether or not it was influenced by climatic conditions.

Survival of offspring is often dependent on individual size and this is often measured in terms of weight (e.g. Tinbergen and Boerlijst, 1990). All individuals from both cohorts were weighed. In males, no difference was found between the juvenile weights of the cohorts. However, in females, a significant difference between the juvenile weights of each cohort was found. This difference occurs because juveniles from June tend to be heavier than those in August. This may be due to greater parental investment earlier in the breeding season or better conditions for breeding earlier in the season (e.g. lower density). However, why this difference is not evident in males is unknown. By April, there was no significant difference in weight between the two cohorts in either sex. This may explain why, in the case of females born in June, juvenile weight does not directly influence annual survival favourably as it has

been shown to do in other species (e.g. great tits, *Parus major*, Perrins, 1965). Despite weighing more upon first capture after weaning, June born females have a lower annual survival rate than August born females.

Juvenile weight has been previously linked to annual survival in birds (e.g. Perrins, 1965). However, adult weight is more indicative of future fecundity. All individuals from both cohorts were therefore weighed in April 1999, just prior to the breeding season. The results show that adult weight varies according to the time of birth in both males and females. In females, individuals born in June are heavier than those born in August. However, in males, the situation is reversed: individuals from the August cohort are heavier than those from the June cohort. This suggests that fecundity will be higher for females from the June cohort but for males in the August cohort. Although there is no direct evidence in *S. araneus* that heavier individuals have higher fecundity, a study has shown that the less inbred an individual, the higher its fecundity (Stockley *et al.*, 1993). Future studies should therefore look at the relationship between inbreeding, weight and fecundity of both males and females.

The distinction of two groups of males of different reproductive potentials has been made previously by Stockley *et al.* (1994). In their study they identified 'Type A' males which were smaller in March (just prior to breeding) than 'Type B' males. During breeding, both exhibited different movement and mating patterns. It is possible that the August males represent 'Type A' males and the June males represent 'Type B' males. Future studies could investigate this using more intensive field methods and mapping movement patterns during the breeding season. Molecular markers could also be used to identify parents and offspring and therefore gauge the reproductive success of each group. The distinction of two groups of females of different reproductive potentials has not previously been identified and could also be incorporated into such a study.

Dispersal is another factor that may be expected to alter according to time of birth. It can be advantageous because it reduces the chance of future matings with close

relatives and therefore the production of inbred offspring. However, dispersal also brings with it the risk of aggressive interactions, a higher predation risk and therefore higher mortality. Dispersal distances were measured for all individuals of both cohorts that survived until April 1999. The distance measured was the maximum straight-line distance between the first point of capture in 1998 and the first point of capture in 1999. It is possible that such measurements do not actually represent a dispersal movement but that each of these trap locations is in the individual's home-range. Of those re-caught in April 1999, 22 % were at some point re-caught in their original trap thus indeed suggesting that these individuals had not dispersed as such but were merely holding a home-range. However, for the purposes of this study, such a distinction is not crucial. Holding a large home range carries with it the same risks of aggressive interactions and also the added benefits of more varied mating opportunities as does dispersal. This aim of this study was to see if differences occurred between the cohorts in terms of spatial behaviour (hereafter referred to as 'dispersal distance').

In both sexes, differences were found between the cohorts in terms of dispersal distance. Individuals born in June have larger dispersal distances than those born in August. The June cohort will therefore be exposed to more mating opportunities than the August cohort. However, they are also exposing themselves to higher risk situations which may be reflected in their lower survival rates and in the case of males, their lower body weight and therefore lower competitive abilities.

Previous studies have shown that hind foot and tibia length in *S. araneus* is related to dispersal ability (Hanski *et al.*, 1991). Hind foot measurements were therefore taken for each animal that survived until April 1999. The results show that no differences were found between the two cohorts in either males or females. It is possible that this is either because no such differences existed or because such differences did exist but are not detectable in live individuals. Hanski *et al.* (1991) used bones from dead animals which are easier to measure with a high degree of accuracy. It is also not possible to measure the tibia of a live *S. araneus*.

S. araneus suffers damage to the tail during aggressive interactions (Crowcroft, 1957). The extent of tail scarring was therefore assessed in every individual caught during April 1999 and the two cohorts compared. The results, unless very clear-cut, are inevitably difficult to interpret. In males, it can be seen that there is very little difference in the extent of tail scarring between the cohorts. However, in females, there is an absence of individuals from June in the most severe tail-scarring categories. This is unexpected given that they disperse further and have a lower survival rate (i.e. more aggressive interactions would have been predicted). However, it is possible that those individuals that did suffer severe interactions did not survive. This would explain their absence from the data.

Sexual characteristics were measured from each animal to see if any differences existed between the cohorts in terms of sexual maturity. In males, lateral gland length was measured. No differences were detected between the cohorts. There were also very few differences in testes score between the cohorts. However, a higher proportion of August males than June males were in category 3 and a lower proportion in category 1. This indicates greater sexual maturity and is in accordance with their heavier weights. In females, presence of nipples/nipple patches was recorded. No difference was found in the number of females with nipple patches between the two cohorts. The state of moult was not used as an indicator of any kind for either sex because it was not possible to distinguish with a high degree of accuracy which animals had completely finished moulting and which animals had not yet started. It may be that weight is a more efficient indicator of maturity and general vigour than sexual characteristics themselves when the animals are not dead (and it is not possible to measure e.g. testes size properly). Given the higher weights of the June cohort females, it can be predicted that they will breed prior to those of the August cohort. In males, the opposite is predicted where August males are heavier and will therefore be expected to breed prior to June males.

Having ascertained that some differences exist between the cohorts, it is necessary to re-examine the three points raised at the beginning of the discussion. Firstly, it is necessary to explore how this affects theories regarding their reproduction. Due to its promiscuous mating behaviour, *S. araneus* has been the focus of attention in terms of different mating strategies (Searle, 1990; Stockley *et al.*, 1993). Female *S. araneus* general produce 2 – 3 litters during the summer and most offspring within a litter are sired by different males. Recently, Stockley and Macdonald (1998) put forward the 'Sibling Competition Hypothesis' to account for the multiple mating strategies of the common shrew. This theory states that if a female mates singly, all the offspring in the subsequent litter will be directly related to each other by having the same mother and father. This scenario is shown in Figure 4.16 (after Stockley and Macdonald, 1998). Within each litter, due to sibling competition, the weaker individuals will die. Under the singly-mating scenario, it can be seen that due to this, some of the more genetically favourable offspring will be out-competed by their related siblings. However, if the female mates multiply and there is multiple paternity within a litter, these genetically favourable offspring will occur in litters alongside genetically inferior individuals. These individuals will therefore be pushed out by the genetically favourable individuals allowing the total number of surviving genetically favourable individuals to be greater. The multiple mating scenario can be seen in Figure 4.16 (after Stockley and Macdonald, 1998). This theory depends on the existence of inter-sibling competition, hence its name.

The theory makes the assumption that all three litters are equal in every way. However, this study has shown that this is not the case. By taking just one factor, survival, it can be seen that the theory must be re-examined. This study has shown that survival is greater in later litters. Therefore if the assumption is made that the first litter does not survive but the latter two do (which is no more extreme than assuming they are all equal in terms of survival and is actually more realistic), a different result is obtained. Figure 4.17 shows the three different scenarios for a singly mating female. If the first litters do not survive, it can be seen that the probability of survival of genetically favourable offspring is equivalent for both

mating strategies. As well as this, the high risk of mating multiply (e.g. aggressive interactions and disease transmission) must be taken into account. The fact that weather may also influence the survival rate in different cohorts further complicates this. This study therefore shows the importance of considering real-life variables in such theories. The situation would become more complex if other variables such as weight and future fecundity were included.

Secondly, it is necessary to explore whether or not such differences need to be taken into account in the construction of models of shrew ecology. This will depend on the types of questions that the models are attempting to answer but it does highlight the need to examine carefully the source of the model parameters. This study shows that it would be especially important to ascertain how long juveniles were trapped for during the summer and whether the values represent both cohorts. If this is not done, the results may be very biased in terms of a particular cohort.

Thirdly, in terms of reproductive biology, this study is important as it shows that in some mammals, like birds, timing of reproduction does have an effect on future behavioural and physiological traits. Further studies based in the field and in the laboratory would be required to assess the full impact of these differences on the future reproductive success of the two cohorts.

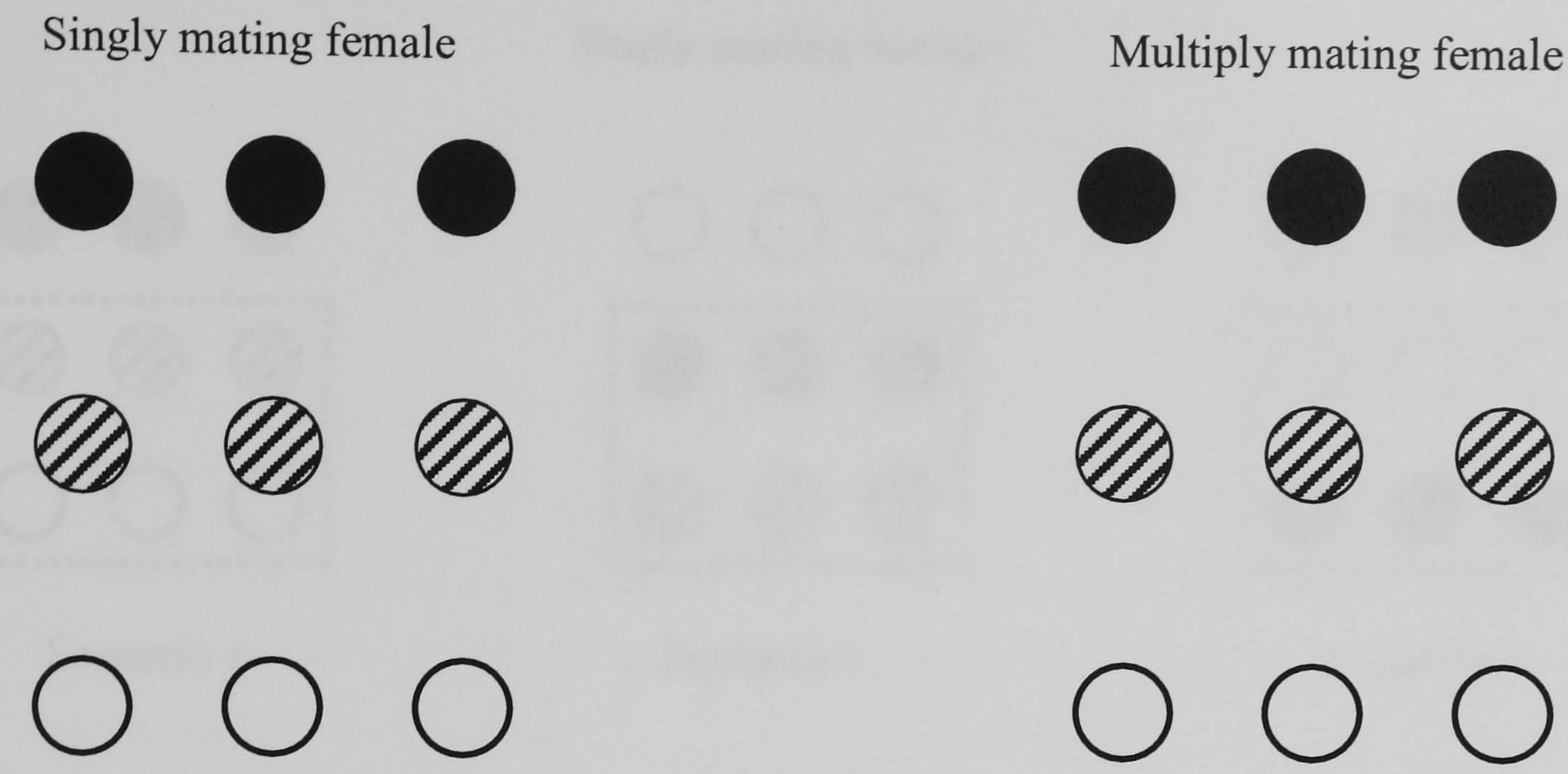
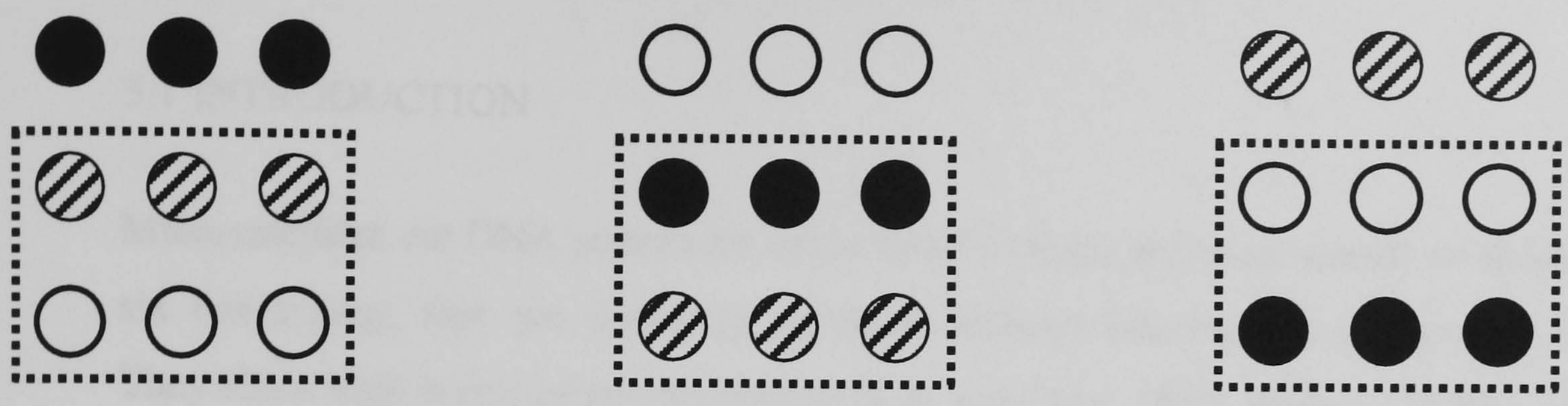


Figure 4.16 Illustration (after Stockley and Macdonald, 1998) to show the two different mating scenarios. Under the 'singly mating female' regime, the female mates with only one male to produce each litter, but each of the three litters is sired by a different male. Under the 'multiply mating female' regime, the female produces litters each sired by three different males. In the example shown, one in three males is a close relative. The figure shows that each female will produce the same number of offspring sired by closely related males. If there is sibling competition, and only a proportion of young from each litter survive to sexual maturity, then the multiply mating female will produce more surviving offspring by unrelated males over her life-time than will the singly mating female. This is because the offspring of unrelated males produced by the singly mated female must each compete with one another, ultimately causing their numbers to be reduced. In contrast, the offspring of unrelated males produced by the multiply mating female will each do well at the expense of more inbred siblings and are therefore more likely to survive.

Singly mating female:

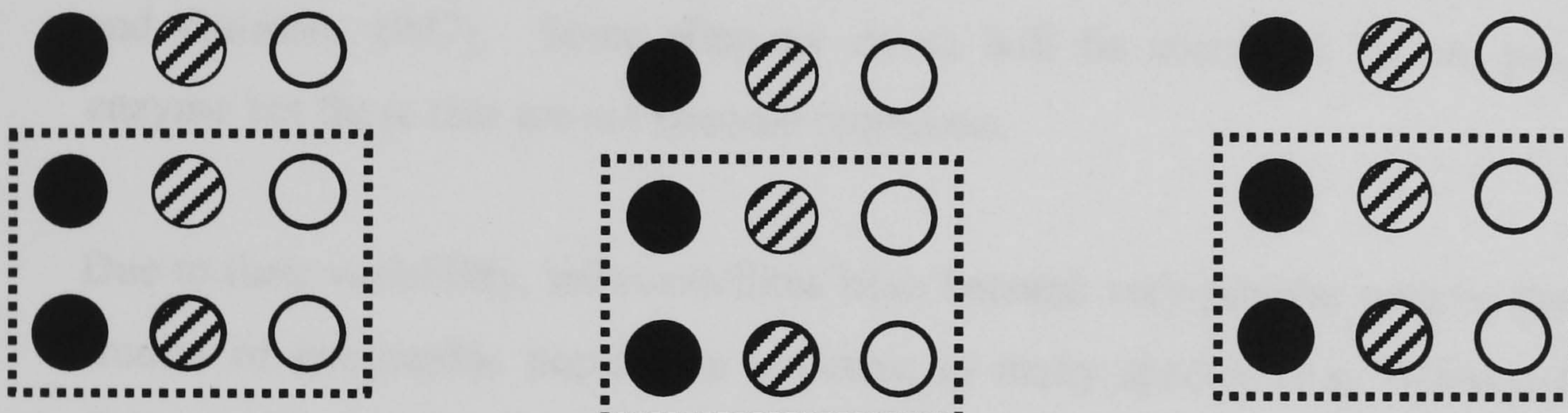


Scenario 1 Scenario 2 Scenario 3

Number of unrelated offspring:

6/9 3/9 3/9 **= 12/27**

Multiply mating female:



Scenario 1 Scenario 2 Scenario 3

Number of unrelated offspring:

4/9 4/9 4/9

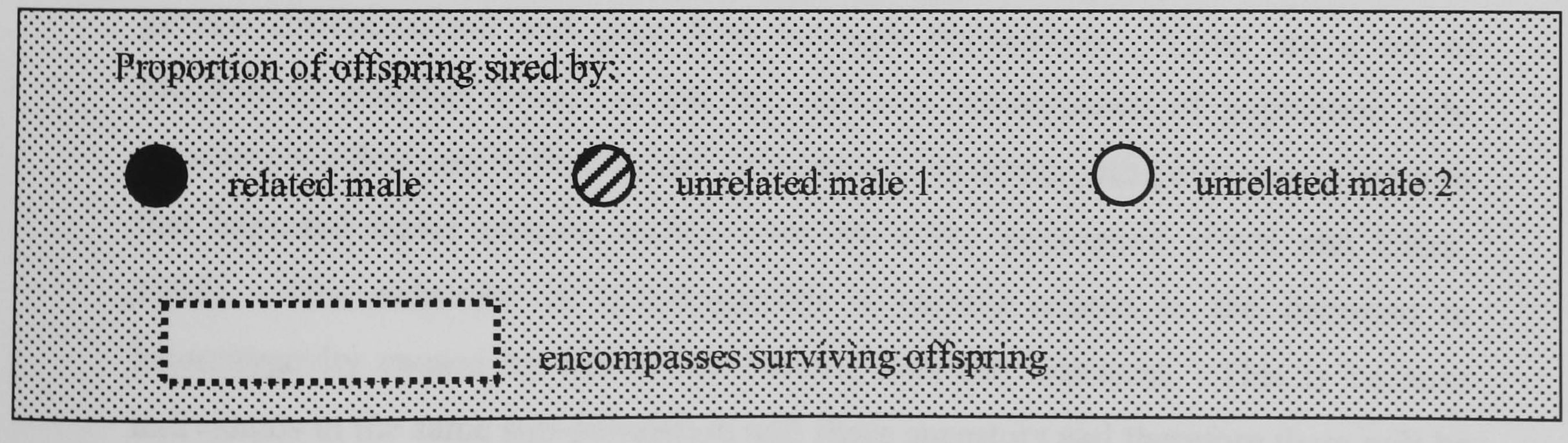


Figure 4.17 Figure to show that given the study findings that survival is different between individuals born in June and those born later in the summer, a multiply mating female does not necessarily have an advantage over a singly mating female.

CHAPTER 5

GENETIC POPULATION STRUCTURE

5.1 INTRODUCTION

Microsatellites are DNA sequences made up of a single sequence motif, no more than six bases long, that are tandemly repeated without interruption (Hancock, 1999). They show high levels of polymorphism (Litt and Luty, 1989, Weber and May, 1989, Tautz, 1989) and exhibit co-dominant inheritance. These, combined with their presence in every organism so far analysed, make them very useful genetic markers (Eisen, 1999). The highly polymorphic nature of microsatellites is due to their high mutation rate (Eisen, 1999). Mutational mechanisms at microsatellite loci are still not fully understood but their high mutation rate is thought to be mainly due to slipped strand mispairing (slippage) during DNA replication (Streisinger *et al.*, 1966, Levison and Gutman, 1987). Some slippage errors will be corrected by the polymerase enzyme but those that are not become mutations.

Due to their variability, microsatellites have become very popular genetic markers in studies of geographic population structure in many species (e.g. Atlantic Salmon, *Salmo salar*, Tessier *et al.*, 1997; the Canyon Tree Frog, *Hyla arenicolor*, Barber, 1999). In *S. araneus*, the development of eight sets of primers for microsatellite loci (Wyttenbach *et al.*, 1997) has enabled such studies to be carried out in this species. These studies have used Wright's F statistics (Wright, 1921), to assess the extent of genetic differentiation and gene flow between populations. These are a set of hierarchical statistics based on the fact that one consequence of population sub-structure is a decrease in the average proportion of heterozygote genotypes relative to that expected under random mating over the entire population (Hartl and Clark, 1997). This reduction in heterozygosity is closely related to the decrease in heterozygosity caused by inbreeding (mating between relatives). This is because individuals in the same sub-population will share ancestors and therefore there will be mating between relatives within a sub-population. Wright's F-statistics (1921)

quantify the inbreeding effect of population sub-structure i.e. each statistic measures the decrease in heterozygosity relative to that expected under random mating at any one level of a population's hierarchy relative to another, more inclusive level of the hierarchy. F_{IS}, for example, measures the decrease in heterozygosity of a group of inbred organisms relative to the sub-population to which they belong. It is also known as the 'inbreeding co-efficient' because a significant decrease in heterozygosity will indicate that random mating is not occurring in the sub-population. F-statistics are a useful index of genetic differentiation because they allow objective comparisons to be made between different organisms. F_{ST} measures the extent of differentiation between sub-populations by measuring the reduction of heterozygosity among sub-populations within the total combined population ($H_T - H_S$) relative to the heterozygosity of the total combined population (H_T). It is calculated:

$$F_{ST} = H_T - H_S / H_T \qquad \text{[Equation 5.1]}$$

F_{ST} has a theoretical minimum of 0 (no genetic divergence) and a theoretical maximum of 1 (indicating fixation for alternative alleles in different sub-populations). A value of 0.07, for example, indicates that only 7 % of the total genetic variation is ascribable to genetic differences among sub-populations and 93 % is found within sub-populations. The apparent deficit of heterozygotes will result in an excess in the average homozygosity of the population. This homozygosity will decrease when sub-populations become one large population due to, for example, the removal of previous geographically isolating barriers. This is known as the Wahlund effect. It can be measured as the reduction in the average frequency of homozygotes if the two sub-populations become one. From this value, F_{ST} can be measured, where it is the variance in allele frequencies among populations $\theta^2 p$, standardised by the mean allele frequency (p) at that locus (Weir and Cockerham, 1984)

$$F_{ST} = \theta^2 p / [p(1-p)] \qquad \text{[Equation 5.2]}$$

$$F_{ST} = \theta^2 p / [p(1-p)] \qquad \text{[Equation 5.2]}$$

The method of obtaining F_{ST} using Equation 5.2 is preferable to that obtained using Equation 5.1 because the value obtained will be independent of sub-population and organism sample sizes. Wright (1931) introduced a simple model of population structure, 'the island model', which predicts a simple relationship between the number of migrants a population receives per generation and F_{ST}. Under the assumptions of the island model,

$$Nm = 1 / F_{ST} - 1 / 4 \qquad \text{[Equation 5.3]}$$

where N is the effective population size of each sub-population and m is the migration rate (the proportion of alleles that are replaced by alleles from migrant organisms) between populations.

When compared with the difficult and time consuming methods involved in collecting such data from the field, this method of calculating the number of migrants between populations per generation is relatively easy. F_{ST} can be estimated from data gathered using molecular techniques and from this 'Nm' can be calculated. As a result, such methods are frequently used (for example in the journal '*Heredity*', 13 papers did this in 1997 alone, Whitlock and McCauley (1999)). However, due to the assumptions of the island model on which this relationship is based, the results must be viewed with caution (Whitlock and McCauley, 1999). The model assumes no selection, no mutation, equal population sizes, no spatial structure and that all processes are at equilibrium. Many of these assumptions are unlikely to hold in natural populations.

Despite the problems with obtaining 'Nm' from F_{ST}, F_{ST} itself remains an effective indicator of population structure (Whitlock and McCauley, 1999). However, most molecular markers that are used to calculate this value are assumed to mutate under the 'K-allele model' (Jarne and Lagoda, 1996) . This assumes that the loci have a

very low mutation rate and also that the mutation process erases any memory of the prior allelic state (Slatkin, 1995). The high mutation rate found at microsatellite loci (which may be up to 10^{-3} per generation (Weber and Wong, 1993)) may, therefore, cause Wright's F_{ST} to give erroneous results (Lugon-Moulin *et al.*, 1999). Slatkin (1995) demonstrated that it will tend to underestimate the true level of genetic differentiation and therefore over-estimate the number of migrants if microsatellites are used.

To overcome this problem, Slatkin (1995) proposed a statistic that better accounts for high mutation rates and such a specific mode of mutation:

$$R_{ST} = \bar{S} - \bar{S}_w / \bar{S} \qquad \text{[Equation 5.4]}$$

Where $\bar{S}_w$ is the average of the estimated variances of allele size within each sub-population and $\bar{S}$ is twice the estimated variance in allele size in the collection of populations together, where the estimated variances are obtained using unbiased estimators. Both are proportional to the within population and total variances. R_{ST} is therefore the fraction of the total variance of allele size that is between populations. Although it can be written similarly to Weir and Cockerham's (1984) equation for F_{ST}, allele sizes and their relationship to each other are taken into account whereas in Weir and Cockerham's model, only identity or non-identity of allelic state is entered. Under a step-wise mutation model, values of F_{ST} are expected to be smaller than the R_{ST} values and therefore migration will not be over-estimated (Slatkin, 1995). Valsecchi *et al.* (1997) compared different R-statistical methods to calculate genetic distances from microsatellite data. They concluded that the 'unbiased R_{ST}' (Goodman, 1997) was the most reliable as unlike others, it allows for unequal sample sizes. It is also able to account for loci with vast differences in the variance of allele sizes.

The genetic population structure of *S. araneus* hybrid zones has recently been examined using microsatellite data. At present, 50 chromosome races in *S. araneus*

are recognised (Zima *et al.*, 1996). Studies of population structure have therefore concentrated on differences between these different chromosome races (e.g. Lugon-Moulin *et al.*, 1996, 1999; Wyttenbach and Hausser, 1996,). This has greatly expanded understanding of the spatial structuring of these populations, because protein polymorphism in this species has generally been too low to be an effective indicator of population structure over a small spatial scale (Ruedi, 1998). Over a relatively large geographic distance (20 kilometres, Lugon-Moulin *et al.*, 1996, 1999) where two chromosome races are separated by a mountain river in the Alps, a small amount of genetic structuring was found to occur (F_{ST} = 0.081; Nm = 12) using microsatellites. A study carried out on shrews separated by a river found less genetic structuring (F_{ST} = 0.017; Nm = 58) (Wyttenbach and Hausser, 1996). These results suggest that geographic barriers contribute to genetic isolation and therefore genetic structuring.

Studies looking at genetic differentiation between geographically divided *S. araneus* populations have previously only been able to estimate 'Nm' from genetic data and have not been able to compare their value with field movements. This is because the scale on which their studies are carried out make it impossible. The present study aims to examine the genetic structure of a population of *S. araneus* over a site that covers an area of 1.5 x 0.5 kilometres. This area is small enough so that comparable field-data can be collected and the different estimates compared. The site is made up of a series of suitable habitat patches separated by unsuitable habitat (see Chapter 1). The unsuitable habitat has been shown to be a barrier to movement to some extent (see Chapters 2 and 3). This chapter aims to assess the genetic population structure of *S. araneus* and *S. minutus* at the site using F-statistics (Wright, 1931, Weir and Cockerham, 1984, Goudet 1995) and R-statistics (Slatkin, 1995; Goodman, 1997). From the values obtained, Nm will be calculated and these values will be compared with individual movement observed at the site.

5.2 METHODS

5.2.1 Study site

For a description of the study site, see Chapter 1.

5.2.2 Live-trapping

Individuals were live-trapped at the site during June 1998 using the methods described in Chapter 2. All juveniles caught were included in the genetic analysis. No adults were included. The aim was to trap individuals as they emerged from their nests and before they had had time to move to other areas. The number of individuals trapped in each patch can be seen in Table 5.1. DNA sampling was performed by toe-clipping which was also used to individually mark the individuals (under Home Office licence). Toe-clippings were stored in absolute ethanol and the shrews released at their trap site. The scissors used for the toe-clipping were sterilised between each individual using clean cotton wool and 100 % ethanol.

5.2.3. DNA extraction and amplification of microsatellite loci

Total genomic DNA was extracted from toe-clippings using standard protocols which involved treatment with SDS (sodium dodecyl sulphate) and proteinase K followed by extraction with phenol chloroform (e.g. Sambrook *et al.*, 1989).

For *S. araneus*, four microsatellite loci were amplified by four separate reactions using the following primer pairs (Wyttenbach *et al.*, 1997):

L9F (TCATGGACTTTTCTGTGCTG),

L9R (CTTTGGCATGAATTTGCC),

L62F (CAGTCTCTCACTGTGGCACTATG),

L62R (GTCATTCTGGATAAGAACCATATGC),

L69F (CTTTATGGTAGAAAATGGTG),

L69R (GACCATATACTAAGTTGTTTTG),

L67F (GAAGTGATACATGAGTGCATGAG) and

L67R (GTTGTTAACAAGAGAGGTATTACACC).

For *S. minutus*, these loci were also amplified, with the exception of L67. All PCR amplifications were performed in a Primus 96 plus thermal cycler (MWG Biotech). Cycling parameters consisted of 32–35 cycles under the following conditions: 45 s at 94 °C, 45 s at 52–56 °C and 45 s at 72 °C preceded by an initial denaturation step (3 min at 94 °C) and followed by a final elongation step (5 min at 72 °C). All amplifications were performed in 12.5 µl volumes containing: 10 mM Tris-HCl (pH 9.0), 50 mM KCl, 0.1% Triton-X-100, 1.0–2.0 mM $MgCl_2$, each primer at 400 nM, each dNTP (Promega) at 60 µM, 0.5 unit Taq polymerase (Promega) and 20 µg/ml Bovine Serum Albumin (Sigma).

One primer from each pair was synthesised with a fluorescent dye group – either FAM, HEX or TET (MWG Biotech) – on the 5' end. These dyes allowed detection and sizing of fragments on an Applied Biosystems 377 automated sequencer. The different dyes enabled more than one sample to be run per lane. Loci were scored relative to an internal lane marker. A detailed description of detection and analysis using this system can be found in Ziegle *et al.* (1992).

5.2.4 Data analysis

Genetic polymorphism and linkage disequilibrium

Genetic polymorphism (expected heterozygosity, He) was estimated using Nei's unbiased gene diversity (Nei, 1987). Exact tests for genotypic linkage disequilibrium were computed using GENEPOP 1.2 (Raymond and Rousset, 1995). For all cases, the Markov chain was set to 100,000. The loci were tested to see if they were in Hardy-Weinberg equilibrium using GENEPOP 1.2 (Raymond and Rousset, 1995).

Genetic subdivision

F-statistics (F_{ST} and F_{IS}) were computed according to Weir and Cockerham (1984) using the software package FSTAT 1.2 (Goudet, 1995). One-tailed tests of the significance of F_{IS} and F_{ST} were obtained from a minimum of 5000 permutations of alleles within samples for F_{IS} and among samples for F_{ST}. In this way, the distribution of the null hypotheses ($F_{IS} = 0$; $F_{ST} = 0$) is obtained and tested against the alternative hypotheses ($F_{IS} > 0$; $F_{ST} > 0$) (Excoffier *et al.*, 1992; Goudet, 1995).

R_{ST} was calculated using the program R_{ST} Calc (Goodman, 1997). A one-tailed test of significance was carried out in a similar way to that done for F_{ST}.

5.3 RESULTS

The raw data can be seen in Appendix 3 (*S. araneus*) and Appendix 4 (*S. minutus*).

5.3.1 Polymorphism, heterozygosity and linkage disequilibrium

S. araneus

Table 5.2 shows that polymorphism at the four microsatellite loci ranged from 10 to 28 alleles. Gene diversity varied between 0.78 and 0.94. Average gene diversity over all marker loci was 0.89. Analysis for linkage disequilibrium resulted in non-significant values, suggesting no genetic linkage between loci. None of the loci showed a significant deviation from Hardy-Weinberg equilibrium.

S. minutus

Table 5.3 shows that polymorphism at the six microsatellite loci ranged from 13 to 15 alleles. Gene diversity varied between 0.77 and 0.88. Average gene diversity over all marker loci was 0.84. Analysis for linkage disequilibrium resulted in non-significant

values, suggesting no genetic linkage between loci. None of the loci showed a significant deviation from Hardy-Weinberg equilibrium.

5.3.2 Gene flow and population structure

Inter-patch comparisons

The distribution of alleles at Locus 69 in three non-neighbouring patches (Patches 1, 7 and 11) can be seen in Figures 5.1 a) – c) for *S. araneus* and 5.2 a) – c) for *S. minutus*.

S. araneus

The overall F_{IS} value (- 0.027) was not found to be significantly different from zero indicating random mating. F_{IS} values were negative or extremely small except in Patches 3 (F_{IS} = 0.200) and 6 (F_{IS} = 0.114). In Patches 3 and 6 there were only two and six individuals respectively and therefore these results cannot be interpreted reliably. The overall F_{ST} value (0.019) was significantly greater than zero indicating a small, but significant heterozygote deficiency between patches. F_{ST} appeared concordant across all marker loci (except for Locus 69 where the value of 0.01 was non-significant). The overall F_{ST} of 0.019 is equivalent to approximately 52 'island model immigrants' (Nm) arriving at each locality per generation.

The overall R_{ST} value (-0.029) is smaller than the overall F_{ST} value. Per locus estimates ranged from -0.072 to 0.029, showing much more variation across loci than F_{ST}. Out of the four loci, three had lower R_{ST} than F_{ST}. The overall R_{ST} did not provide an estimated number of 'island model immigrants' due to its negative value. The overall R_{ST} value was not significantly different from zero.

S. minutus

Table 5.3 shows that the overall F_{IS} value (-0.01) was not found to be significantly greater than zero indicating random mating within sub-populations. F_{IS} values were negative or extremely small in all patches. The overall F_{ST} value (0.032) was significantly greater than zero indicating a small, but significant heterozygote deficiency between patches. F_{ST} was large and highly significant at Locus 69. The other two loci had small and positive, but non-significant values. The overall F_{ST} of 0.032 is equivalent to approximately 31 'island model immigrants' (Nm) arriving at each locality per generation.

The overall R_{ST} value (0.047) is larger than the overall F_{ST} value. Table 5.3 shows that per locus estimates ranged from 0.005 - 0.169, showing much more variation across loci than F_{ST}. Out of the three loci, two had lower R_{ST} than F_{ST}. Although the overall R_{ST} provided an estimated number of 'island model immigrants' of 21, the overall R_{ST} value was not significantly greater than zero. As a result, the number of immigrants cannot be estimated legitimately.

	No. individuals	
PATCH	***S. araneus***	***S. minutus***
1	4	4
2	18	6
3	2	0
5	0	0
6	4	0
7	12	9
9	16	18
10	3	0
11	19	6
12	0	0
13	5	0
Total	83	43

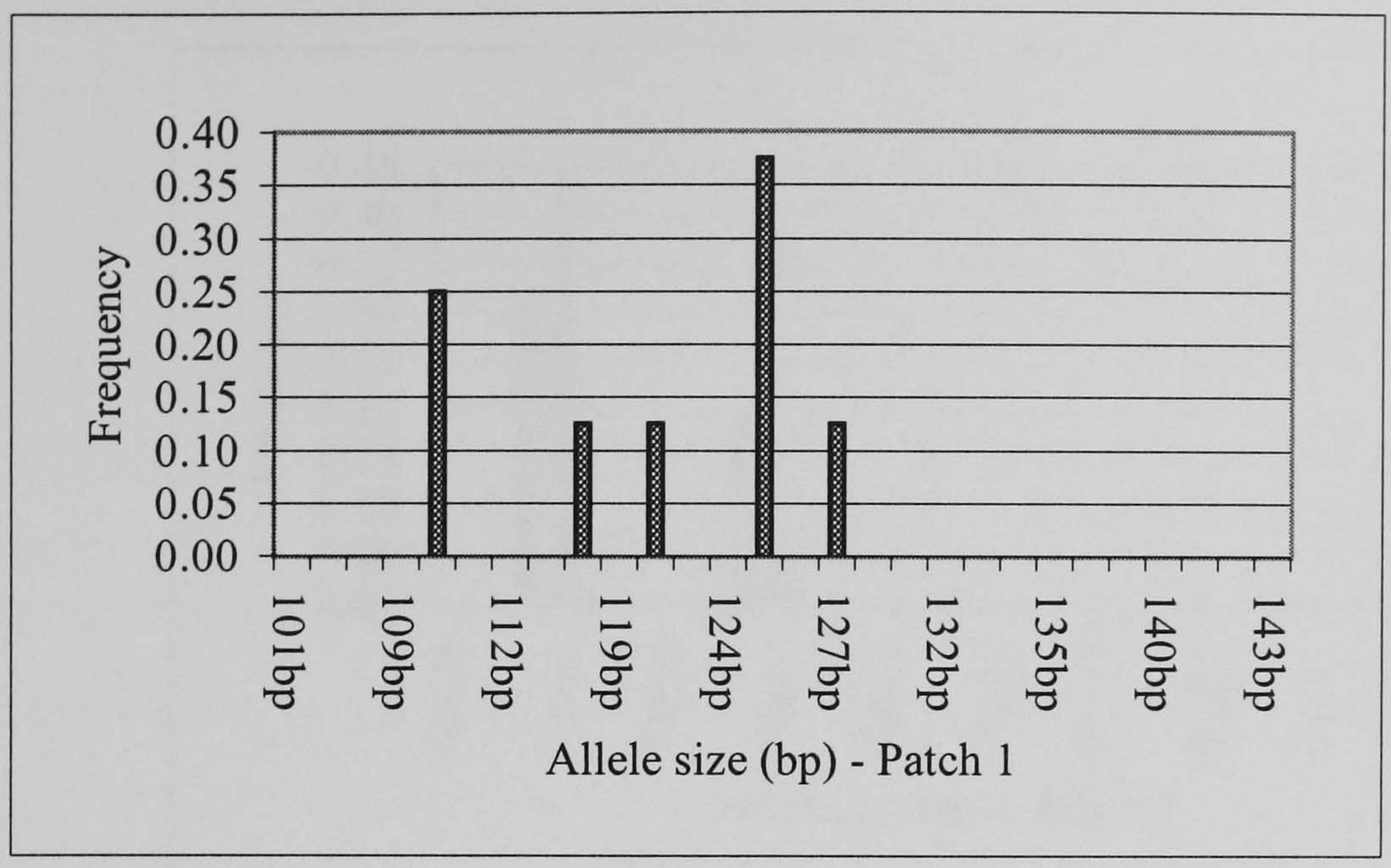
Table 5.1 The number of *S. araneus* and *S. minutus* individuals from each patch that were included in the genetic analysis of population structure

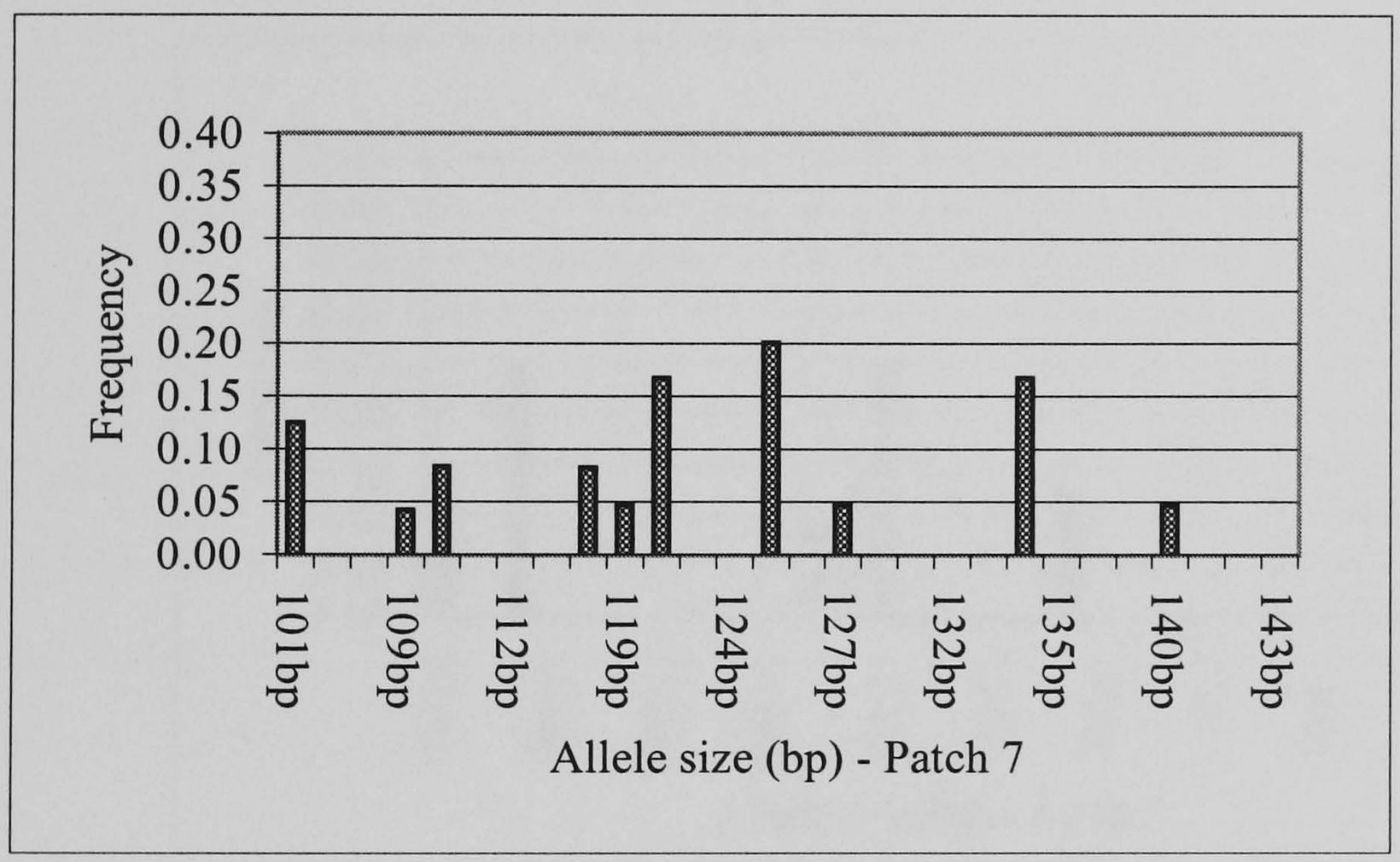
Locus	Na	He	F_{IS}	F_{ST}	R_{ST}	$R_{ST} > F_{ST}$
69	28	0.90	-0.005	0.01	-0.034	No
62	20	0.93	-0.019	0.017*	-0.072	No
9	28	0.94	-0.006	0.017*	0.029	Yes
67	10	0.78	-0.088	0.032*	-0.035	No
All	86	0.89	-0.027	0.019**	-0.029	No
Nm				52	/	

Table 5.2 The number of alleles (Na), expected heterozygosity (He) and F- and R-statistic results, per locus and over all loci for *S. araneus* .
(* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Due to the negative RST value, it is not possible to calculate Nm.

Locus	Na	He	F_{IS}	F_{ST}	R_{ST}	$R_{ST} > F_{ST}$
69	15	0.88	0	0.063*	0.005	No
62	13	0.77	0.005	0.007	0.169	Yes
9	13	0.86	-0.034	0.022	0.019	No
All	41	0.84	-0.01	0.032**	0.047	Yes
Nm				31	21	

Table 5.3 The number of alleles (Na), expected heterozygosity (He) and F- and R-statistic results, per locus and over all loci for *S. minutus* .
(* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).





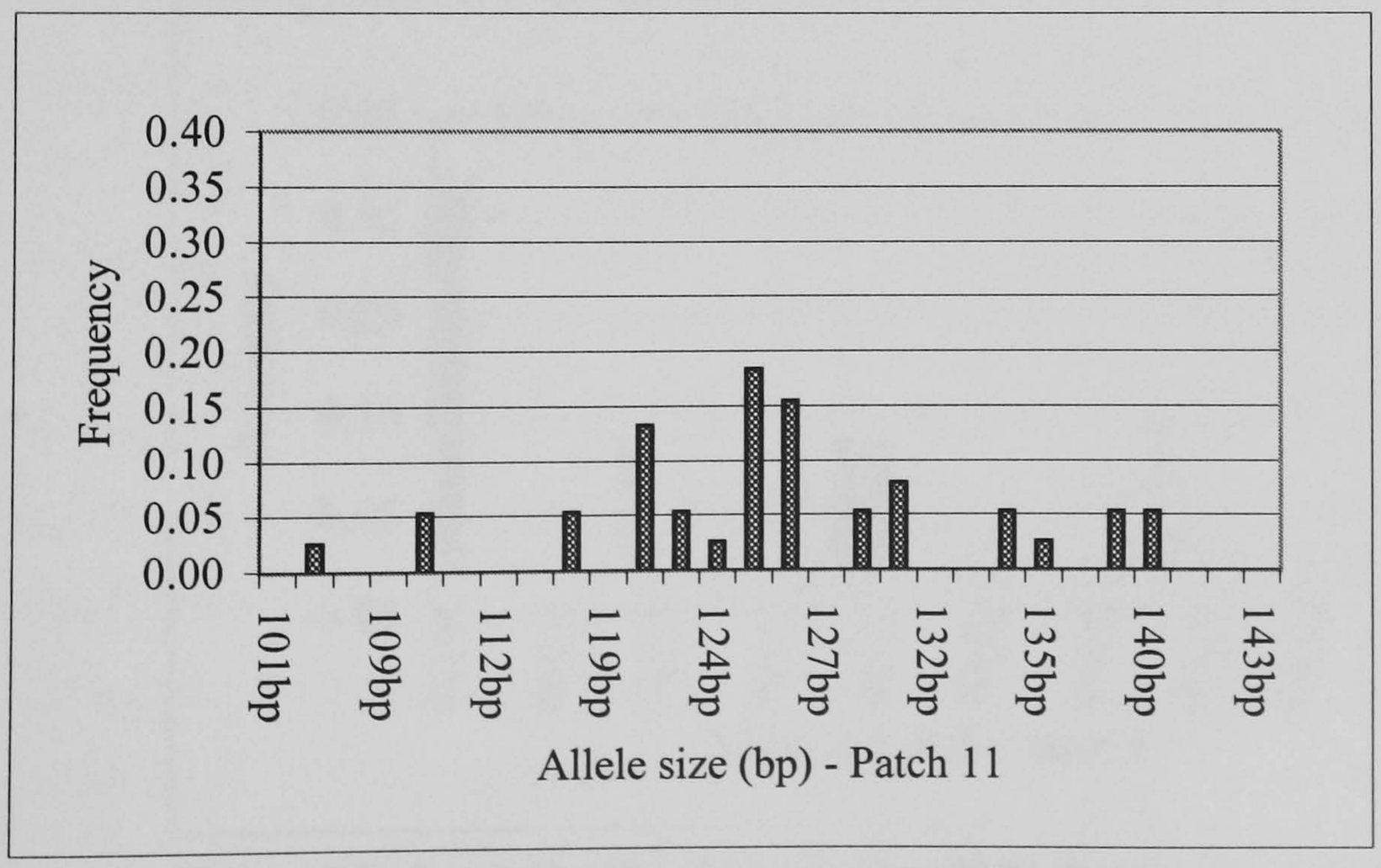
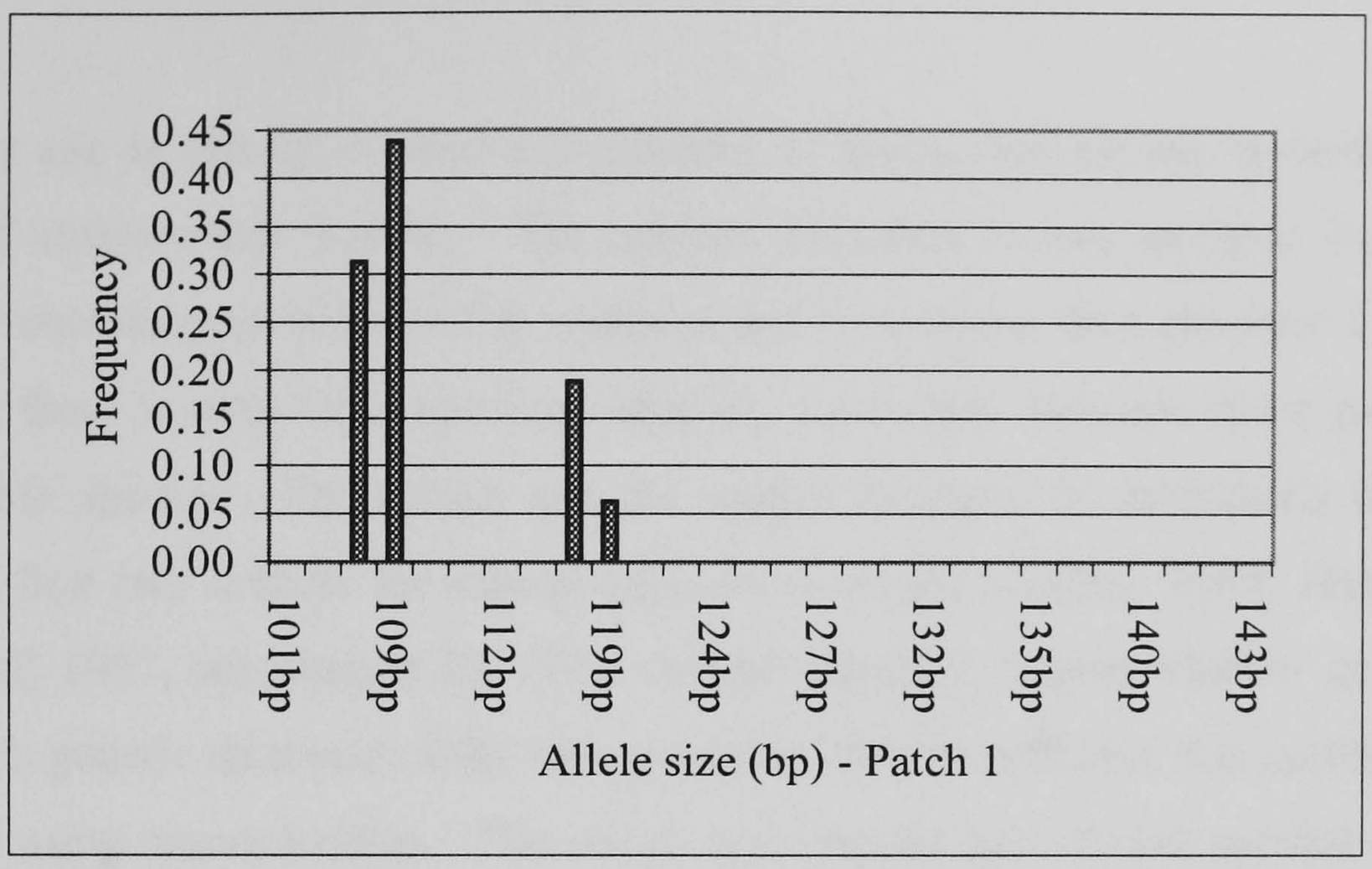
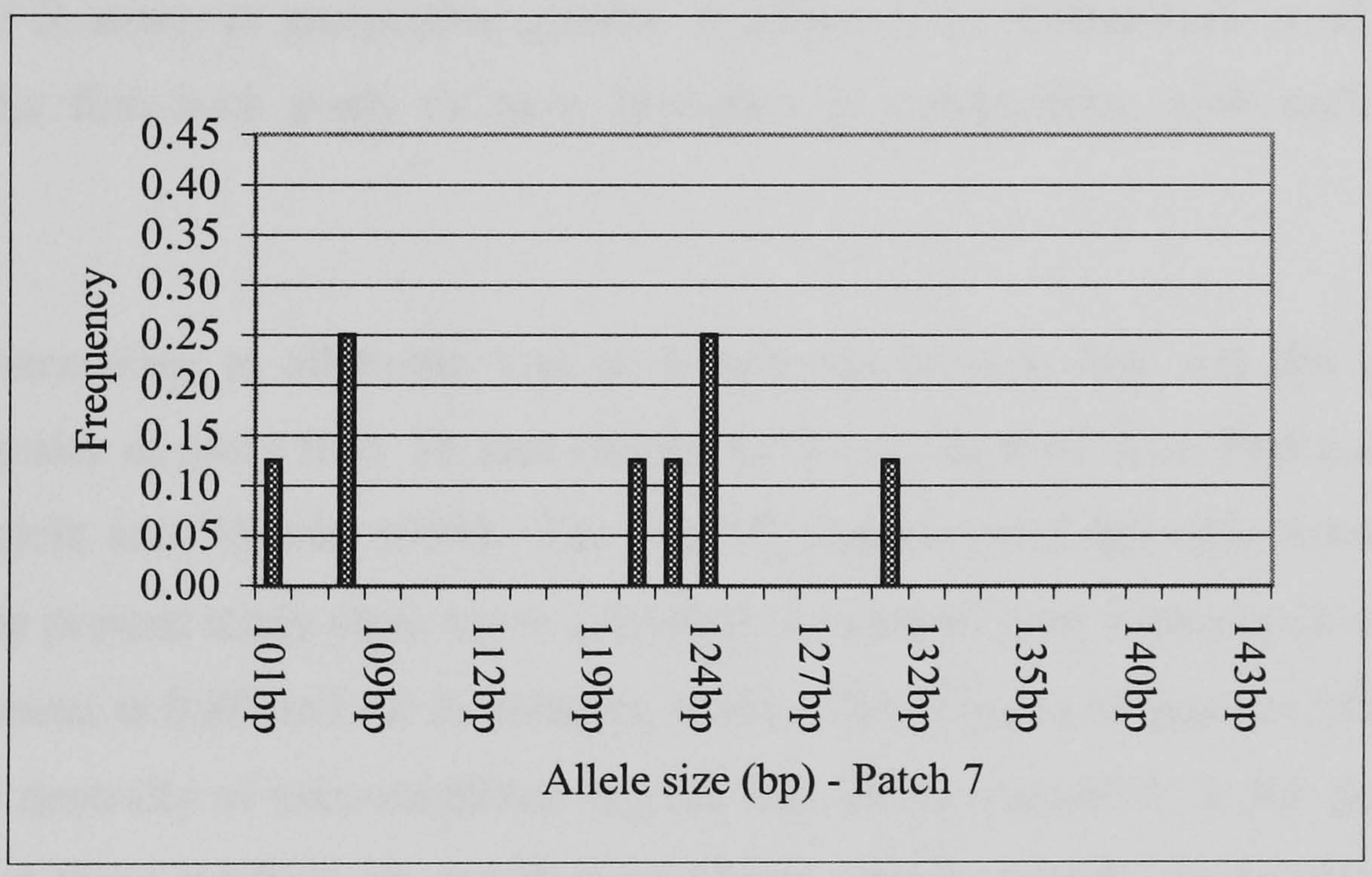


Figure 5.1 a) - c). Graphs showing the allele distribution at L69 in Patch 1, Patch 7 and Patch 11 for *S. araneus* .





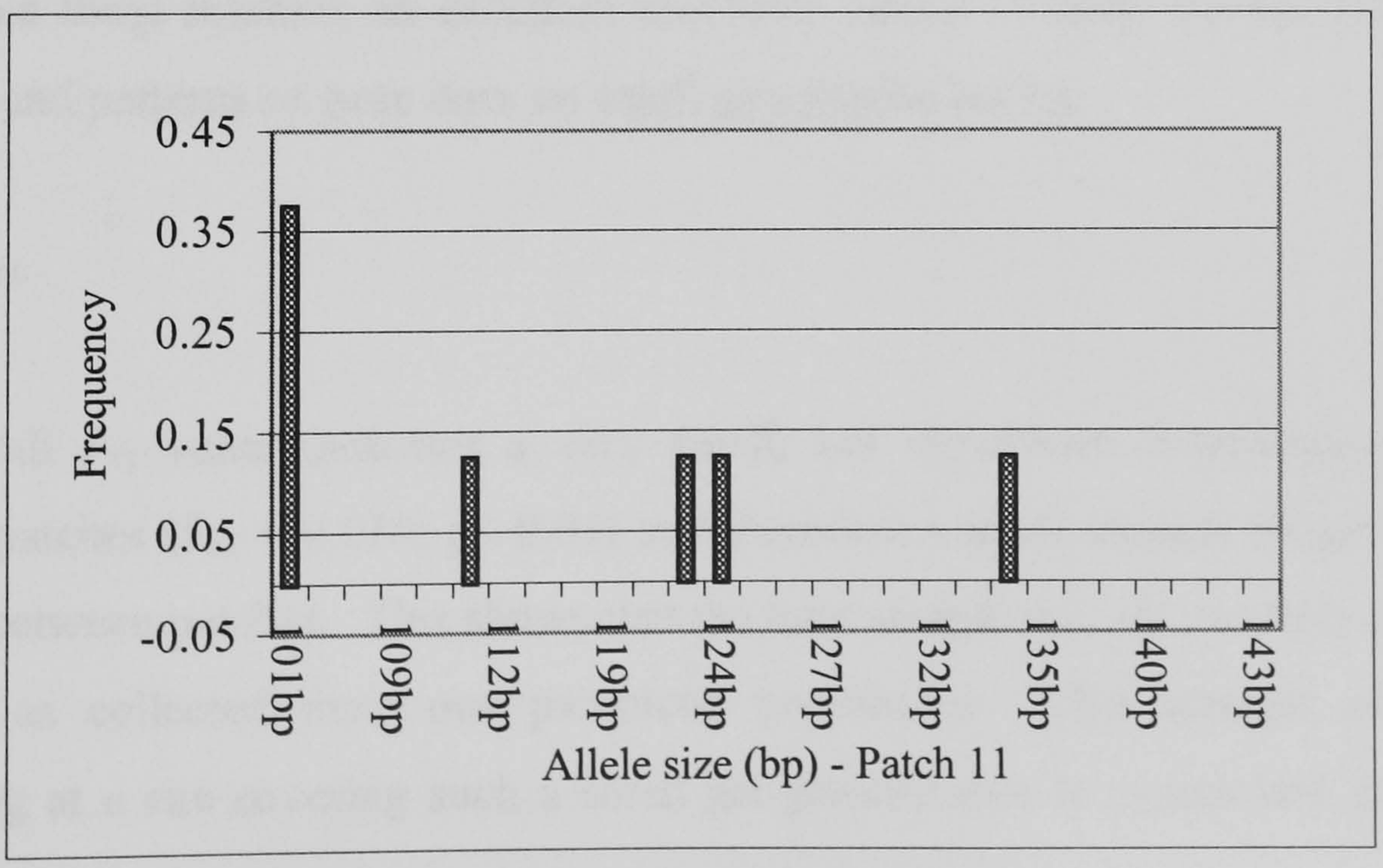


Figure 5.2 a) - c) Graphs showing the allele distribution at L69 in Patch 1, Patch 7 and Patch 11 for *S. minutus* .

5.4 DISCUSSION

The study site is clearly divided into patches of favourable habitat embedded in a matrix of unfavourable habitat. The patches included in this analysis have been shown to contain populations of *S. araneus* and *S. minutus* (see chapters 2 and 3). Although there is some inter-specific variation, movement between these patches is low in both species. The habitat and the spatial structure of individuals therefore fulfil the first two criteria for metapopulation structure (Levins, 1969; Hanski and Simberloff, 1997, see chapter 2). This chapter aimed to assess whether or not the geographic genetic structure of the two species at the site reflected this pattern. This was done using microsatellites. The results will then be put into the context of other studies of *S. araneus* geographic genetic structure (e.g. Wyttenbach *et al.*, 1999). This is the first such study to have field-data in combination with such genetic analysis.

Genetic variability at allozyme loci in *S. araneus* is very low and the observed heterozygosity at more than 30 loci ranged from 0.03 to 0.07 (e.g. Frykman *et al.*, 1983; Wojcik and Wojcik, 1994). The four (*S. araneus*) and three (*S. minutus*) loci used in the present study show up to a 20-fold increase in gene diversity (average He for *S. araneus* is 0.89 and for *S. minutus*, 0.84). The absence of genetic linkage, the presumed neutralty of microsatellites and the high allelic variability at the population level make these markers an excellent tool with which to study genetic population structure and patterns of gene flow on small geographic scales.

S. araneus

The overall F_{ST} value indicates a very small, but significant heterozygote deficit between patches ($F_{ST} = 0.019$; $p < 0.01$) and therefore a small amount of genetic sub-division between patches. This shows that the total sample (i.e. all patches) cannot be regarded as collected from one panmictic population. This amount of genetic structuring at a site covering such a small geographic area is concordant with other

studies carried out over different geographic scales. Wyttenbach *et al.* (1999) examined the genetic structure of two chromosome races of *S. araneus* in Sweden which are separated by a river 50 – 60 metres wide. Approximately 70 % of it freezes over in winter. They obtained a very similar F_{ST} value of 0.017 ($p< 0.05$). Wyttenbach *et al.* (1999) also trapped and sampled *S. araneus* at 24 different localities in four distinct valleys in the Swiss and French Alps. They obtained an overall F_{ST} value of 0.032 ($p<0.001$). Lugon-Moulin *et al.* (1999) collected *S. araneus* samples along a 13 kilometre transect in the Alps which included two different chromosome races. Their overall F_{ST} value was 0.07 ($p<0.05$). In both the latter two studies, populations were separated by mountain ranges. The F_{ST} value therefore appears to increase with the size of the area sampled and the geographic barriers separating the populations. Additional studies at different spatial scales would enable further validation of this.

Figure 5.1 shows the frequency of the different alleles at each locus show great overlap illustrating the lack of genetic differentiation between the patches. These contrast with Figure 3 in Lugon-Moulin *et al.* (1999) where there is a clear difference between the two chromosome races from different Alpine valleys ($F_{ST} = 0.07$). However, the fact that the F_{ST} value is significant shows that although structuring is small, it is real. This result supports the field-work finding that individual movement is restricted to some extent between habitat patches.

The extent to which movement appeared to be restricted in the field, however, (see Chapters 2 and 3) was not directly reflected in the genetic results. Field observations showed that eleven individuals moved between patches in one generation (see Chapter 3). The 'Nm' value derived from the F_{ST} value states that 52 individuals are received by each patch per generation. Although this must be taken as a rough estimate, due to the stringent assumptions of the island model affecting the validity of the relationship between F_{ST} and Nm, there is a discrepancy which must be explained. Firstly, it is likely that the field results do not represent exactly what is happening in the field. It is possible that a few more individuals than are recorded move between

patches. In each patch, a small number of new individuals were caught throughout the year (see Chapter 2) and at the end of the year (Chapter 3). Some of these may have moved from other patches and others from outside the study site. The strategy of multiple mating in this species (e.g. Stockley *et al.*, 1994) also means that if a pregnant female were to move between patches, she would carry with her up to ten young of different genetic make-up. It is also possible that the landscape structure of the site has not been constant since the golf-course was created in 1906. The exact history is unknown but some patches may have been separated only recently. The fact that two patches disappeared during the study period (see Chapter 3) supports the view that landscape change does occur.

The genetic structuring is not reflected in the overall R_{ST} value (-0.029, $p > 0.05$). Slatkin (1995) demonstrated that F_{ST} may give erroneous results due to the mutational mechanisms it assumes. However, Wyttenbach *et al.* (1999) showed that in *S. araneus*, there is no trend in favour of either the infinite 'K' allele model (Jarne and Lagoda 1996) appropriate for F-statistics or the SMM (step-wise mutation model) (e.g. Valdes *et al.*, 1993) appropriate for R-statistics. This supports the use of both methods and indicates that there is no defined mutation model that universally explains the process of mutation at microsatellite loci (Feldmann *et al.*, 1997). However, the fact that the genetic structuring is not reflected in the R_{ST} value supports the fact that the F_{ST} value is very low. The fact that the R_{ST} value is smaller than the F_{ST} value shows that these loci are not obviously following a step-wise model of mutation. This supports Wyttenbach *et al.* (1999) who showed that there is no defined mode of mutation for microsatellite loci in *S. araneus*.

The overall F_{IS} value of –0.027 ($p > 0.05$) shows that *S. araneus* is mating randomly within patches throughout the site. This is in concordance with previous studies on shrew mating behaviour (e.g. Stockley *et al.*, 1994; Michielsen, 1966). F_{IS} values for two patches were high: Patch 3 ($F_{IS} = 0.200$; $n = 2$) and Patch 6 ($F_{IS} = 0.114$; $n = 4$). This is thought to be due to the small sample size in these patches. The analysis was re-run without these two patches and the same overall F_{ST} value was obtained.

S. minutus

The overall F_{ST} value for this species is 0.032 ($p<0.01$). This indicates a slight geographic sub-division between localities and is similar to the value obtained for *S. araneus* by Wyttenbach *et al.*, (1999) when this species was trapped in four distinct Alpine valleys. The R_{ST} value (0.047) reflects the F_{ST} value despite being non-significant. Such analysis has not been carried out in this species before and therefore it is not possible to make intra-specific comparisons. However, the values for F_{ST} are not concordant across loci and this value indicating strong geographic structuring may be soley due to the high value obtained for Locus 69 (F_{ST} = 0.063; $p< 0.05$). Wyttenbach *et al.* (1999) found that a high overall F_{IS} value in their study was solely due to the alleles at one particular locus in one particular sub-population. The reason for this could not be explained as *S. araneus* are thought to be a species that mates randomly on a local level (Stockley *et al.*, 1994).

These loci were not developed for this species and null alleles may be biasing the analysis. In addition, some microsatellites have been associated with disease in humans (e.g. Huntington's disease (Huntington's Disease Collaborative Research Group 1993)) and they may therefore be subject to selection in other species as well. However, as all three loci were at Hardy-Weinberg equilibrium, it is unlikely that this was occurring. This study should be extended to include more loci to determine whether or not this pattern is consistent.

Although there is only a small amount of movement between patches in *S. minutus*, inter-patch movement has been shown to occur at greater frequencies in this species than in *S. araneus* (see Chapter 2). This is not reflected in the F_{ST} values which suggest that there is less inter-patch movement in *S. minutus* (F_{ST} = 0.032; Nm = 31) than in *S. araneus* (F_{ST} = 0.19; Nm = 52). It is possible that *S. minutus* have a less regular capture rate than *S. araneus* (e.g. they are sometimes able to enter and leave traps without setting them off) and therefore the results for the two species are not

equally representative. However, inter-specific comparisons must always be viewed with caution when the microsatellite primers have been developed for only one of the species.

The overall F_{IS} value for *S. minutus* is not significantly different from zero and this is concordant across loci. This shows that this species is mating randomly at the site. This is also concordant with previous studies on movement and mating in this species (Michielsen, 1966).

This study is the first to present genetic population structure data in *S. araneus* and *S. minutus* in combination with comparable field data. The FST value expected for the eleven migrants observed is 0.08 which differs from that obtained (0.019). Further studies should evaluate the difference between these two values by determining whether there is any overlap between the confidence intervals of the values obtained. The discrepancy in the results shows the importance of field data in understanding a population in nature. A purely genetic based study would draw entirely different conclusions regarding movement at the site. The results of the genetic study suggest that there is a high frequency of movement between habitat patches. Field-work data will inevitably under-estimate the number of individuals moving between patches. However, the very low number of movers recorded combined with the very high number of individuals caught overall suggest that there are other reasons, such as landscape history and mating strategies of the species concerned, that contribute to this lack of genetic structure between patches.

CHAPTER 6

GENERAL DISCUSSION

The aim of this study was to obtain data on the movement and spatial distribution of *S. araneus* and *S. minutus* individuals in relation to the habitat structure found at the study site. This was in order to ascertain the amount of movement occurring between habitat patches and therefore to predict gene flow between them. This was done for three main reasons. The first was to determine whether individual movement in these species was influenced by landscape structure. The second was to determine whether the habitat patches at the site represented 'patches' in the metapopulation sense (Hanski and Simberloff, 1997), thus making the concept a good starting point from which to understand the dynamics of the overall population. The third was to use *S. araneus* and *S. minutus* as model species from which general patterns of animal movement in a heterogeneous landscape can be observed.

Much previous work looking at the effect of landscape structure on individual small mammal movement has concentrated on roads. This is because a road network is anticipated to contribute considerably to the resistance between habitat patches (Bennett, 1991). A previous study on small mammals (Richardson *et al.*, 1997) showed that roads greater than 20 metres wide were barriers to small mammals (bank voles, *C. glareolus*, field voles, *Microtus agrestis* and wood mice, *A. sylvaticus*) and that movement across the road occured at a very low rate. This study also demonstrated that road traffic intensity contributed to this barrier effect.

Such work has also been carried out in other species, with important implications for conservation. Habitat destruction leading to habitat fragmentation has been cited as one of the most important factors causing amphibian decline in industrialised regions (Blaustein *et al.*, 1994). The results of a recent study (Vos and Chardon, 1999) also showed a negative effect of road density on the probability of occupation of moorland ponds by moor frogs (*Rana arvalis*). This is interpreted as an indication that roads increased the isolation between ponds and therefore contributed to habitat

fragmentation. The results of both the above studies showed that roads increased the isolation between suitable habitats due to the reluctance of individuals to cross them (or being killed while they are trying) and therefore contributed to habitat fragmentation. The exchange of individuals in the landscape matrix between patches will decrease and as a result, rates of colonisation will be lower. This, combined with the increased mortality of individuals on exposed habitat, will increase the extinction risk of the entire population.

A road is a visually clear-cut potential barrier to animal movement and roads are becoming increasingly numerous throughout the world. These two reasons may explain why many studies looking at the effect of landscape structure on individual movement have focused on roads. However, other types of landscape heterogeneity may be equally important in influencing individual movement and therefore also deserve attention. Due to the difficulties of quantifying movement between habitat patches under less clear-cut conditions, approaches have tended to be either experimental or indirect. An experimental approach to the effect of landscape structure on individual movement was adopted by Bright (1998) in a study of the dormouse, *Muscardinus avellanarius*. This species is an arboreal habitat specialist and had previously been shown to travel through corridors of trees to avoid gaps in woodland (Bright and Morris, 1991, 1992). Bright (1998) carried out habitat manipulation and translocation of individuals and showed that this species will not cross even small gaps in hedgerows. This has important implications for conservation: hedgerows can only provide corridors for dormice if they have no gaps in them.

Indirect approaches are also used to assess the effect of landscape structure on individual movement. Bank voles have specific habitat requirements and live in forests and woodlots. Work has shown that in a Polish agricultural landscape, the degree of isolation of patch populations affected factors such as density and exchange rate of individuals (Kozakiewicz, 1985; Szacki, 1987). This strongly suggests that this species is affected by landscape structure and individuals are reluctant to cross

large areas of unfavourable, exposed landscape. More recent work on this species has been carried out in the Netherlands (van Apeldoorn *et al.*, 1992) in an area of maize fields and pasture containing well-defined patches of woodland. This study also showed that in small patches, as the distance to permanently inhabited forest increased, the number of females decreased (although no change was found in the number of males). This work supports the previous studies but also suggests that different sexes may be responding differently to the same landscape structure.

A similar study carried out in Britain also suggested that landscape structure influences individual small mammal movement (Fitzgibbon, 1997). This study was carried out in an intensive arable region of Great Britain which contained thirty-eight small woodlands. This result showed that isolation variables such as the distance to the nearest large wood influenced the density of wood-mice and bank vole populations. Fitzgibbon (1997) also showed that woods that were well connected by hedgerows supported higher densities of both species. Her results supported the fact that exposed habitat is a barrier to movement. These studies illustrate the importance of understanding how individual movement patterns can be affected by landscape structure. However, they also show that most studies are either carried out on roads, involve experimental manipulation and translocation of individuals or use indirect approaches. These approaches are thought to be due to movement between habitat patches being a relatively rare event and therefore difficult to observe.

The present study was carried out in a landscape where suitable habitat patches were separated by unsuitable habitat. However, it avoided using the above approaches and does not rely on any kind of experimental manipulation. As a result, an intensive trapping regime was required in order to try and quantify directly how many individuals were moving between suitable patches. The results show that both *S. araneus* and *S. minutus* are sensitive to landscape structure and do not move freely between patches. However, *S. minutus* males tend to move more frequently between patches than *S. minutus* females. An advantage of using a golf-course as a study site, in addition to the fact that many landscape variables were eliminated, is that traffic

density is not a feature and so is yet another variable eliminated from the study. This study has shown that, even in the absence of traffic and the prospect of venturing onto tarmac, both shrew species are reluctant to leave habitat providing suitable cover in order to venture onto exposed habitat. The difference between male and female *S. minutus* highlights the importance of understanding the expected sex ratio of the species in question in studies such as these. If the ratio of males to females was high in a similar study, a different conclusion may be reached. This study has therefore highlighted the vulnerability of this species to fragmented habitat due to the effect it can have on individual movement. This finding is not supported by the only similar study on these species which suggested that they regularly cross back and forth to a traffic island (Korn, 1991). However, Korn's study also showed an irregular capture rate for these species which may explain the difference in results. In addition, no individuals were marked or sexed and therefore the results do not offer any information on individual movement.

The second reason for quantifying movement between the habitat patches at the study site was to determine whether or not a metapopulation approach was suitable for understanding the dynamics of the overall system. Previous studies have explained shrew distribution through the Theory of Island Biogeography (MacArthur and Wilson, 1967; Hanski, 1986; Peltonen *et al.*, 1989). Despite proving information on shrew dispersal ability, these studies were specific to mainland-island situations (literally) and were not directly applicable to terrestrial fragmented habitats where a 'mainland' may not be present. They also concentrated on explanation of patterns and did not focus on conditions for persistence of the overall population. In order for *S. araneus* and *S. minutus* populations in fragmented terrestrial habitats to be understood and conditions for persistence obtained, a different approach is needed. A metapopulation approach has never been used for these species or the suitability of such an approach assessed. This study aimed to do this.

It is necessary to know whether a population is functioning as one large population or as a collection of sub-populations before an understanding of their dynamics can be

obtained. The migration rate between the sub-populations must be therefore be quantified. However, this is generally a labour-intensive and time-consuming process. A recent study of the house sparrow (*Passer domesticus*) aimed to determine spatial and temporal variation in demography between four islands off the coast of Norway (Saether *et al.*, 1999). The authors examined each island ('patch') separately due to the small number of migrants that were exchanged between them. This approach was taken only after five years of an intensive mist-netting and colour ringing scheme which showed the low inter-patch migration rates. As a result of this, Saether *et al.* (1999) adopted a metapopulation approach to understanding the overall dynamics of the sparrows on the four islands. The results of the present study show equally low rates of migration between the habitat patches.

The third reason for quantifying inter-patch movement in *S. araneus* and *S. minutus* was because they were anticipated to be good model organisms from which to deduce the response of other species to heterogeneous landscapes. Their abundance and readiness to enter traps at the site became apparent during preliminary trapping work and was confirmed during the course of the study. High numbers of both species were caught in both the 1997 and 1998 cohorts (see Chapters 2 and 3 respectively). This study therefore provides data that can tentatively be extrapolated to other mammal species for which fragmentation may be a threat, but which may not be caught in such large numbers (e.g. hedgehogs, *Erinaceus europaeus* and badgers, *Meles meles*). However, such comparisons must always be viewed with caution as an organism's response to landscape structure has been shown to be highly species/race specific (Ims and Rolstad, 1993). This may be due to differences in social structure between the species which will also affect how it interacts with its environment. Differences in resource requirements also occur between species. This will also affect how an organism interacts with the landscape.

The results discussed above are purely field-based and it is therefore necessary to discuss their validity based on the findings of similar studies. There is often unavoidable bias in dispersal distributions obtained from a mark-recapture study

(Koenig *et al.*, 1996). Such distributions are usually highly skewed towards short-distance dispersal due to study areas being finite in size (Barrowclough, 1978; Stenseth and Lidicker, 1992). Previous studies on *S. araneus* illustrate this point. As the study site size increased, so does the maximum distance moved by an individual in that study: Shillito (1963) recorded a maximum dispersal distance of 144 metres (study site length, 168 metres); Stockley *et al.* (1993) recorded a maximum dispersal distance of 200 metres (study site length 1,050 metres); and Michielsen (1966) recorded a maximum dispersal distance of 250 metres (study site length 2,500 metres).

The present study also supports the fact that the maximum distances recorded will be a function of study design. It has produced the longest movements ever recorded for *S. araneus* and *S. minutus* using a live-trapping regime: male shrews were shown to move distances of up to 1,026 metres and female shrews distances of up to 513 metres. The maximum length of the field site was 1,700 metres. This was shorter than Michielsen's (1966) site but her site was broken into three areas with no traps in between them. The present study recorded 446 metres as a maximum movement distance for *S. minutus*. Prior to this, 355 metres was the longest distance recorded (Michielsen, 1966). These results show that maximum distances recorded for individuals will tend to be dependent on study site length but also on trap density and trapping intensity within that site.

This study is the first to display movement distance distributions for either species of shrew. For *S. araneus*, the distribution is highly skewed towards short-distance dispersal as predicted by Barrowclough (1978). However, there is an important difference between this distribution and others where dispersal drops off with distances and reaches zero at or near a distance corresponding to the length of the study site (e.g. acorn woodpeckers, *Malanerpes formicivorus*, Koenig and Mumme, 1987). The results show a large gap between the majority of the values and the outlying long-distance values. There is no drop off corresponding to the length of the study site. This result suggests that the data do represent reality. Although there will

be some bias, the results clearly illustrate the dichotomy between the majority of low-distance dispersers and the fewer number of longer-distance dispersers. This dichotomy cannot be caused by the patchiness of the habitat because some of the long-distance movements were undertaken within habitat patches and some of the smaller movement distances were undertaken between habitat patches.

In contrast with *S. araneus*, the results for *S. minutus* do not show the highly skewed distribution as predicted by Barrowclough (1978). They also do not show a clear dichotomy between short- and long-distances movements. This, combined with their low 'survival' at the site suggests that for this species, long distance movement is under-estimated and the results obtained may be directly related to study design. Potentially, this species has good dispersal ability. Like *S. araneus*, *S. minutus* is found on islands in lakes in Finland where they must have dispersed by themselves (Hanski, 1986).

These results highlight the fact that in order to obtain information regarding long-distance dispersal using mark-recapture data, a huge effort is required. In order to increase the size of the current study site, more field-work personnel would be needed or the number of days required to trap the whole area would have to be increased (which would make the four sections of each trapping session less comparable). Radio-tracking is an effective way to increase the size of a study area because this results in it becoming as big as the dispersal distances of the individuals. Studies on yellow-bellied marmots (*Marmota flaviventris*, Van Vuren and Armitage, 1994) compared radio-tracking data with dispersal distributions obtained from long-term plot-based studies using marked individuals. Their study demonstrated that long-distance dispersal based on radio-tracking was strikingly more frequent than was suspected (mean dispersal distances were 332 % greater in males and 282 % greater in females than shown in the trapping study). The study by Tegelström and Hansson (1987) showing *S. araneus* moving several kilometres over ice, and studies by Hanski (e.g. 1986) showing shrews swimming between islands in a lake, also suggest that

longer distance dispersal movements are undertaken by a few *S. araneus*. Such distances are far greater than could be recorded through a terrestrial trapping regime.

There is no doubt that radio-tracking of *S. araneus* and *S. minutus* would greatly improve understanding of movement and dispersal. It would also improve understanding of how they are responding to patch edges and unfavourable habitat. However, shrews are currently unable to be radio-tracked due to their head and neck shape being unsuitable for a collar and implanted transmitters being too large. Externally placed transmitters are also unsuitable due to shrews being able to reach every part of their body with their teeth. The high cost involved combined with this latter fact would make radio-tracking an impractical option for these two species.

Alternative approaches in addition to live-trapping can provide further information on long-distance/dispersal movements. The use of genetic markers to determine dispersal distributions and patterns is becoming increasingly popular and was the approach chosen in this study. This widespread popularity reflects the relative ease with which genetic data can be collected and analysed (Avise, 1994) and the frequent belief that such estimates may be more valid than those obtained through direct studies of movement (Bossart and Pashley Prowell, 1998). However, conclusions are often drawn from genetic data about population structure and levels of gene flow between populations even though there are often multiple, equally viable ways to interpret the results. For example, present day patterns of genetic structure often reflect historical patterns such as the effects of Pleistocene glaciations and post-glacial range expansions (e.g. Larson *et al.*, 1984; Merila *et al.*, 1997). In turnstones (*Arenaria interpres*), the lack of genetic population structure (in mitochondrial DNA) on a world-wide scale is thought to be due to recent expansions from a bottlenecked refugial population rather than from global gene flow (Wenink *et al.*, 1994). Such studies emphasize the different time-scales that the two approaches are measuring. Direct, field-based measurements are limited to a maximum of a few hundred individuals and only a few generations. Indirect measures based on gene flow infer rates of effective dispersal by a large number of individuals over a much longer

period of time. There will, therefore, be problems if genetic data are used in isolation as a means by which to understand contemporary ecological processes. Slatkin (1985) and Bossart and Pashley Prowell (1998) strongly advocate the key role direct studies of movement play in understanding contemporary ecological processes and state that this is the only valid approach to studying gene flow in an ecological context.

Many studies depend entirely on genetic data to understand migration, population sub-division and barriers to gene flow in a species. In the case of marine organisms, this is often because reliable field data are almost impossible to obtain. This is the case for the veined squid, *Loligo forbesi*. Using microsatellite loci, Shaw *et al.* (1999) showed a genetic uniformity across the populations occupying the European shelf seas of the North-east Atlantic and extreme genetic differentiation of the Azores population. They also demonstrated subtle, but significant levels of differentiation between the populations of the North-east Atlantic offshore banks (Rockall and Faroes) and the shelf population. Such a study had implications for the interpretation of dispersal and management of such a commercially exploited species. It also provided information about marine barriers to gene flow such as water depth and current regimes. However, although such a study greatly improves what is known about this species, it gives no information on important factors such as population size and structure (in terms of age-classes etc.) which may be of a more immediate conservation value. In addition, as with glaciation patterns in terrestrial ecosystems, ocean currents and water depths change with time. The fact that these patterns may represent past gene flow must also be taken into account when interpreting these results.

Smaller-scale, terrestrial-based studies do allow comparable field data to be collected in addition to genetic data. However, such studies have accumulated at a much slower rate than purely indirect (genetic) studies (Bossart and Pashley Prowell, 1998). A study by Dallas *et al.* (1995) on genetic sub-division and gene flow in the European house mouse, *Mus musculus musculus* in Denmark, produced genetic data that were

compatible with known ecological characteristics of this sub-species. The results (using microsatellite loci) were consistent with two types of gene flow. The first was constant migration among stable sub-populations and the second was continual extinction and re-colonisation of sub-populations. This species has been studied in two Danish farms (Carlsen, 1993) and has been shown to emigrate from the farms to surrounding fields in spring, returning in the autumn. Such seasonal movements may represent re-habitation by the same sub-population (with possibly some new immigrants) or instead, extinction/re-colonization events. Thus in this case, the data collected from the field and also from genetic based techniques produced compatible results.

However, it is rare that field and genetic data show such similar results and it is more common that the results are conflicting. Waser and Elliot (1991) examined the local population structure of bannertailed kangaroo rats (*Dopodomys spectabilis*) using allozyme loci and found no evidence for the spatial clustering of alleles in populations up to 1 kilometre apart. This was despite extensive long-term trapping data indicating that virtually all individuals dispersed less than 400 metres away from their natal area. They reconciled the data by saying that long-distance movement forays were undertaken by males to mate with females and this was going undetected. Their results were therefore important in highlighting possibly hidden behavioural characteristics in their population. A similar result was found in the Colombian ground squirrel (*Spermophilus colombianus*) where an F_{ST} value of 0.026 was obtained from allozyme data, indicating very little genetic population structure (Dobson, 1994). This was contrary to field-based data which showed that dispersal was very low. Their result was explained by saying that short-distance dispersal was the norm but that it was so frequent that it was able to homogenise allele frequencies among relatively distant populations. However, this would only work if the populations were continuous which they are not (due to the mountain habitat requirements of the species). Both these results may be due to their choice of genetic marker as variability at allozyme markers is often very low compared with other

genetic markers (e.g. as it is in *S. araneus* allozyme loci compared with microsatellite loci, Wyttenbach *et al* (1997)).

A more recent study of oystercatchers (*Haematopus ostralegus*) using microsatellites also found a lack of genetic variation between different populations which was contrary to the results expected on the basis of field observations (Van Treuren *et al.*, 1999). The study was carried out in the Netherlands where this species is found in large numbers along the coast and on islands in the north part of the country. Breeding individuals always return to the same site each year (Ens *et al.*, 1993). Genetic differentiation between populations was examined on a local scale and also in geographically separated breeding localities. On both scales, no genetic differentiation was found between populations, indicating one panmictic population in the North of the Netherlands. This result supported a very small amount of field data indicating that juvenile dispersal occurred occasionally. The results therefore suggested that juvenile dispersal was more common that previously thought and thus provided a direction for future field-based research. However, the results in the above three studies may all relate to past patterns of gene flow rather than present ones.

The present study provides field-based and genetic-based data sets for *S. araneus* and *S. minutus* and is the first to do so in these species. Population genetic studies have previously been carried out in *S. araneus* (e.g. Wyttenbach *et al.*, 1997). However they were carried out at such large scales that comparable field-work was impossible. This study is important because it covers a small area and is therefore able to compare the two approaches and discuss possible conclusions on the basis of both data sets. It is also important because studies with both sets of data are rare.

The results from the microsatellite data show that genetic variation is high and inbreeding is not an immediate threat in this population. The field-based results show very little movement occurring between the patches, thus predicting that there is some genetic sub-division between them. However, the genetic results show that there is in

fact very little genetic sub-division (based on F-statistics) or none at all (based on R-statistics). This study is therefore similar to other studies which have shown conflicting information when comparing field-based results with genetic results. It is therefore necessary to explore reasons why this may be. The first reason is that the lack of genetic sub-division may be a result of past rather than present levels of gene flow. This is very likely as the habitat patches at the site were separated at most, 93 years ago (and is equivalent to 93 generations of *S. araneus* and *S. minutus*). The second reason may be that the field-data are misrepresentative of what is actually occurring at the site: there may be more inter-patch movement occurring than is being recorded. The third reason may be that, due to the mating strategy of *S. araneus*, genetic diversity at microsatellite loci is high. This, coupled with the fact that a small amount of long-distance dispersal does occur (and is probably slightly under-estimated) may be enough to explain the lack of variation found. Although radio-tracking studies in this species would probably increase the number of long-distance dispersal movements recorded, the results suggest that they are still undertaken by only a few individuals relative to the total population.

This study, along with those mentioned above, highlights how genetic data must be interpreted in combination with field-based data (including ecological aspects of the species of concern, such as dispersal characteristics and mating strategies) and an understanding of past landscape processes. Often such processes can only be guessed at but a historical perspective to such results must be taken. In terms of predicting the persistence of a population, genetic data can show whether lack of genetic variation is a serious problem and may lead to inbreeding and inbreeding depression (as it has shown in wild muskox, *Ovibos moschatus*, populations, Laikre *et al.*, 1997). However, if such lack of genetic variation is not found, a different approach should be taken. In terms of modelling the persistence of populations, a demographic approach based on field-data should be taken. Such an approach will probably under-estimate inter-population dispersal due to the limitations of field-based approaches. However, genetic-based approaches may over-estimate migration (depending on the influence

of historical landscape processes which will difficult to quantify). This may result in unrealistic predictions being made about a population's persistence.

As well as comparing dispersal estimates from field- and genetic-based data, this study also shows that dispersal characteristics can be influenced by timing of birth. Individuals born earlier in the summer tend to disperse further (or have larger home ranges) than those born later. Other studies have also shown that timing of birth can affect dispersal characteristics. Crested tits (*Parus cristatus*) have been studied in Belgium where they occur in isolated pine plots ('habitat fragments') and large pine forests ('continuous habitat') (Lens and Dhondt, 1993). Proportionately more second brood emigrants (fledged up to three weeks after the first broods) were recovered in habitat fragments compared with continuous habitat. First brood immigration into the fragments was three weeks later than into continuous habitat, thus supporting the fact that the fragments are second choice habitat. However, in this species it appears that the landscape structure itself determines timing of fledging and dispersal. Young from first broods dispersed one week later if they were born in fragments compared with individuals in continuous habitat. In second broods, the delay was even longer. The present study does not implicate landscape structure in the timing of birth of the different *S. araneus* cohorts. However, timing of birth does affect dispersal characteristics. In northern Belgium, *P. cristatus* is totally restricted to coniferous woodland and this study was carried out in an area where such favourable habitat was easily distinguished from the surrounding inhospitable agricultural matrix. In species with less specific habitat requirements, such links may be more difficult to determine. However, as landscapes become more fragmented, the relationship between landscape structure, timing of birth and dispersal characteristics may become apparent in an increasing number of species.

The aim of this study was to describe spatial distribution and movement of *S. araneus* and *S. minutus* in a heterogeneous landscape, using a mixture of direct (field-based) and indirect (genetic-based) methods. Such a study is important for several reasons. It is the first study to present the results of a live-trapping regime for the two species

over such a large and consistently trapped area. As a result, it has produced longer movements by both species than has ever previously been recorded using live-trapping. It is also the first study to examine the effect of landscape structure on either species. Such studies are becoming increasingly important as landscapes become increasingly fragmented. This study is also one of few to compare movement data obtained through field-work and genetic work. It also contributes to previous studies on the genetic sub-division of *S. araneus* as it is the first to present comparable field-data in such a study.

The results have shown that although movement between patches is low, genetic variability is high and not strongly partitioned according to the habitat patches at the site in either species. This highlights the potential influence of a small amount of long-distance dispersal, a mating strategy that promotes genetic variability within litters and the history of the landscape in preventing genetic differentiation between sub-populations occupying well-defined habitat patches. This study has therefore provided a direction for future research at the site. The demographic data can be used to construct a mathematical model which can, in turn, be used to predict population persistence of both species at the site.

FUTURE WORK

The field-based results show that *S. araneus* at the study site is not operating as one large population but is made up of a series of patches, inter-linked by occasional migration. This finding means that a metapopulation approach would be the most appropriate means by which to model the system. The classical Levins model (Levins, 1969) is a non-spatial and deterministic model. It requires two parameters, a colonisation rate and an extinction rate. Patches are all identical. They can be occupied or empty and colonisation only occurs into empty patches.

The results of the field study show that different patches tend towards different extinction rates (this is primarily due to the differences in patch size: big patches have

lower extinction rates than small patches). In addition, the movement rate between pairs of patches differs (for example, Patch 12 received more immigrants than any other patch probably due to its proximity to Patch 11). Using such a model, the colonisation rate would have to be deduced from the recorded movement data and the extinction rate averaged over all the sub-populations. The results from such a model could therefore not be expected to produce reliable results. This would hinder understanding of how the overall population was operating.

It would therefore be necessary to produce a model that is spatially explicit and able to model the patches on an individual level. This would allow the variation between patches to be incorporated. Movement rates based directly on the field-data could then be used. The explicit spatial variation would allow features such as the more commonly observed movement between neighbouring patches to be incorporated. In its deterministic form, such a model would allow direct exploration of the consequences of changes, such as an increase or decrease in movement rates.

In order to develop such a model further and to explore how variation of processes within and between patches would affect the overall population dynamics, stochasticity should be incorporated into the model. This would result in different parameter values being selected for at each iteration according to probability distributions. By changing the levels of stochasticity, it would be possible to determine how sensitive the system is to temporal fluctuations. Such a model would allow exploration of how the overall system is working. Future manipulations, such as the removal of the largest patches, would give further insight into this and allow such a model to be validated.

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Common Name	Latin Name	Method of observation
Order Rodentia		
Wood Mouse	*Apodemus sylvaticus*	Longworth trapping
Bank Vole	*Clethrionomys glareolus*	Longworth trapping
Field Vole	*Microtus agrestis*	Longworth trapping
Grey Squirrel	*Sciurus carolinensis*	Visual
Order Insectivora		
Mole	*Talpa europaea*	Visual
Hedgehog	*Erinaceus europaeus*	Visual
Order Lagomorpha		
Hare	*Lepus europaeus*	Visual
Rabbit	*Oryctolagus cuniculus*	Visual
Order Carnivora		
Domestic cat	*Felis catus*	Visual
Stoat	*Mustela erminea*	Visual
Weasel	*Mustela nivalis*	Longworth trapping

Appendix 1. Table showing the mammal species observed at the study site, Fulford Golf-Course, in addition to the two study species, *S. araneus* and *S. minutus* .

Common Name	Latin Name	Method of observation
Mammals		
Domestic cat	*Felis catus*	Visual
Stoat	*Mustela erminea*	Visual
Weasel	*Mustela nivalis*	Longworth trapping
Birds		
Little Owl	*Athene noctua*	Visual
Sparrowhawk	*Accipiter nisus*	Visual
Carrion Crow	*Corvus corone*	Visual
Kestrel	*Falco tinnunculus*	Visual
Tawny Owl	*Strix aluco*	Visual

Appendix 2. Table showing the potential predators of *S. araneus* and *S. minutus* observed at the study site, Fulford Golf-Course.

		LOCUS 69		LOCUS 62		LOCUS 9		LOCUS 67	
PATCH	**Individual**	**P 1**	**P 2**	**P1**	**P 2**	**P 1**	**P2**	**P1**	**P2**
1	**82A**	110	125	184	184	152	160	98	102
1	**83A**	121	127	174	184	162	179	102	104
1	**84A**	125	125	174	197	162	191	94	104
1	**87A**	110	117	183	191	183	185	104	104
2	**68A**	101	111	186	197	162	191	104	104
2	**69A**	101	132	186	190	163	165	102	102
2	**70A**	110	134	174	176	165	179	102	104
2	**71A**	110	141	174	176	142	179	95	104
2	**72A**	121	125	182	185	160	161	102	104
2	**73A**	125	125	185	191	158	191	94	104
2	**76A**	110	117	188	195	139	139	98	102
2	**77A**	132	141	174	193	139	183	98	104
2	**78A**	0	0	189	193	141	183	102	104
2	**79A**	101	125	186	197	162	191	102	104
2	**80A**	125	125	187	187	152	167	102	102
2	**81A**	117	140	174	195	139	141	98	102
2	**85A**	110	110	194	197	152	158	102	104
2	**86A**	101	125	175	183	162	167	98	102
2	**89A**	117	125	188	195	139	162	94	102
2	**90A**	125	132	175	187	162	163	102	104
2	**91A**	110	117	187	195	163	165	98	98
2	**92A**	110	125	188	190	165	165	98	102
3	**74A**	117	140	176	188	164	164	94	102
3	**75A**	110	110	189	193	188	193	94	98
6	**20A**	110	117	185	186	162	191	94	94
6	**37A**	117	123	185	193	160	160	104	108
6	**39A**	121	132	191	191	139	183	98	102
6	**42A**	110	117	190	195	139	141	98	104
7	**11A**	101	125	184	195	158	191	97	104
7	**12A**	121	134	176	182	139	163	96	100
7	**13A**	101	109	185	195	160	160	104	104
7	**14A**	117	141	187	193	163	201	96	104
7	**15A**	125	134	187	189	156	167	104	108
7	**16A**	119	127	187	189	159	201	102	104
7	**17A**	121	125	191	195	175	191	98	108
7	**18A**	125	134	174	193	152	162	102	104
7	**19A**	125	134	187	195	156	201	102	104
7	**87B**	101	121	183	191	163	203	94	102
7	**91B**	110	110	182	195	139	158	102	102
7 - 3	**88A**	117	121	187	189	163	191	98	108

Appendix 3. Table showing the microsatellite alleles (in base pairs) at each locus amplified for *S. araneus* . P1 = 'Peak one' and P2 = 'Peak two'. A zero shows that no alleles were amplified at this locus.

		LOCUS 69			LOCUS 62			LOCUS 9			LOCUS 67	
PATCH	**Individual**	**P 1**	**P 2**		**P1**	**P 2**		**P 1**	**P2**		**P1**	**P2**
9	**45A**	110	110		177	193		161	203		94	104
9	**46A**	133	143		191	195		181	191		104	104
9	**47A**	121	125		189	193		158	161		94	102
9	**49A**	117	121		183	191		163	203		98	104
9	**50A**	0	0		185	193		160	175		102	104
9	**51A**	117	121		186	200		0	0		94	98
9	**52A**	115	125		185	195		164	201		102	104
9	**53A**	107	121		182	191		152	204		98	104
9	**54A**	117	125		193	195		160	191		98	102
9	**55A**	117	125		191	193		162	201		102	104
9	**56A**	125	143		182	186		160	184		94	104
9	**61A**	125	127		176	188		162	191		102	108
9	**62A**	110	125		182	190		163	179		94	98
9	**63A**	127	142		189	189		158	162		102	108
9	**64A**	107	140		176	188		160	203		104	104
9	**65A**	112	136		182	186		158	179		98	104
10	**38A**	110	121		175	183		160	161		93	104
10	**43A**	0	0		191	191		181	183		94	102
10	**44A**	109	127		187	191		181	183		102	104
11	**21A**	117	140		185	201		158	179		94	102
11	**22A**	121	126		184	193		181	183		94	94
11	**23A**	126	141		176	191		158	203		94	102
11	**24A**	130	134		184	193		158	179		94	102
11	**25A**	130	135		191	193		158	199		94	102
11	**26Aa**	121	125		189	193		160	183		102	108
11	**26Ab**	123	125		0	0		162	203		94	94
11	**27A**	121	125		176	190		162	183		102	108
11	**29A**	110	117		183	201		141	179		94	102
11	**31A**	125	130		185	193		141	181		94	102
11	**32A**	106	126		185	195		152	181		93	104
11	**33A**	126	141		189	191		183	203		93	102
11	**34A**	126	140		189	191		158	161		94	108
11	**35A**	128	128		187	195		141	162		98	102
11	**36A**	124	134		182	185		152	161		94	108
11	**41A**	110	126		177	183		161	199		98	102
11 - 5	**28A**	121	125		177	191		152	161		102	108
11 - 9	**30A**	123	125		189	195		162	202		104	108
11 - 9	**40A**	121	125		185	189		158	160		94	102
13	**48A**	117	132		183	193		160	165		102	104
13	**59A**	125	132		190	193		139	162		94	102
13	**60A**	110	121		176	195		160	185		98	98
13	**66A**	121	125		193	201		158	160		102	102
13	**67A**	126	139		176	182		163	201		102	104

Appendix 3 cont. Table showing the microsatellite alleles (in base pairs) at each locus amplified for *S. araneus* . P1 = 'Peak one' and P2 = 'Peak two'. A zero shows that no alleles were amplified at this locus.

		LOCUS 69			LOCUS 62			LOCUS 9	
PATCH	**ndividu**	**P 1**	**P 2**		**P1**	**P 2**		**P 1**	**P2**
1	**44P**	107	124		176	185		134	140
1	**45P**	124	130		176	180		136	140
1	**94P**	107	121		174	176		136	152
1	**98P**	103	123		176	176		150	150
2	**42P**	124	130		176	182		136	138
2	**43P**	117	130		176	180		140	140
2	**46P**	103	107		183	187		136	140
2	**47P**	115	130		174	178		145	152
2	**97P**	0	0		180	180		138	140
2	**99P**	109	119		181	190		138	140
6	**16P**	109	111		178	180		124	136
6	**17P**	0	0		0	0		0	0
6	**20P**	109	130		174	178		140	140
6	**21P**	107	111		174	178		124	147
7	**13P**	117	119		176	189		137	139
7	**3LP**	107	109		0	0		137	137
7	**75P**	107	109		183	187		138	140
7	**76P**	107	109		178	180		140	142
7	**77P**	107	109		178	180		136	138
7	**79P**	109	117		178	180		136	138
7	**80P**	109	117		176	176		138	140
7	**100P**	107	109		180	182		137	139
7	**101P**	0	0		0	0		139	139

Appendix 4 Table showing the microsatellite alleles (in base pairs) at each locus amplified for *S. minutus* . P1 = 'Peak one' and P2 = 'Peak two'. A zero shows that no alleles were amplified at this locus.

		LOCUS 69			LOCUS 62			LOCUS 9	
PATCH	ndividu	P 1	P 2		P1	P 2		P 1	P2
9	24P	103	130		176	180		136	138
9	25P	103	130		176	176		136	138
9	26P	123	130		176	180		134	146
9	27P	117	132		176	180		146	152
9	28P	123	130		176	181		124	134
9	29P	103	103		176	176		138	146
9	30P	103	107		0	0		136	138
9	31*P	0	0		0	0		0	0
9	31P	0	0		0	0		0	0
9	32P	107	115		172	181		134	138
9	33P	111	130		176	176		136	138
9	34P	130	132		176	180		138	140
9	35P	107	107		166	174		137	137
9	36P	125	128		176	178		136	146
9	37P	103	103		174	180		140	146
9	38*P	0	0		0	0		0	0
9	38P	0	0		0	0		0	0
9	39P	107	130		174	180		138	140
9	41P	130	130		176	180		136	140
9	89P	107	107		176	180		136	140
11	18P	111	134		174	180		124	145
11	19P	0	0		0	0		0	0
11	22P	103	124		176	180		138	140
11	23P	123	130		174	180		138	140
11	85P	103	103		176	176		134	146
11	86P	0	0		0	0		134	140
11	92P	107	119		180	180		137	139
11	93P	0	0		176	176		136	138
12	12P	117	130		176	180		138	142
12	14P	109	130		180	180		140	146
13	91P	123	123		176	178		140	140

Appendix 4 cont.Table showing the microsatellite alleles (in base pairs) at each locus amplified for *S. minutus* . P1 = 'Peak one' and P2 = 'Peak two'. A zero shows that no alleles were amplified at this locus.