THE INVASION ECOLOGY OF COMMON WALL LIZARD (*PODARCIS MURALIS*): POPULATION DYNAMICS, INTERACTIONS AND ADAPTATIONS

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The candidate confirms that the work submitted is his own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Myself and C.H. conceived the ideas and designed methodology; I collected and analysed the data; C.Q., A.D. and C.H. provided guidance on the final Q set. I led the writing of the manuscript. All co-authors contributed critically to the drafts and gave final approval for publication.

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Abstract

The potentially damaging outcomes of species introductions to areas outside of their natural range are well known, and invasive non-native species are regarded as one of the most significant threats to biodiversity worldwide. Social perceptions of non-native species are open to subjective influence, and in a rapidly changing world the implications of species introductions are becoming less defined. Understanding the ecology of invasions and the human perceptions of them, is therefore fundamentally important for managing all stages of species introductions, relying on a multidisciplinary approach to understanding the invasion process. Invasions can also provide opportunities to study adaptive responses of organisms to novel or changing environments, which in turn can provide insight into mechanistic workings of the invasion process and range expansion. In this study I investigate the ecology of introduced populations of the Common Wall lizard (*Podarcis muralis*). Using a multidisciplinary approach including population ecology, functional ecology, predictive modelling, social science, and behavioural experiments, I focus on the species' invasion potential, adaptive responses, and implications for ecological impacts on native lizards in the UK and on Vancouver Island, British Columbia. I found that morphological differences between populations were associated with ancestral origins and infer a greater invasion potential for animals of Italian origin over French. Comparison of physical and performance traits, and a broad dietary niche of *P. muralis*, indicate considerable overlap between *P. muralis* and native lizards, suggesting high potential for competitive interaction. However, the varied behavioural responses observed towards scent cues in *P. muralis* and native lizards suggests an interplay between naivety and threat sensitivity may influence interspecific interaction. Models of predicted range expansion suggest *P. muralis* populations are likely to remain localised, but that potential for secondary translocation is likely to increase with increasing population size, particularly in urban habitats. I also found clear indication that charismatic non-native species such as *P. muralis,* may have use as model species with which to raise awareness and minimise the subjectivity shaping perceptions of invasive species in general.

Table of Contents

List of figures

List of Tables

Abbreviations

AB – Abbotsbury
BC – Bournemouth coast
BF – Bite force
BU – Bury
CMR – Capture-mark-recapture
DS – Durlstone
EA – Eastbourne
EC – *Elgaria coerulea*
FE – Felixstowe
FO –Folkestone
HH – Head height
HL – Head length
HS – Head size
HW – Head width
KW – Kingswear
LA – *Lacerta agilis*
NDVI – Normalised difference vegetation index
NLSI – Normalised land shape index
NA – Newton Abbot
NF – Newton Ferrers
PM – *Podarcis muralis*
PO – Portland
PQ – Purbeck quarries
SH – Shoreham
VI – Vancouver Island
WE – Wembdon
WW – West Worthing
ZV – *Zootoca vivipara*

Chapter 1: Alien reptile and amphibian introductions in Europe: a review

1.1 Abstract

Biological invasions are simultaneously a contributor to, and result of global change. As such, research interest into the processes driving biological invasions and the range of subsequent ecological, economic, and health impacts has greatly increased over the last 30 years. Understanding the ecology of invasions is fundamentally important for risk assessment, prevention, and management of potentially damaging species introductions; relying not only on comprehensive species data and monitoring, but also advancements in both applied and theoretical approaches that aim to explain the nature of biological invasions.

Within the literature there is disparity in the available data and current knowledge regarding species introductions across taxa - a bias that may be the result of some groups having more pronounced effects as invaders than others. This review considers the representation of reptiles and amphibians in invasion ecology research, a group for which introduction data is relatively sparse and for which ecology of introductions is poorly understood. Particular focus is given to non-native herpetofauna in Europe, and I review the existing knowledge surrounding the mechanisms implicit in driving the invasion process in this group, and the ways in which introduction of non-native herpetofauna may have impact on resident communities. Climate matching emerges as the most consistent factor determining establishment success in this group, and the diverse suite of potential impacts on native communities is comparable to better-studied taxa.

I highlight the specific nuances and research gaps associated with introductions in this group with an introductory case study of non-native lizard species established in the UK, which then forms the basis of the research presented in this thesis. I conclude by identifying current research needs and suggest that life history traits, potential for rapid adaptive response to introduction, and introduction histories make lizards ideal model species for gaining insights not only into invasion biology, but also ecological and evolutionary processes more generally.

1.2 Introduction

1.2.1 Alien species in a changing world

Economic growth and increasing transport efficiency have driven an era of globalisation, which, in turn, has shaped the origin, frequency and magnitude of species movements along introduction pathways worldwide (Hulme, 2009; 2015). The potentially damaging outcomes of species introductions to areas outside of their natural range are well known (Blackburn et al., 2014), and invasive non-native species (INNS, see Box 1) are justifiably regarded as one of the most significant threats to biodiversity worldwide (Simberloff et al., 2013). In addition to having undesirable impacts on native species through predation, genetic pollution, competition, and transmission of disease, invasions can also have significant economic and social impact by interfering with commercial crops, industrial operations, public health, and ecosystem services (Hulme et al., 2008b; Keller et al., 2011). Other authors have also highlighted the role that invasive species might play – by virtue of their generalist habits – in replacing specialist species and thus contributing to worldwide "functional homogenization" of biodiversity that could alter ecosystem functioning and productivity, as well as result in the deterioration of ecosystem goods and services (Clavel et al., 2011).

Not only are introduced species, in themselves, a significant component of human-induced global change (Ricciardi, 2007), but invasions also interact synergistically with other drivers of global change, notably land use and habitat disturbance (Dukes and Mooney, 1999), and climate (Walther et al., 2009; Bellard et al., 2013; Hulme, 2017), both of which are likely to influence the frequency and outcomes of species invasions. For instance, the differential effects of anthropogenic habitat disturbance and climate changes between invaders and resident communities can modify niche and fitness differences, thus affecting mechanisms determining species coexistence and modulating the impact of biological invasions (Valladares et al., 2015).

Box 1. Definition of terms

The term 'non-native species' (NNS) is used throughout this document and is the equivalent of 'alien species' as used by the Convention on Biological Diversity (CBD). INNS or 'Invasive non-native species' (the equivalent of 'invasive alien species' or 'IAS') are broadly defined as species whose introduction and/or spread threaten biological diversity or have other unforeseen impacts.

Not all non-native species introductions have negative outcomes, however, and emergent perspectives over negligible harmful effects and potential benefits of NNS introductions have led to advocacy for a reappraisal of the ‘native good, non-native bad’ maxim (Low, 2007; Goodenough, 2010; Davis et al., 2011; Thomas and Palmer, 2015), stimulating much debate in the research community (Simberloff et al., 2011; Vitule et al., 2012; Hulme et al., 2015; Rejmanek and Simberloff, 2017). For example, some authors have brought attention to the conservation value that can be gained from facilitative interactions between non-native and native species (Schlaepfer et al., 2011; Ward-Fear et al., 2017). And whilst some have drawn attention to a misrepresentative bias focusing on negative contexts of alien species pervading the literature and media (Warren et al., 2017; Guerin et al., 2018), others have argued that the predisposition against non-natives exists because of the exponential increase in the frequency of invasions and the far greater probability of negative impacts by non-natives than for natives (Simberloff et al., 2013; Rejmanek and Simberloff, 2017).

1.2.2 A European perspective

With increasing evidence of the impacts of biological invasions reported in the late 1990’s, recognition of invasive alien species as an emerging issue of environmental importance prompted significant policy change within the European Union to implement measures to prevent such invasions, and to effectively manage non-native species following introductions (see Hulme et al., 2008b for an historical overview of European policy and legislative commitments to non-native species; Keller et al., 2011). In Europe, the effective control of INNS has historically been hampered by the lack of (a) monitoring for alien species at frequent enough intervals in regions of concern; (b) a means to report, verify the identifications, and warn of new sightings; and (c) risk assessments that predict the likelihood of a particular species becoming invasive (Hulme et al., 2008b). To address these shortcomings a pan-European inventory of alien species was created as part of the European Commission’s DAISIE project (Delivering Alien Invasive Species Inventories for Europe). Launched in 2005, the online database provides the most comprehensive species lists and information of non-native species in Europe (www.europe-aliens.org). Contributing to and benefiting from this resource has been a wealth of research assessing risks and impacts posed by NNS across taxa: plants (Lambdon et al., 2008; Kumschick et al., 2015), fish (van der Veer and Nentwig, 2015), mammals (Nentwig et al., 2010), birds (Kumschick et al., 2013), and invertebrates (Vaes-Petignat and Nentwig, 2014; Roques et al., 2016; Smith et al., 2018). Further innovative EU-wide regulation (Regulation 1143/2014) to combat INNS came into force in January 2015, with the aim of prevention, eradication, management, and control of the most invasive and threatening species of EU concern, promising a step-change in the global response to biological invasion threats (European Parliament, 2014; Beninde et al., 2015; Genovesi et al., 2015).

There are currently more than 14,000 alien species recorded in Europe (EASIN Catalogue, https://easin.jrc.ec.europa.eu/) (Roy et al., 2019). Included on the DAISIE inventory of alien species are some 88 mammal, 2481 invertebrate, 5789 vascular plant, and 77 established bird species (DAISIE, 2009). Reptiles and amphibians have smaller numbers of recorded alien species (55 species established, see below), and information on introductions and impacts is less detailed in many cases (Kark et al., 2009). However, one amphibian and one reptile species feature on the '100 worst list' in terms of impact on biodiversity, economy and health – the American bullfrog (*Lithobates catesbeianus*) and the freshwater turtle (*Trichemys scripta*) (www.europe-aliens.org/speciesTheWorst.do). The following review aims to synthesise the available literature on non-native reptiles and amphibians in Europe with the aim of providing an overview of the current understanding about the pathways, establishment patterns, and impacts of introductions. A case study focusing on the introduction of alien lizard species that have established breeding populations in the UK is also presented, which will form the basis for the research presented in this thesis.

1.2.3 Historical pattern of amphibian and reptile introductions in Europe

In compiling information for the DAISIE project, data were sourced on 172 introduction events of 29 amphibian species (8 families) and 183 introduction events of 48 reptile species (14 families) recorded from Europe between 1900 and 2000 (Kark et al., 2009). Although likely to be greatly underestimated due to a lack of documentation, the number of introduction events and the number of species introduced throughout the 20th century show an increase towards later years (Fig 1.1).

The analysis of the available records also highlights an additional shortfall in documentation on the outcome of these introductions. More data were available on successful introduction attempts that led to established populations (159 introductions of 55 species) than on failed introductions (54 introductions of 15 species) - a bias created presumably as a consequence of successful introductions being easier to detect and more likely to be documented than unsuccessful ones. In addition, the outcome of 46 events (accounting for 23 species) was unclear, and in 96 cases (44 species) no information on the fate of the introduction was available (Kark et al., 2009). The overview provided by Kark et al. (2009), whilst making a valuable contribution to the compilation of the DAISIE itinerary at the time, also serves to illustrates how under-recorded introduction events and outcomes of introductions (past and future) can be in this group of animals.

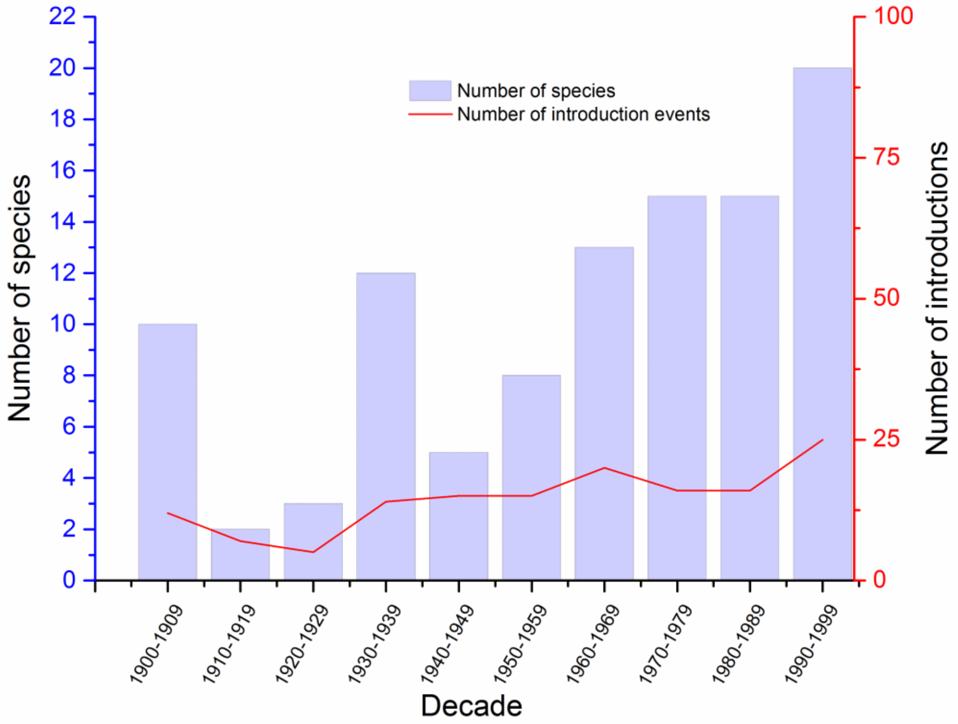


Figure 1-1 Trend in the number of documented reptile and amphibian species introduced to Europe in relation to the number of introduction events between 1900-2000 (after Kark et al., 2009)

1.2.4 Patterns of establishment and invasion

The process by which an alien species invades can be placed in a framework involving a series of four consecutive stages: transport (beyond native range limits), introduction (into the wild in a new environment), establishment (of a viable population) and finally (invasive) spread (Blackburn et al., 2011) (Fig 1.2). In each stage there are barriers that need to be overcome for a species or population to pass on to the next stage.

A central question underlying much of the research in invasion science is 'how and why do some species become established following introduction when others fail to establish self-sustaining populations?' Predicting the likelihood of introduction and potential for subsequent establishment is critical to identifying future INNS and maintaining biosecurity (Roy et al., 2014; Roy et al., 2019), and several studies have investigated the role of biogeographic (Sax, 2001; Pysek et al., 2010a; Guo et al., 2012), climatic (Walther et al., 2009; Bellard et al., 2013; Gallardo et al., 2015), species traits (Machler and Altermatt, 2012; Liu et al., 2014), and economic and demographic (as proxies for 'propagule pressure', see below) (Hulme, 2009; Pysek et al., 2010b; Gallardo, 2014) influences driving general patterns of establishment for non-native species from multiple taxa. Amphibians and reptiles have however been generally poorly represented in these models, primarily due to a lack of synthesis of documented introductions. A compendium by Kraus (2009) has since addressed this shortfall and has become a primary source of global data for researchers modelling patterns of invasion in this group (Tingley et al., 2010; Ferreira et al., 2012b; Poessel et al., 2013; Mahoney et al., 2015).

Following successful establishment, a second key question arises: 'why do some established species go on to become invasive in the resident community and cause negative impacts, whereas others seemingly coexist with native species causing no detrimental impact, or perhaps even have positive effect on native biodiversity?' In answering this, numerous individual hypothesis have been proposed – based on specific individual drivers of invasions (e.g. propagule pressure, biotic resistance, resource fluctuation, ee.g. propagule pressure, biotic resistance, resource fluctuation, enemy release hypothesis, evolution of increased competitive ability; reviewed by Catford et al., 2009) – to provide conceptual frameworks to explain, at least in part, invasion success. It is becoming increasingly clear, however, that there is no single cause of invasion, and the invasiveness of species and invasibility of communities are context dependent; varying across temporal and spatial scales, requiring a conceptual framework that synthesises the fundamental ecological and evolutionary processes involved, and the interactions and feedbacks between multiple causal factors (Gurevitch et al., 2011). To this end, emergent views suggest a move away from the metaphor of invasions based on a hierarchical linear filtering scheme (Fig 1.2), to one that embraces network thinking and explores the adaptive ecological network centred on the focal species (Hui and Richardson, 2019).

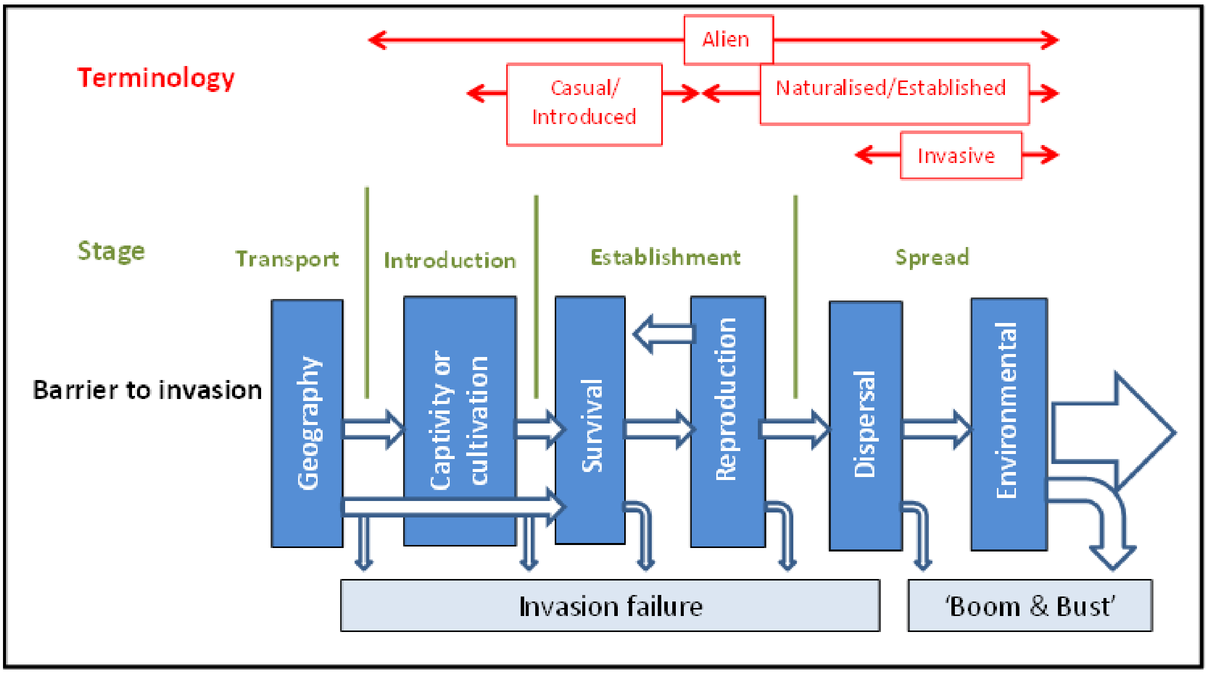


Figure 1-2 A proposed framework for biological invasions recognising that the invasion process can be divided into a series of stages, that in each stage there are barriers that need to be overcome for a species or population to pass on to the next stage, and that species can be referred to by different terms in the terminology depending on where in the invasion process they have reached. The unfilled block arrows describe the movement of species along the invasion framework with respect to the barriers (Blackburn et al., 2011).

1.2.5 Pathways to introductions

Cargo hitch-hikers, deliberate introductions for personal aesthetic pleasure, food, and plant nursery-trade hitch-hikers are important pathways for introduction of non-native reptiles and amphibians globally (Bomford et al., 2009). However the contribution of the pet trade to new introductions of amphibians and reptiles far exceeds any other recognizable pathway (Hulme et al., 2008a; Kopecky et al., 2013). The influence of the pet trade is illustrated by the 2,108 recorded introduction events (worldwide) of freshwater turtles of the family *Emydidae* – the most traded and commonly introduced reptile taxon in the world (Kopecky et al., 2013; Masin et al., 2014). Escapees and deliberate release of pets, animals intended for food, and intentional releases for fauna 'improvement' are reportedly the most common pathways for alien reptiles and amphibians in Europe (Hulme et al., 2008a). An example of the latter is the deliberate introduction of the visually striking Western green lizard (*Lacerta bilineata*) to the UK, an addition that seems not entirely unwelcome judging by this statement found on the website of a local reptile and amphibian group "It is indeed an illegal alien invader and its excessive spread should be actively discouraged. However, we can also be thankful and delight that such a magnificent member of the European herpetofauna can be found in isolated areas of the UK for us to enjoy." (www.surrey-arg.org.uk).

The role of secondary introductions, whereby non-native individuals are transported from areas where they have previously become established to un-colonised areas, is prevalent within this group in Europe (Ficetola et al., 2007; Michaelides et al., 2015). The incidence of secondary introductions is likely to be a primary factor confounding efforts to compile detailed, up to date, information on species introductions within Europe, with many deliberate introduction events potentially still going undetected.

1.2.6 Biogeography

In accordance with robust patterns in biogeography (Pianka, 1966), predictable latitudinal gradients in species richness and geographic range size have been demonstrated for established alien (naturalised) plants, mammals, and birds in temperate regions, with general declines in number of species and geographical range increases at northerly latitudes (Pysek and Richardson, 2006; Pysek et al., 2010a; Guo et al., 2012). In contrast, numbers of naturalised reptile and amphibian species in Europe have been shown to increase above 50° N latitude (Pysek et al., 2010a). There is however reasoning that this latitudinal effect seen in non-native herpetofauna is possibly confounded by the magnitude of intentional releases that are undoubtedly the primary pathway for this group (Pysek et al., 2010a). The effect of latitude is also irrevocably linked with climatic influences and, as would be expected for ectotherms, successfully introduced species have better climate matches between the areas where they have been introduced and their geographic range elsewhere in the world than do species that fail to establish (Hayes and Barry, 2008; Bomford et al., 2009). Further to this, establishment for species from temperate regions may be easier in the relatively mild climates of ~50 N°, such as the maritime climates of the UK, than the much hotter and drier regions of southern Europe (Pysek et al., 2010a). These explanations for the biogeographical pattern of non-native establishment in Europe are further supported by the fact that nearly half (46%) of the amphibians and reptiles successfully introduced have at least part of their native range in other parts of Europe, and that for most introduction events animals were not brought to non-native areas directly from their native range but rather from other European areas where they had previously been introduced (as in secondary introductions) (Kark et al., 2009).

1.2.7 Climate matching and species traits

Across models, the role of climate matching emerges as one of few consistent predictors influencing the establishment of alien reptiles and amphibians (Hayes and Barry, 2008; Bomford et al., 2009; Pysek et al., 2010b). Climatic similarity between native range and introduction locality has also been shown to have far stronger influence on establishment success compared to relatively weak effects of species specific characteristics (e.g., minimum body size at maturity, minimum clutch size, presence of free-living aquatic larval stages, and habitat breadth) in amphibians (Rago et al., 2012). However, species traits such as taxonomic position and body size (e.g., large body size is a desirable trait for species that have been intentionally introduced for food or bio-control) may underlie biases in the anthropogenic mechanisms involved in transporting amphibian species around the globe (i.e., 50% of all introduced species originate from only 5% of all families, and intentionally introduced species are of larger than average body size) (Tingley et al., 2010). In their models focusing solely on global establishment successes of non-native reptiles, Mahoney et al. (2015) found that location-level (e.g., climate matching) factors were most important in describing reptile establishment success, followed by event level (e.g., propagule pressure) and species-level (e.g., parthenogenesis, fecundity) factors, respectively. Similarly, species-level traits (native-range size, aquatic habitat use, lotic breeding habits, body size and clutch size) were found to make little contribution to rates of spread in alien amphibian and reptiles compared to richness of native congeneric species and human-assisted dispersal (Liu et al., 2014). An important point raised by Mahoney et al. (2015) is that the role of species traits in establishment success may be underestimated considering the insufficient knowledge of reptile life history within introduced ranges. When species traits are considered in isolation however, success at establishment and spread stages has been shown to be promoted by fast life history traits (i.e., small body size, large and frequent clutches, early maturity, short reproductive lifespan) in both amphibians and reptiles, demonstrating the importance of potential for rapid growth of small founder populations and subsequent invasive success (Allen et al., 2017).

1.2.8 Propagule pressure

Despite propagule pressure – which is the sum over all release events of the number of individuals released to form a population (Lockwood et al., 2005; Blackburn et al., 2015) – being reported in the literature as an important variable in establishment of alien species across taxa (Lockwood et al., 2005; Jeschke and Strayer, 2006; Hayes and Barry, 2008; Pysek et al., 2010b), a lack of recorded data on the number of release events and animal numbers has meant quantification of the influence of this parameter for establishment of alien amphibians and reptiles has proved difficult (Rago et al., 2012; Van Wilgen and Richardson, 2012; Liu et al., 2014). As such, classifying introduction attempts as intentional/unintentional – with the rational that intentional releases are most often associated with larger number of individuals released, more release events, and small scale location of the introductions – has been employed as an indirect measures of propagule pressure for both amphibians (Rago et al., 2012) and reptiles (Mahoney et al., 2015). In both cases intentional releases were found to increase the probability of establishment, although interpretation relies heavily on this mode of introduction being an appropriate surrogate for propagule size. Bomford et al. (2009) also highlighted the importance of propagule pressure influence on alien amphibian and reptile establishment. They found the number of jurisdictions into which a species was introduced was a significant predictor of the probability the species had established in at least one jurisdiction, but could only quantify the number of recipient jurisdictions to receive introductions and not numbers of released animals or numbers of independent release events (due to lack of records). Multiple introductions of the American Bullfrog (at least 25 introductions into Europe since the 1930’s and the years shortly after introductions became prohibited in 1997) and subsequent secondary translocations throughout European countries have undoubtedly contributed to the invasion of the species in Europe (Ficetola et al., 2007).

1.2.9 The role of native biodiversity

In addition to the confounding interplay between the factors already mentioned as being predictors of non-native herpetofauna establishment, the role of native biodiversity in the area of introduction has also been considered. Such studies stem from two theories first put forward by Darwin. Some studies take as their foundation Darwin’s hypothesis of ‘naturalization’, which predicts that the success of alien invaders will decrease with increasing taxonomic similarity to the native community because less closely related species are less likely to encounter direct competitors or to share natural enemies with native species. Other studies focus on Darwin’s ‘preadaptation’ hypothesis, in which shared traits between aliens and the native assemblage may preadapt aliens to their novel surroundings, thereby facilitating establishment (Darwin, 1859). For amphibians, evidence that supports the latter theory is found in analysis of successful and failed introductions of amphibian species across the globe, where the probability of successful establishment is higher when congeneric species are present at introduction locations and increases with increasing congener species richness (Tingley et al., 2011). Similar results have also been found for reptiles, leading to the conclusion that presence/richness of native congeners indicating environmental conditions appropriate for closely related non-native species outweighs potential competition for niche space in regard to establishment success (Ferreira et al., 2012a). These conclusions are perhaps unsurprising, considering the intrinsic association between environmental conditions and life history in this group of animals. And relations between establishment success and congener presence/richness can largely be regarded as a manifestation of climate matching. This connection between non-native establishment success, native species richness, and climate is illustrated in the models of Poessel et al.

(2013), where the inclusion of a climate variable (measured as potential evapotranspiration) appears to drive the relationship between native and non-native species seen in previous models.

1.2.10 Impacts in Europe

Research into the threat posed by introduced species into Europe (and globally) has, necessarily, focused attention on taxon groups having large and obvious ecological, evolutionary, economic and health impacts such as birds, mammals (Kumschick et al., 2013) freshwater invertebrates (Gallardo and Aldridge, 2015) and plants (Kumschick et al., 2015). Such high profile impacts appear relatively uncommon with regards to introductions of herpetofauna (particularly reptiles) into Europe, which is again likely to be a result of nearly half of the introduced species having at least part of their native range in other parts of the continent (Kraus, 2009). Unsurprisingly, the most pronounced impacts reported have been caused by herpetofauna introduced from outside Europe and from species introduced to islands that are home to vulnerable endemic fauna (Cadi and Joly, 2004; Moore et al., 2004a). Overall, however, the impacts of herpetofauna introductions within Europe have received little scientific attention, perhaps because perceived impacts are considered to be benign or negligible, or are subtle enough, context dependant, or so cryptic as to go unnoticed. For example, the introduction and range expansion of the Mediterranean Painted Frog, *Discoglossus pictus*, outside of its natural range in Europe has not led to a general decline in native anurans in the Catalonia region of Spain, despite similarities in morphological traits, functional guild and niche breadth with some species (Escoriza and Boix, 2012). In such cases it is theorized that there are native communities which are not species-saturated, which can therefore be invaded without apparently deleterious effects on the original pool of species – the introduction of new species therefore producing an overall increase in species richness (Escoriza et al., 2014). An overview of the negative ways in which introduced herpetofauna can impact on native biodiversity is given below.

1.2.11 Disease

The spread of disease to European amphibians is perhaps the most prominent threat caused by the introduction of non-native herpetofauna species. *Batrachochytrium dendrobatidis* (Bd) is a non-hyphal, zoosporic chytridiomycete fungus that is the causative agent of the amphibian disease chytridomycosis, and has been associated with mass mortalities of several European amphibian species (reviewed by reviewed by Duffus and Cunningham, 2010). Introductions of the American Bullfrog and African clawed frog (*Xenopus laevis*)*,* both vectors of the disease, have been implicated in the spread of Bd throughout Europe and worldwide (Weldon et al., 2004; Garner et al., 2006). In addition, the number of ranaviruses affecting amphibians, and the number of amphibian mortality events associated with ranavirus infections have greatly increased since the 1980s (Duffus and Cunningham, 2010), and although species introductions have not been directly implicated as a mechanism in this increased prevalence, evidence suggests that both *L. catesbeianus* and *X. laevis* can act as potential vectors (Robert et al., 2007; Mazzoni et al., 2009; Teacher et al., 2010). Although ranaviruses can also infect reptiles there is very little research on ranavirus pathology in wild animals. However, interclass transmission of Frog Virus 3 (FV3)-like ranavirus between ectothermic vertebrates in aquatic environments has been proven in laboratory experiments, where the red-eared slider (*Trichemys scripta elegans*) was able to transmit ranavirus to Cope's grey tree frog (*Hyla chryscocelis*) tadpoles, causing 50% mortality (Brenes et al., 2014). The potential for *T. scripta elegans* to act as a reservoir for ranavirus in invaded habitats is therefore a distinct possibility.

1.2.12 Competition and predation

There are very few examples in the literature of direct competition and predation from non-native herpetofuana having significant impact on native European species populations. Although the American Bullfrog is a voracious predator of a variety of prey across taxa (Détaint and Coïc, 2001), to the best of my knowledge there has been no quantification of the impacts of predation on European native fauna. On the island of Mallorca the once widespread Midwife toad (*Alytes muletensis*) has suffered population declines that have been attributed to predation from the viperine snake (*Natrix maura*) (Moore et al., 2004b). The introduction of *N. maura* also appears to have impacted on the endemic snake *N. natrix* *cetti* on the island of Sardinia. Here, the introduced species is now widespread and abundant whereas the endemic species is extremely rare and confined to a handful of sites from which the other competitor is generally absent. Evidence also suggests that the growth of the endemic snake is suppressed in the presence of its competitor (Luiselli, 2006). European pond turtles (*Emys orbicularis*) have been shown to suffer fitness costs (i.e., weight loss) and higher mortality when kept in mixed groups with introduced *T. scripta elegans* (Cadi and Joly, 2004). And although attributing these outcomes directly to competitive dominance of the latter is speculative, *T. scripta elegans* has shown to be able to out-compete the native turtle in exploiting preferred basking sites (Cadi and Joly, 2003).

1.2.13 Genetic pollution

Owing to the patterns of introduced species establishment within Europe described earlier, the risk of introduced species hybridising with closely related native species is arguably the most pressing threat posed by these introductions. Interbreeding between the great crested newt (*Triturus cristatus*) and introduced populations of the Italian crest newt (*T. carnifex*) are well documented, and asymmetric introgression of *T. cristatus* mitochondrial DNA into *T. carnifex* suggests displacement through hybridization of *T. cristatus* by *T. carnifex* can occur at least on a localised scale (Brede, 2015; Meilink et al., 2015). The potential for introduced water frog *Pelophylax ridibunda* to dramatically affect the viability and maintenance of hybrid water frog populations (*Pelophylax esculentus* complex) native to Western and Central Europe has also received attention, although likelihood of species replacement and severity of impacts appear to vary geographically (Holsbeek and Jooris, 2010; Leuenberger et al., 2014). Similarly, genetic consequences and the loss of genetic integrity in native populations of Common wall lizard (*Podarcis muralis*) have arisen following intraspecific hybridization with introductions of non-native conspecifics in Germany (Schulte et al., 2012a; Schulte et al., 2012c).

1.3 Case study: Alien lizards in the UK

Two lizard species have been introduced to the UK from their natural range in continental Europe, the Wall lizard (*Podarcis muralis*) and the Western green lizard (*Lacerta bilineata*). Multiple populations of *P. muralis* (currently 31 known) have become established, primarily on the South Coast, following numerous introduction events and subsequent secondary translocations to disused quarries, cliff side areas, and private gardens (Michaelides et al., 2015) within the UK since the 1920's (Foster, 2015) (Fig 1.3). Currently only one population of *L. bilineata* is known from cliff tops in Bournemouth, Dorset – established since at least the early 1990's (Deichsel et al., 2007). The establishment of both these lizard species to the UK, which now represents the northernmost extent of their distribution, raises interesting questions about the outcome of these introductions. Such questions naturally fall into four areas of investigation: the population ecology of the non-native species; interactions with native reptiles (particularly Common lizard, *Zootoca vivipara*, and Sand lizard, *Lacerta agilis*) and other fauna; factors influencing the persistence/spread of these populations; and evolutionary implications for the introduced species at the northern limits of their range. Rather surprisingly, considering the length of time for which these species have been present in the UK, these questions have received little attention. The following is a synthesis of pertinent research work carried out to date.

1.3.1 *Podarcis muralis*

Podarcis muralis has successfully colonized regions in north-western Europe outside of its native range which covers most of Western and Southern Europe. In Central Europe human mediated introductions have resulted in more than 150 self-sustaining populations that can be assigned to eight geographically distinct evolutionary lineages (Schulte et al., 2012c). Due to this distribution pattern the majority of research regarding introduced populations of *P. muralis* has focused on the genetic consequences of introductions and the loss of genetic integrity through intraspecific hybridization with native conspecifics (Schulte et al., 2012a; Schulte et al., 2012c). Where clades have mixed following introductions, rapid genetic assimilation of native populations by strong introgression from introduced lineages can occur, as exemplified in Germany by the dominance of Italian lineage haplotypes over native *P. muralis* populations (Schulte et al., 2012c). Experimental and genetic evidence suggests that divergence in male sexual characters (i.e., ventral and dorsal colouration, head length, bite force, testes mass) between lineages promotes strong asymmetries in male contest and mating success, thus resulting in the asymmetric hybridisation and rapid introgression observed in contact zones arising from introductions (While et al., 2015a). There are no native species that can hybridise with *P. muralis* in the UK. However, the introduced *P. muralis* populations have been shown to have origins from multiple locations within the native range, with representatives from five geographically distinct clades (Michaelides et al., 2015). The human introduction of these populations has thus facilitated opportunities for hybridization between genetically and phenotypically distinct lineages which may have important consequences for the success and long-term viability of these UK populations (Michaelides et al., 2013).

1.3.2 *Lacerta bilineata*

This species is native to parts of Western Europe, including Jersey, Channel Islands. Reports of deliberate introduction attempts to the UK date back as early as 1872, although the only currently known established population was not formally discovered until 2002 (Gleed-Owen, 2015). The UK population is reported to have increased considerably in the years since the introduction and available information is still sparse regarding any impacts the species may be having (Beebee et al., 2005; Mole, 2010).

1.3.3 Direct impacts of introduction

Despite there being sound rationale for suspecting that *P. muralis* may affect native species negatively through competition or interference (i.e., high density, niche overlap with native species, high fecundity)(i.e., high density, niche overlap with native species, high fecundity i.e., high density, niche overlap with native species, high fecundity Foster, 2015), evidence for impacts of *P. muralis* on native species (reptile and non-reptile) is scarce. Suspected declines in native lizards following introductions of *P. muralis* have been reported in the literature, primarily concerning case studies of introductions in Germany (Münch, 2001; Kühnis and Schmocker, 2008; Schulte et al., 2008; Schulte, 2009). In all cases, supporting evidence for the introduction of *P. muralis* as the cause of declines to native lizards is lacking, and the influence of other factors on native species (e.g., habitat loss, impact of introduced predators) must be considered. A 75% decline in the native *Z. vivpara* and increases of 40% and 36% for *P. muralis* and *L. bilineata* respectively at a single site in Bournemouth, UK, has been observed for the period 2002 – 2007 (Mole, 2010). Again, there is no evidence attributing the decline in *Z. vivipara* directly to the presence of the introduced lizards, although observations of the native species now being found primarily at the periphery of the site (Mole, 2010) is persuasive of a negative impact from the non-natives. Conversely, Heym et al. (2013) found no shift in habitat use or thermoregulatory behaviour of Sand lizard in the presence of introduced Wall lizards at a site in Germany.

Even less is known about the potential impacts of introduced *L. bilineata* on native fauna. Research may be limited because there is currently only a single known population in the UK, and that co-occurrence with many other species native to southern Britain is a natural scenario in neighbouring parts of Europe (Gleed-Owen, 2015). Nevertheless, the potential competition risk from both *P. muralis* and *L. bilineata* to native reptiles, particularly to *L. agilis* (one of the UK's rarest reptiles), should they continue to extend their UK range, is a concern highlighted in recent risk assessments for the GB Non-Native Species Secretariat (Foster, 2015; Gleed-Owen, 2015).

1.3.4 Range expansion

The spread of both these non-native lizard species in the UK by natural dispersal is considered to be slow, with range expansion taking place along linear features (cliff sides, verges) and being limited by fragmentation of suitable habitat and climatic suitability, thus neither species is regarded as truly invasive and wider impacts are considered to be minimal (Foster, 2015; Gleed-Owen, 2015). Recent work however, has shown that a rapid adaptive response to cool climates (compared to native range), in the form of embryo retention and faster developmental rate, confers survival benefits for offspring in the introduced UK *P. muralis* population (While et al., 2015b). This response could, theoretically, enable expansion into other areas of the UK over the long term.

Figure 1-3 Distribution of known breeding populations of *Podarcis muralis* in the UK. Map inset shows native range (red) in Europe.

1.4 Conclusions, future directions

European legislation on non-native species requires that the existing/potential risks from species introductions are fully assessed in order that preventative measures and management operations can be appropriated accordingly. Owing to the geographic patterns of reptile and amphibian introductions in Europe outlined above, this means undertaking an objective (and current) evaluation of the ecological implications of introductions, regardless of how similar the ecological scenarios may be at the region of introduction with the non-native's natural range (i.e., species occurring together naturally in other parts of their range), and time since establishment. The scenario of the Wall lizard and Western green lizard in the UK is a good case in point. Although considered to have low 'invasive' capacity and minimal impact on native lizards (due to isolated populations and natural sympatry with native UK species elsewhere in Europe), these assertions have not been quantified and are lacking in rudimentary baseline data in the time since introduction. Furthermore, the current assessments for these species give little consideration to impacts at a community level, and as such indirect effects on congeners and other species of conservation importance, such as endangered invertebrates may be less obvious. In addition, although their range expansion may be limited, the human mediated introduction of these species to sites of conservation value such as disused quarries could undermine the quality of such sites depending on the community level effects they may have. Where non-native species have been present for a long time, with no immediately obvious negative ecological impacts (as with *P. muralis* in UK), there is the potential for long term impacts, or sudden shifts in invasive capacity to go unnoticed. This is particularly true for herpetofauna which are generally a poorly surveyed/monitored group. There is therefore a need for an improved evidence base for risk assessment of herpetofauna introductions that is case specific, utilises standardised population monitoring, and also considers impacts at a wider ecological level.

The introduction of species to regions beyond their natural range provides opportunity for research into evolutionary adaptations in response to novel environmental conditions at limits of natural tolerance. In lizards, such responses can occur rapidly, as seen with adaptive response in reproduction phenology of Wall lizards introduced to cooler northern regions at the limits of their climate tolerance (While et al., 2015b). Such adaptive responses in reptiles and amphibians, coupled with climate change scenarios, could influence the invasion process in the long term, and facilitate range expansion and negative impacts on native species that are not currently realised. Predictive modelling of habitat availability and microhabitat use, coupled with improved knowledge of species traits and adaptive responses will be useful in forecasting future changes in the invasion process and management options.

The presence of an analogous introduced population of *P. muralis* on the Saanich peninsula of Vancouver Island, British Columbia – firmly established and spreading since the release of 12 individuals in 1970 (Bertram, 2004) – provides a rare opportunity for investigating intercontinental variation in this model system through comparative study. Such a study may yield important insights into how invasive performance and adaptive responses may vary with geographical context in a single model species.

It is clear that there is a need for greater representation of reptiles and amphibians in regard to studies of invasion ecology. This need is not only because data on this group is lacking compared to other taxa, but also because the life histories of reptiles and amphibians and their capacity for adaptive response to novel environmental conditions outside of native ranges makes them model species for gaining insight into biogeographical, ecological and evolutionary responses of species to a changing world.

1.5 Thesis outline

In this thesis I aim to make a comprehensive investigation into the ecology of introduced populations of *Podarcis muralis* in the UK and the introduced population on Vancouver Island, British Columbia, with focus on invasive potential, adaptive responses, and implications for ecological impacts on native lizards. A broader aim of this work is that it serves as a detailed case study in which the findings regarding ecological ramifications and societal perceptions of the introduction contribute to our wider understanding of the invasion process and emergent attitudes towards non-native species against the backdrop global change.

Demographic processes are central to invasion outcomes and play into all of its components; population increase, local dominance and range expansion. In Chapter 2, I assess the status of UK populations through capture-mark-recapture data, and compare aspects of population and individual fitness that may indicate invasive potential of introduced populations – namely microhabitat use, body size, body condition, predation pressure, and parasite load.

Chapter 3 focuses on the spatial aspects of the species' introduction in the UK. Since long distance jump dispersal via translocation is important in facilitating spread of this species, I seek to predict the national extent of the area potentially available for further colonisation by running species distribution models (SDM) based on climatic suitability at these northern extremes. To make predictions of population growth and identify environmental and landscape features important to future range expansion at a local level, I combine SDMs with a high resolution (15x15 m) spatiotemporal individual based model (IBM) simulating local population dynamics and spatial patterns of spread.

In Chapter 4 I explore the possibility of rapid adaptive morphological and functional responses of introduced populations of *P. muralis* through analysis of population divergence in body size, head dimensions, bite force and diet. Secondly, I consider how these traits compare with those of native lizards with which *P. muralis* may be in direct/indirect contest and the implications for niche overlap, interaction outcomes, and invasion success.

Chapter 5 builds on the theme of competitive interactions and takes a closer look at the potential for, and likely outcome of, competitive interaction between introduced *P. muralis* and native lizards from the UK and Vancouver Island. For this, I take an experimental approach to measuring recognition and subsequent behavioural responses of lizards to interspecific scent cues.

In recognising the importance of human elements to this particular model of invasion by a charismatic and appealing non-native species, Chapter 6 investigates emerging opinions and perceptions about the presence of *P. murails* in the UK. Through novel application of the Q method for qualitative and semi-quantitative analysis of discourse, I explore subjectivity in stakeholder opinion and perceptions, and discuss the implications of these in relation to invasion success and species management.

The results of preceding chapters are discussed in Chapter 7, along with identification of areas for further research. Key findings are synthesised in regard to the case specific implications of the invasion potential of *P. muralis,* and discussed in relation to existing theoretical and applied research of the invasion process.

Chapter 2: Population and individual fitness as indicators of invasion potential in multiple populations of non-native wall lizards (*Podarcis muralis*)

2.1 Abstract

Key to the management of biological invasions is the assessment of an invading species' potential for progression from introduction to establishment to invasion. Heterogeneity within the introduced range as well as variation in the nature of the introductions (timing, source, propagule pressure) create spatial and temporal variation in invasion dynamics, while population lags can mask the true potential for invasion success and subsequent impacts, and should be a consideration when making management decisions.

I studied several measures of individual fitness, namely body condition, hemoparasite prevalence, and tail damage, in 12 established populations of the common wall lizards, *Podarcis muralis* (Laurenti, 1768), introduced to southern England and Vancouver Island, British Columbia. As introduction history, habitat occupied, and native origins differ between populations, I hypothesised that aspects of morphology and fitness may therefore also vary between populations, thus influencing invasive potential.

Capture-mark-recapture (CMR) methods used to estimate population sizes indicated densities generally lower than those reported for native and introduced populations in the literature. Lineage was a significant factor for variation in body size, with male and female lizards of Italian origin being 4.5% and 4% larger than counterparts of French lineage, respectively. Differences in body condition were site specific, with little effect of habitat type or lineage. Tail damage was more prevalent in lizards inhabiting urban sites than those from more rural habitats. I found hemogregarine infection in only one of nine populations screened (prevalence 54%). Intensity of infection was low compared to data in the literature with no detectable effect on body condition.

Estimates of low wall lizard density compared to densities elsewhere suggest UK populations, although established for >40 years in some cases, may be exhibiting a lag phase in population growth post-introduction. Furthermore, significant variation in aspects of individual fitness between populations may influence the dynamics of their invasion potential making some populations more 'high risk' than others for transition to invasion. These findings, in addition to the effectiveness of capture methods and high levels of recapture during CMR, provide the first indication that targeted eradication/control may be feasible at some UK sites and that decisions to initiate such efforts need to consider the possibility of acting prior to a potentially abrupt breakthrough in apparent lag phase.

2.2 Introduction

European legislation on non-native species requires that the existing and potential risks from species introductions are fully assessed in order that preventative measures and management operations can be appropriated accordingly (European Parliament, 2014 Regulation (EU) No 1143 Regulation (EU) No 1143). This means undertaking an objective (and current) evaluation of the ecological implications, range expansion and invasive status of introductions, regardless of species origins and time since establishment. Central to making such evaluation is an understanding of the biological principles that form the basis of frameworks modelling the invasion process (Facon et al., 2006; Hulme et al., 2008a; Blackburn et al., 2014).

A fundamental aspect of managing the impact of biological invasions is assessment of the invading species' potential for progression through the invasion model framework from first introduction to establishment success, culminating in an invasive status where negative ecological, economical, and/or social impacts are measurable (Kumschick and Richardson, 2013; Dick et al., 2017). Driving the dynamics of this invasion process are the performance, physiology, demography, and biological fitness of the invading species (van Kleunen et al., 2010), which in turn are influenced by the biotic and abiotic characteristics of the novel space to which the species is introduced and capacity for adaptive responses (Davidson et al., 2011). Spatial and temporal variation in invasion process dynamics are therefore inherent following introductions and lags in population growth, range expansion, and impacts can mask the true nature and future outcomes of invasions confounding management decisions (Blackburn et al., 2015).

Theory for explaining why some species introductions become invasive is commonly based on assumptions that introduced populations perform better (compared to in the native range) in some aspect of their ecology by virtue of responses to altered ecological and evolutionary pressures of the invaded environment (reviewed by reviewed by Parker et al., 2013). Increases in organism size (Campbell and Echternacht, 2003; Meyer and Dierking, 2011), fecundity (Taniguchi et al., 2017), and abundance (Lopez-Torres et al., 2012; Licata et al., 2019) have all been considered as indicators for whether novel conditions in the new range are imparting benefits to population fitness. Such enhancement to performance is often regarded as evidence for the enemy release hypothesis, in which introduced species are distanced from pressures of predation (Wilson et al., 2018) and parasites (Torchin et al., 2003; Dunn, 2009) encountered in their native ranges (see review by Colautti et al., 2004).

Population fitness (increase) is a function of the lifetime reproductive contribution of individuals (their realised fitness) within the population, which is in turn determined by their genotype, phenotype, and the environments they experience, including interactions with conspecifics and other species (Coulson et al., 2006; Edelaar and Bolnick, 2019). Since resources are not equally distributed across space and time, the microhabitat an animal occupies thus has profound impacts on its growth, survival, reproduction, and, ultimately, fitness (Paterson and Blouin-Demers, 2018). For example, habitat use by ectotherms is often primarily influenced by specific thermal requirements of the species and opportunities for thermal regulation (Adolph, 1990; Harvey and Weatherhead, 2010). For diurnal species this involves selection of habitat that offers thermal heterogeneity that can be exploited using a suite of behavioural mechanisms such as varying activity time, shuttling between sun and shade, and adjusting posture and perch types (Huey, 1991). However, habitat use can also be influenced by biotic determinants such as inter- and intraspecific competition, and predator avoidance (Downes and Shine, 1998; Shah et al., 2004), creating conflicting priorities for habitat selection that can significantly affect individual fitness (Amo et al., 2007b).

Body condition is tightly linked to fitness and represents an individual’s physical or nutritional status as a marker of general health (Labocha et al., 2014). A decrease in body condition may therefore have important consequences for short- and long-term fitness of individuals and survival. For example, the loss of condition could lead to a decrease in the ability to mount an immune response to infection from parasites, reduced physical performance and capability to deal with environmental pressures, and a compromised reproductive output (Amo et al., 2006b; 2007a; Lazic et al., 2017).

The capacity for introduced populations to grow and become invasive is thus ultimately determined by the ability of individuals to exploit resources and maximise fitness against the environmental conditions and species interactions encountered at introduction sites. Successful establishment can be achieved through individual-level processes of phenotypic change, selection of optimal microhabitat conditions available, and adjustment of the environment to suit individual needs (Edelaar and Bolnick, 2019). In this regard, invasion success is often associated with species being habitat generalists with a degree of preadaptation to a variety of habitats and tolerance to disturbance (Marvier et al., 2004).

In this study, I investigate aspects of individual and population fitness in introduced populations of the common wall lizard (*Podarcis muralis*) in the UK and on Vancouver Island, British Columbia, in order to assess current population status and inform predictions of invasive potential. With variation in time since establishment, origin, habitat at introduction site, propagule size and secondary introductions, there is potential for multiple geographically isolated introduced *P. muralis* populations to vary in their invasion potential. Furthermore, with representatives from five geographically distinct clades (Michaelides et al., 2015), the human introduction of these populations has facilitated opportunities for hybridization between genetically and phenotypically distinct lineages which may have important consequences for the long-term viability and invasive potential of these UK populations (Michaelides et al., 2013).

2.3 Methods

Locations of known UK *P. muralis* populations have been documented by Surrey Amphibian and Reptile Group (http://www.surrey-arg.org.uk). This resource served as a primary guide to identifying survey sites for the present study. Information on population introduction history and lineage have been detailed by Michaelides et al. (2015). Lizard population data were collected from as many sites as possible with focus directed to sites based on accessibility, survey logistics, and population size following initial surveys. Surveys were undertaken between 07.30 and 18.00 on dry, warm, sunny days as considered best practice for reptile surveys (Gent and Gibson, 1998). Sites were walked by 1-4 surveyors searching suitable habitat paying particular attention to likely basking spots which provide greatest opportunity to locate lizards for capture. Lizards were caught by noose or by hand. Upon capture, morphometric data were collected in the form of snout to vent length (SVL), tail length (TL), tail regeneration (TR). All variables were measured to 0.1 mm using digital vernier callipers. Body mass was weighed to 0.5 g using a 60 g Persola spring balance. Sex was determined primarily by examination of the vent and the presence of an enlarged hemipenal bulge and enlarged femoral pores (males).

Morphometric data were obtained from a total of 652 *P. muralis* across 12 introduced populations in the UK (n= 548), the introduced population on Vancouver Island from locations around the Fairfield district of Victoria (n= 79), and a native population from Saulnay, France (n= 25) (Table 2.1) (Fig 2.1). UK populations were sampled between May-August from 2016-2018; the Saulnay population in August 2017; and the Vancouver Island population in July 2018.

Body condition - Measures of body condition were analysed for males alone (n = 365), since females were caught at various stages of gravidity throughout the study period. As a measure of body condition, I used a scaled mass index (SMI) as proposed by Peig and Green (2009) as the most reliable and unbiased measure. SMI standardises body mass for a predefined value of body size according to the equation $SMI = Mi(\frac{L0}{Li})^{bSMA}$, where Mi is the body mass of ith individual; Li body size of ith individual; L0 is an arbitrary, predefined value of body size; bSMA is the scaling exponent calculated by a standardised regression axis (SMA) of log-transformed body mass on log body size; and SMI is the predicted value of body mass for the individual for L0 standardised body size. The arithmetic mean of SVL of the male sample was taken as L0, (60.5 mm). Where individuals possessed incomplete tails at the time of capture, estimates of predicted mass from the regression of mass on total length based on individuals with complete tails were used. Variances in mean values were analysed with nested ANOVAs (site nested in lineage, habitat type) applying Satterthwaite approximation for unequal sample sizes.

Population estimates - Five sites were considered suitable for obtaining estimates of population size using CMR methods due to the manageable size and naturally defined boundaries of the survey areas. A total of ~30 h survey effort (between two surveyors) over a minimum of three CMR sessions were conducted at each site in dry, sunny conditions between 07.30 and 19.00 when lizards were known to be active. On three occasions CMR sessions were conducted twice in the same day, allowing for a minimum of two hours between capture sessions. Attempts were made to capture by noose or hand all lizards encountered (unless previously marked), and all caught lizards were retained in a large, well ventilated container for morphometric data collection, and marked on the head with a black chevron using waterproof marker prior to being released to location of capture at the end of the session. Where there was a period of several days between subsequent CMR sessions at a particular site, and temporary marking of the head was likely to have been lost, recaptures were confirmed by cross referencing caught individuals with morphometric measurements and the record of unique pattern in blue ventral scales. The CMR data were subsequently analysed using Begon’s weighted mean estimator of population size (Begon, 1979), after careful consideration that all assumptions of the model had been met, namely that the population is geographically and demographically closed for the duration of the study, and that all individuals are equally likely to be caught.

Habitat use - I sampled lizard microhabitat use at nine introduced UK populations. Data from 20 microhabitat variables within a 1 m radius of the point where lizards were first seen were collected as detailed in Table 2.2. To establish whether lizard microhabitat use was non-random, data were also collected from random points that simulated lizard sightings. Since habitat structure (e.g., vertical surfaces, raised perches) is important to *P. muralis,* random points were generated by releasing a half inflated, untied balloon from the location of the previous genuine lizards sighting.

Taking the location of first impact of the deflated balloon as a simulated lizard sighting ensured structural features could be accounted for and habitat data collected accordingly. All random points were generated at least 1m away from release point.

Microhabitat use data at each site were explored by principal component (PC) analysis to reduce the habitat variables into a smaller number of components that describe underlying trends in the data. All continuous variables were Log 10 (×+1) transformed and those data recorded as a percentage Arc(Sine) square root transformed prior to analysis. Factors with an eigenvalue >1 and that accounted for over 10% of communal variance were considered significant and used in further analysis. Within factors, correlations of variables with loading values > 0.4 were considered significant (Pernetta et al., 2005; Ross et al., 2008). Variation between mean factor scores for lizard locations and random points were then tested with MANOVA.

Parasitology - For this study 108 *P. muralis* were collected at nine different populations in June 2017; Purbeck quarries (Seacombe and Winspit) (n =19), Portland quarry (Cheyne Wear) (n =10), Abbotsbury (n = 5), Bournemouth (n = 13), Shoreham Beach (n = 13), Eastbourne (n = 13), Newton Ferrers (n = 8), West Worthing (n = 11) and Vancouver Island (n = 16), in July 2018 (Table 2.1).

Thick and thin blood smears were made directly after euthanasia (pithing and decapitation) following anaesthesia with 25% Benzocaine gel via oral administration. Currently accepted best practice for euthanasia of small lizards involves either straight blunt force trauma to cranium, decapitation and/or pithing without prior anaesthesia (Leary, 2013). Recent discussions within the community have recommended the efficiency of Benzocaine as a general anaesthetic for small reptiles and amphibians (G. Hanke pers comms.). As such, its use prior to existing methods exceeds protocols previously considered humane for dispatching small lizards.

Smears were prepared in the same slide for each individual and labelled accordingly, air-dried, and fixed for 3 minutes in absolute Methanol (Sigma-Aldrich) within four hours of collection. Fixed slides were stained in the laboratory with 15 min immersion in Giemsa Stain Modified Solution (Sigma-Aldrich) diluted 1:9 with Sorensen's Buffer Solution and left to air-dry for 24 hours. Slides were examined under 1000x microscope magnification with addition of immersion oil. The blood smears were scanned for blood parasites, both intracellular and extracellular, and where present, were counted using the Miller disc method commonly used for counting reticulocytes in clinical haematology studies. The disk is a reticle that is placed in one ocular of the microscope and is engraved with a small square B surrounded by a large square A, the area of which is nine times that of the small square (Nazi, 1986). The infection status of each individual was recorded. For infected individuals, intensity of infection (% blood cells parasitized) was measured by quantifying the percentage of blood cells that were parasitized. This was quantified by searching for a field on the smear were the RBC's were not touching each other and there were between 3-11 cells in square A on the Millar disk, then counting all the hemoparasites present in square A and the number of RBC's present in square B. This procedure was repeated until the total cumulative count of RBC's in square B reached 111. By enumerating the red cells in square B while counting the reticulocytes in the entire area of square A, the percentage of reticulocytes can be determined. Thus, when a total of 111 red cells have been counted in the small square B, the actual percentage of reticulocytes is based on 1,000 red blood cells (Nazi, 1986). I then applied the formula:

$$\%\ hemoparasites = \frac{total\ hemoparasites\ counted\ square\ A}{111*9} * 100\ .$$

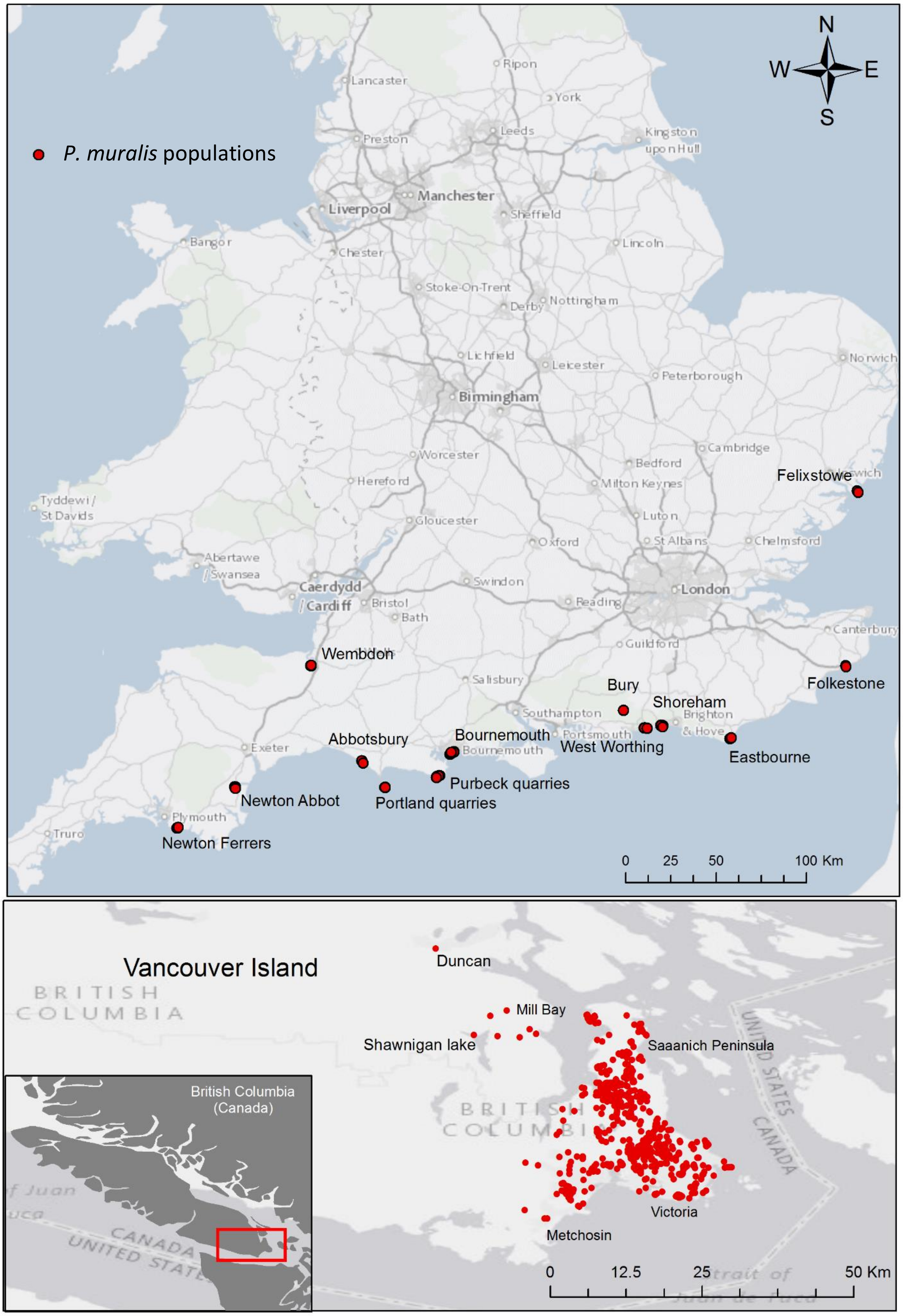


Figure 2-1 Location of introduced *P. muralis* study populations in southern England and confirmed records on Vancouver Island, Canada (data courtesy of G. Hanke)

Table 2-1 Summary of wall lizard survey sites May-August 2016-2017. *Sites where CMR was carried out in 2016

Site	Male	Female	Lineage	Site description
Folkestone* (51.52 °N, 1.12 °E)	7	28	Italian	Campsite situated below chalk cliffs surrounded by broadleaved woodland, scrub and calcareous grassland
Eastbourne (50.45 °N, 0.16 °E)	36	23	Italian	Shrub boarders and scrub between paved walkways and beach front promenade
Shoreham (50.49 °N, 0.15 °W)	41	20	Italian	Vegetated shingle beach and adjacent residential properties
Bury* (50.54 °N, 0.33 °W)	14	23	French	Residential buildings and old walls within a rural village surrounded by calcareous grassland, woodland and scrub
Purbeck* (50.35 °N, 2.02°W)	49	26	Italian	Disused coastal quarries surrounded by lowland calcareous grassland and scrub
Portland* (50.31 °N, 2.26 °W)	43	26	French	Disused coastal quarries surrounded by scrubland
Abbotsbury* (50.39 °N, 2.37 °W)	21	29	Italian	Walls and vegetated boarders within exotically planted sub-tropical gardens. Surrounded by calcareous grassland and broadleaved woodland
Wembdon (51.81 °N, 3.22 °W)	29	22	French	Walls and buildings throughout village on the outskirts of urban area. Surrounded by arable land and urban habitat
West Worthing (50.49 °N, 0.23 °W)	19	24	Italian	Railway station and disused sidings and adjacent allotment. Surrounded by heavily urbanised habitat.
Bournemouth (50.42 °N, 1.54 °W)	19	18	Italian	Cliff side scrub and zig zag walkways. Bordered by beach front and urban habitat
Newton Ferrers (50.18 °N, 4.21 °W)	12	10	Italian	Private gardens surrounded by arable land and woodland
Felixstowe (51.57 °N, 1.21 °E)	4	5	Italian	Public cliff side rockery garden and scrub. Bordered by beach front and urban habitat
Saulnay, France (46.86 °N, 1.26 °E)	11	14	French	Rural cemetery surrounded by arable land
Vancouver Island (48.24 °N, -123.20 °E)	59	20	Italian	Mix of rocky scrubland and residential gardens
Total	365	288		

Table 2-2 Summary of habitat variables recorded at lizard locations and random points, recording methods and equipment used.

Variable	Method	Equipment
Substrate type	Visual assessment of % type within 1m radius e.g. soil, rock, man-made	N/A
Ground cover	Visual assessment of % type covering substrate e.g. leaf litter, ground vegetation < 1m high, bare soil	N/A
Shade	Visual assessment of % shade covering substrate	N/A
Vegetation height	Average height of prevailing vegetation measured within 1 m radius of sighting	Measuring tape
Ambient temperature and humidity	Recorded 1 m above ground level at point location	Combined thermometer/hygrometer accurate to ±1˚C
Substrate temperature	Recorded at point of lizard sighting/ random points	Infrared thermometer accurate to ±1˚C
Distance to nearest refuge	Measured distance (mm) from point of sighting to nearest feature for retreat that offers full concealment e.g. hole, crevice, under rock, dense vegetation	Measuring tape
Frequency and type of refugia	Visual count of all refugia within 25 cm radius classified into types e.g. under rock, hole, man-made etc.	N/A
Perch type & orientation	Visual assessment of substrate on which lizard was seen and vertical/horizontal positioning of the lizard	N/A

2.4 Results

2.4.1 Population Estimates

Population estimates were calculated for five sites: Dancing Ledge (Purbeck) and Cheyne Wear (Portland) quarries, Abbotsbury, Bury, and Folkestone. Population estimates and approximate survey area are summarised in Table 2.3. The density estimates are generally lower than those reported elsewhere in the literature (Fig 2.2).

Table 2-3 Summary of mean (± standard error) population size and density per hectare estimates for *Podarcis muralis* at five UK sites.

Site	Population estimate ± SE	Survey area (ha)	Estimated lizard density per ha
Purbeck	144 ± 23	0.60	237
Portland	103 ± 22	0.81	126
Abbotsbury	50 ± 9	0.40	122
Bury	31 ± 13	0.07	416
Folkestone	47 ± 14	0.22	212

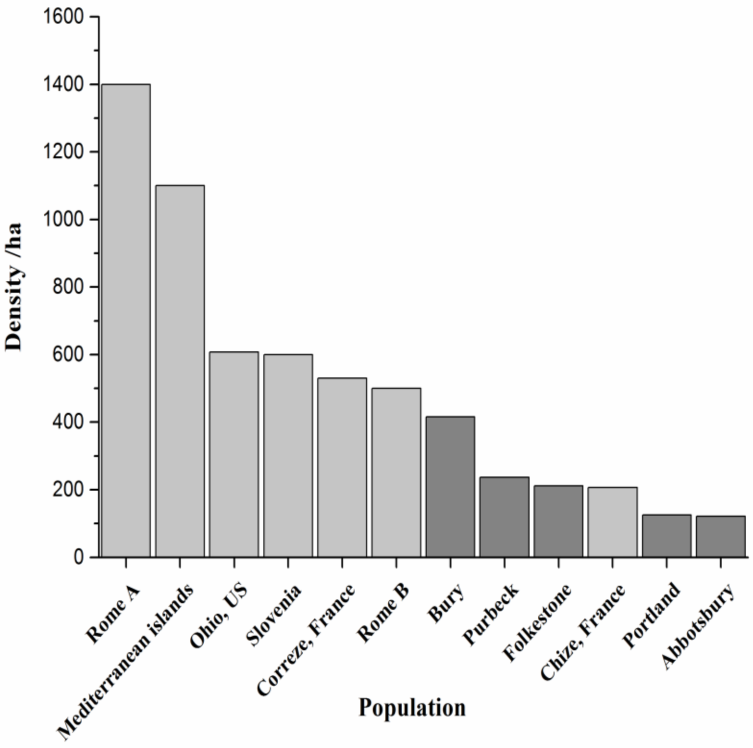


Figure 2-2 Comparison of *Podarcis muralis* density estimates from this study (dark grey) vs literature (Mediterranean islands, Chize, Correze cited Barbault and Mou (1988); Rome A/B, Gracceva et al. (2008); Ohio, Kwiat and Gist (1987); Slovenia, Vogrin (1998).

2.4.2 Microhabitat use

PC analysis and results of tests for variation in means, were carried out for habitat data collected from wall lizard locations (n = 285) and random points (n = 199) from nine UK *P. muralis* populations (separate analysis for each population can be found in Appendix 2.1).

Analysis of 23 habitat variables for lizard locations alone produced three significant factors, cumulatively accounting for 74.1% of variance within the data. Mean scores differed significantly between sites for all three PC's (PC1, $F_{8,276} = 169.83$, $p < 0.001$; PC2, $F_{8,276} = 9.60$, $p < 0.001$; PC3, $F_{8,276} = 11.09$, $p < 0.001$). As such, populations clustered into three distinct groups along the PC 1 (x) and PC 2 (y) axes, which broadly describe prevailing habitat as; quarry sites (Portland, Purbeck), urban/semi-urban (Shoreham, Bury, Wembdon, Folkestone, Worthing), and cultivated/ornamental gardens (Eastbourne, Abbotsbury) (Fig 2.3).

Prominent variables in PC1 describe a gradient from negative loadings of exposed natural stone features (i.e., stone substrate, open rocky ground cover, under rock refugia), and ground level (horizontal) perches, towards positive loadings describing more structured, vegetated microhabitats (i.e., increasing leaf litter, vegetative ground cover, increased vegetation height and shade, vegetation refugia) and man-made features. The PC2 axis then makes distinction between microhabitats that feature soil substrate, leaf litter and areas of vegetation typical of cultivated gardens, from those featuring more man-made surfaces and structure. PC3 highlights the contrast between habitats offering vegetative structure and close proximity to vegetation refugia, to those of exposed, natural and man-made surfaces (e.g., grassland, lawns, paths/pavement) with increasing distances to refuge.

Lizard microhabitat use was non-random within the quarry sites, with significant variation in mean scores between lizard locations and random points for PC1 (lizards mean = -4.30 ± 1.01, random = -2.99 ± 2.00, $F_{1,83} = 15.15$, $p < 0.001$) and PC3 (lizards = 0.70 ± 1.09, random = -0.49 ± 1.30, $F_{1,83} = 21.39$, $p < 0.001$). Lizards tended to be associated more with areas of taller vegetation with plentiful loose rocks providing refuge, as opposed to exposed areas of bare rock or grassland. There was however no significant variation between mean scores with regard to PC2 (lizards = -0.52 ± 1.15, random = -0.21 ± 1.76, $F_{1,83} = 0.92$, $p = 0.34$) (Fig 2.4)

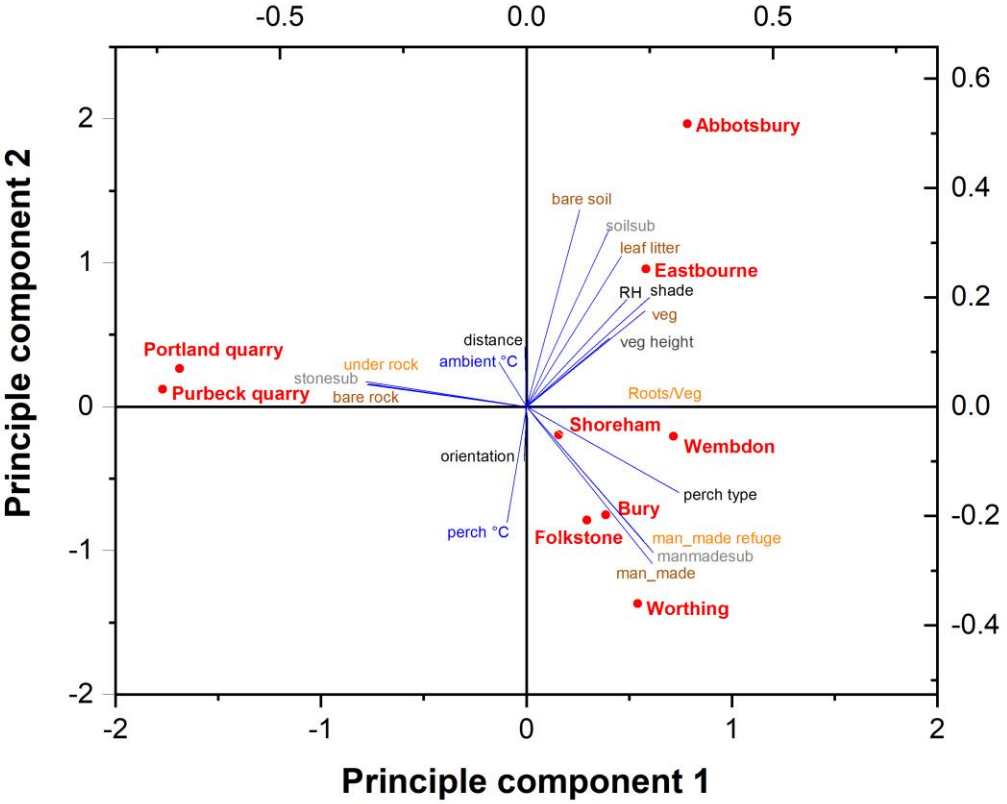


Figure 2-3 Defining variables and site grouping of principle components 1 and 2 characterising habitat use by non-native *P. muralis* at eight UK sites. Text in grey = substrate type, brown = ground cover, orange = refuge type, blue = thermal properties (ambient, perch), RH = relative humidity.

Microhabitat use by lizards in the urban/semi urban sites represented non-random selection for man-made structures and close proximity to refuge that is not so apparent at random points (PC1; lizards = 1.21 ± 1.07, random = 0.32 ± 1.42, $F_{1,266} = 34.02$, $p < 0.001$). There was also significant variation between lizard and random points for PC3 (lizards = 0.83 ± 1.12, random = -0.60 ± 1.14, $F_{1,266} = 105.81$, $p < 0.001$), with selection for some vegetative structure in preference to exposed open areas. Mean scores did not differ significantly for PC2 (lizards = -0.31 ± 1.57, random = 0.02 ± 2.51, $F_{1,266} = 1.87$, $p = 0.17$) (Fig 2.4).

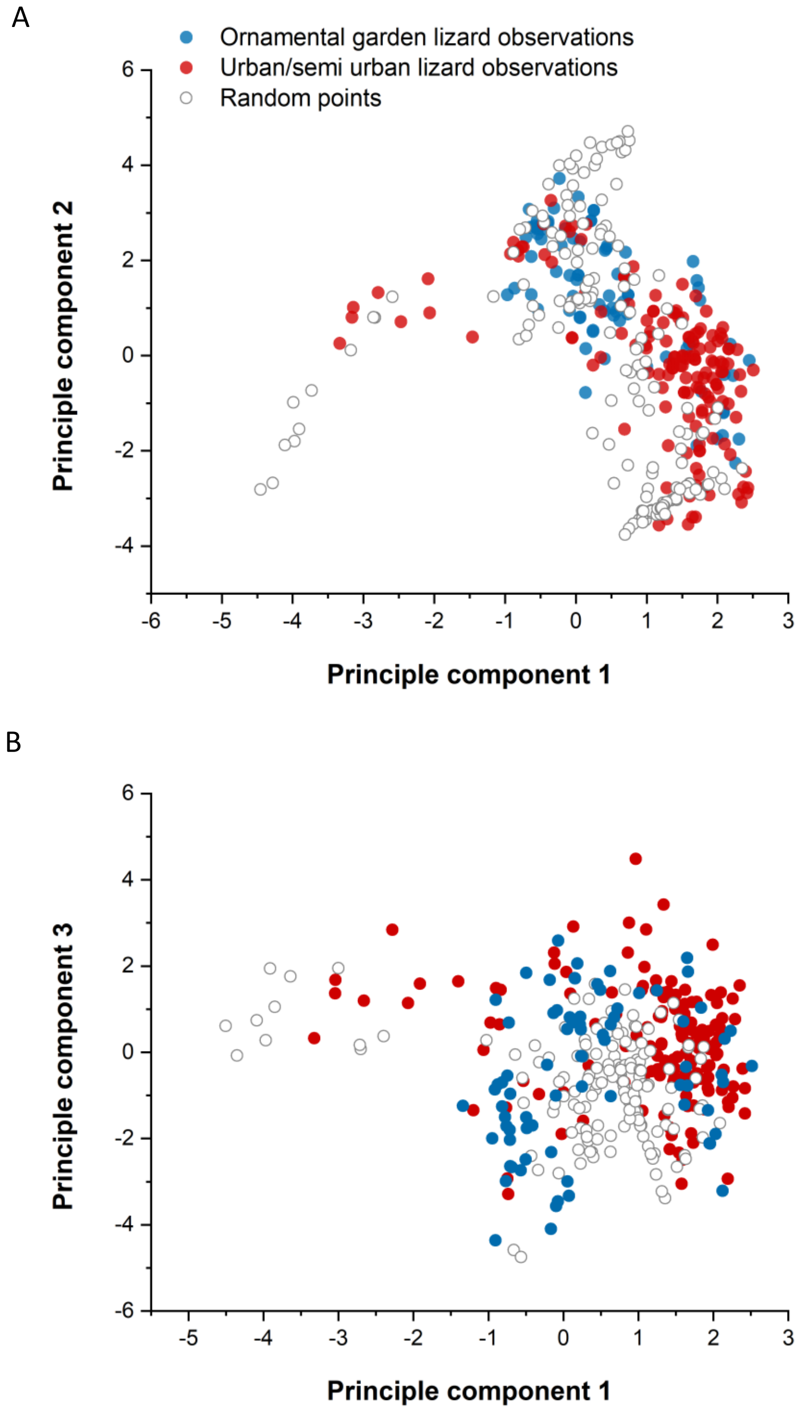


Figure 2-4 Relationship between mean scores of principle components 1 and 2 (A) and 1 and 3 (B) for wall lizard locations and random points at urban/semi urban and ornamental garden habitats.

At sites categorised as ornamental, lizard locations and random points had similar positive mean scores for PC1 (lizards = 0.63 ± 0.81, random = 0.72 ± 0.58, $F_{1,129} = 0.44$, $p = 0.51$), reflective of predominant microhabitat of cultivated vegetation and man-made features. Lizard habitat use was non-random in relation to PC2 (lizards =1.27 ± 1.46, random = -0.49 ± 2.96, $F_{1,129} = 20.74$, $p < 0.001$). Here, lizards selected for microhabitat with vegetative structure, soil substrate, bare soil, leaf litter, and close proximity to man-made and vegetation refugia around shrubs, flower beds, and low walls. In contrast, there was an avoidance of more open areas of man-made substrate and lawn with greater distance to refuge, as represented by the random sample. This contrast is further emphasised by significant difference in scores for PC3 (lizards = -0.20 ± 1.58, random = -1.22 ± 1.26, $F_{1,129} = 14.64$, $p < 0.001$) (Fig 2.4).

2.4.3 Morphometric data

Body size - Excluding juvenile lizards (SVL < 45 mm) an ANOVA analysis of 653 male (n = 365) and female (n = 288) *P. muralis* indicated significant variation in mean SVL between the sexes ($F_{1, 651} = 19.25$, $p < 0.001$), with males having greater mean SVL (60.67, SD ± 0.31) than females (58.91 ± 0.33). This size dimorphism did not change across populations ($F_{13, 651} = 1.39$, $p = 0.15$).

There was a significant variation in mean SVL between males from different lineages (Italian = 61.28 ± 5.27, French = 58.55 ± 4.97 $F_{1,351} = 5.15$, $p = 0.04$) (Fig 2.5), and between populations within lineages ($F_{10,351} = 3.32$, $p < 0.001$). Males from Worthing had the greatest mean SVL (63.06 ± 0.82) and males from Bury having smaller mean SVL (54.49 ± 1.55) (Fig 2.6A).

Mean SVL of females also differed significantly between lineage (Italian = 59.47 ± 5.36, French = 57.11 ± 4.74; $F_{1,287} = 5.04$, $p = 0.04$; Fig 2.5) and between populations within lineage ($F_{11,287} = 2.46$, $p = 0.004$), but not by habitat ($F_{1,287} = 1.84$, $p = 0.16$). Shoreham females had significantly higher mean SVL (61.92 ± 4.09) than Saulnay (54.53 ± 2.43), Bury (55.55 ± 3.78) and Folkestone (56.87 ± 5.58) females (Fig 2.6B).

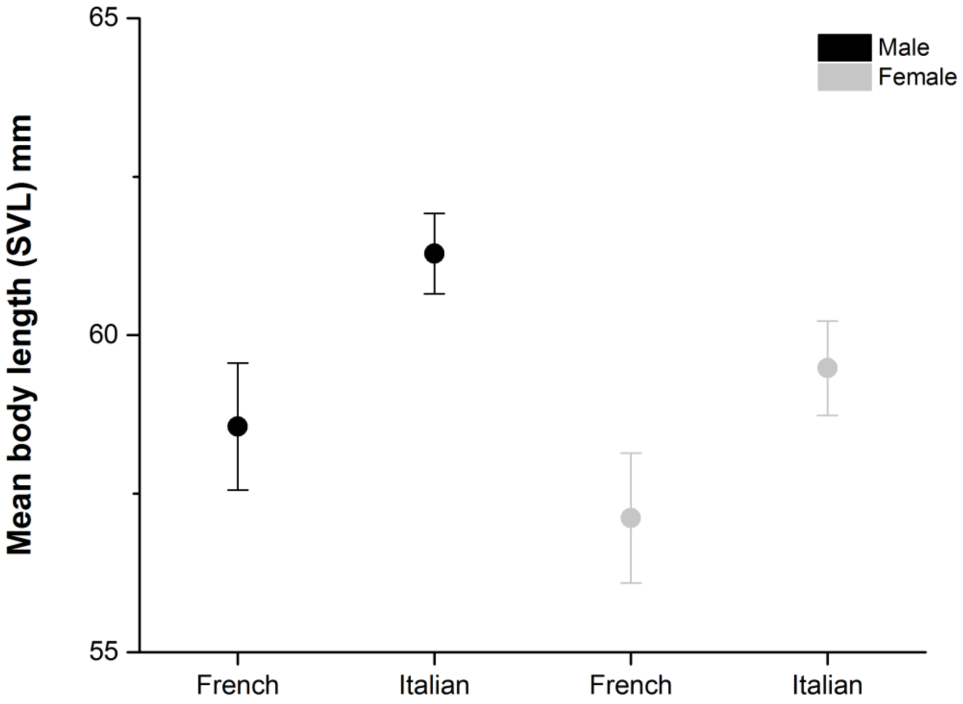


Figure 2-5 Comparison of mean body length (mm) between sex and lineage in introduced populations of *P. muralis* (95% CI error bars).

Body Mass - Male lizard body mass varied significantly between populations ($F_{13,351}$ = 8.01, p <0.001). The Newton Ferrers population had the lowest mean mass (5.31 ± 1.47), a value significantly lower than that of Worthing (7.94 ± 1.00), Purbeck (7.27 ± 1.01), Eastbourne (7.43 ± 1.82), Shoreham (7.14 ± 1.03) and Abbotsbury (7.05 ± 1.08). Worthing males were significantly heavier than 8 of 13 other populations (Fig 2.6C).

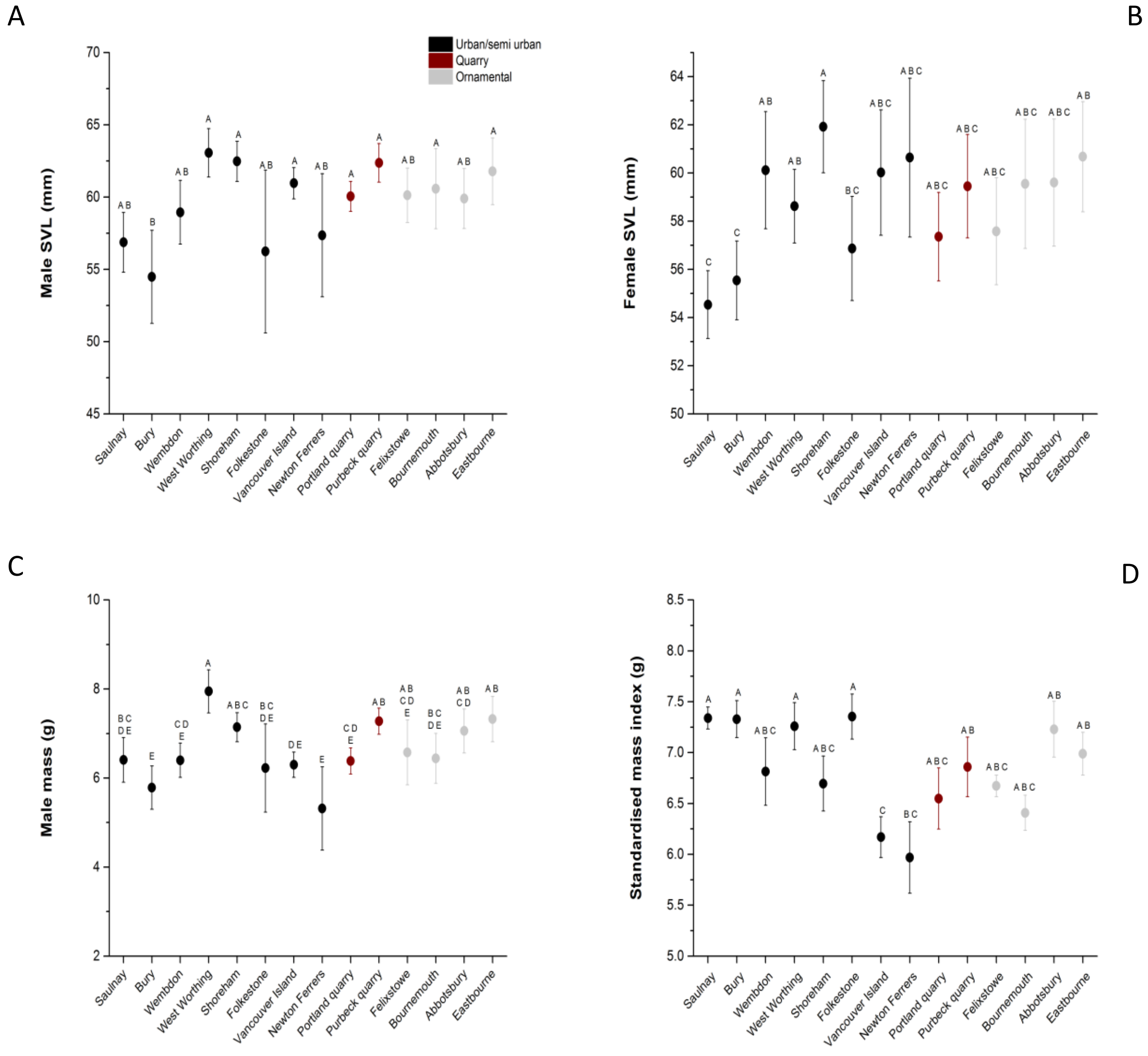


Figure 2-6 Mean interval plots (95% CI error bars) comparing male (A) and female (B) body length; male mass (C) and body condition (D) between introduced populations of *Podarcis muralis* in the UK; Vancouver Island, and a native population in Saulnay, France. Groups that share an initial (A,B,C etc.) are not statistically different. Black markers = urban/rural habitat, red = quarry, light grey = ornamental garden.

Body condition - Linear regression analysis of the log transformed male SVL and body mass measurements showed a significant positive relationship ($F_{1,351}$ = 509.37, p < 0.001, R^2=0.65), where logMass = -2.56 + 1.91 × logSVL. A nested ANOVA indicated that SMI varied significantly between populations ($F_{2,349}$ = 5.46, p < 0.001) (Fig 2.6D) and tail damage ($F_{1,21}$ =

5.09, $p = 0.03$; Fig 2.7A), but not between habitat types ($F_{2,11} = 0.32$, $p = 0.73$; Fig 2.7B) or lineage ($F_{1,11} = 0.22$, $p = 0.64$). The Newton Ferrers population had the lowest mean SMI score (5.96 ± 0.09), significantly lower than four of the other 13 populations tested (Fig 2.6D), and lizards exhibiting tail damage had greater body condition than those with undamaged tails (2.7A).

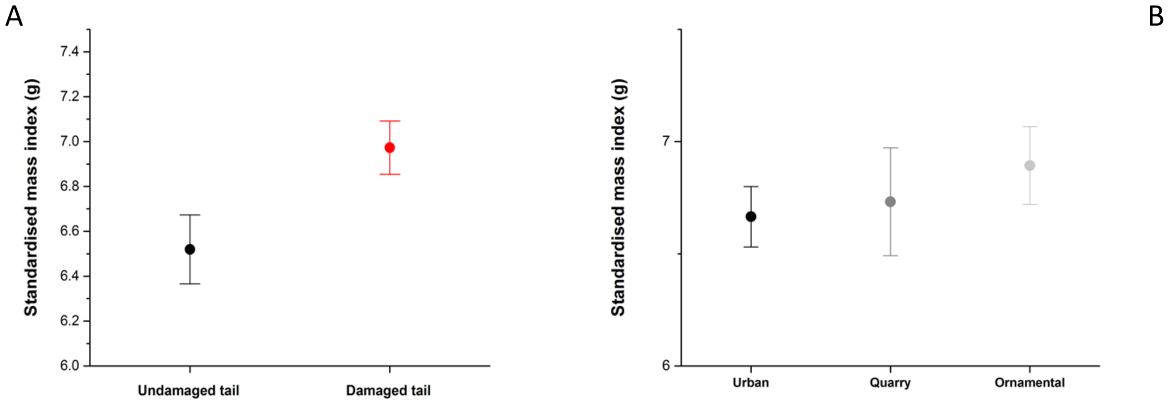


Figure 2-7 Influence of tail damage (A) and habitat type (B) on mean (95% CI error bars) standardised mass index of body condition for introduced populations of *Podarcis muralis* in the UK and Vancouver Island.

Tail damage - Sixty-three percent (n = 410) of all lizards had tails that were incomplete or had regrowth. A chi-square test for association indicated occurrences of tail damage was similar for both sexes ($X^2_{(1, N=652)} = 0.52$, $p = 0.46$). There was however a significant association between population and proportion of tail damage ($X^2_{(13, N=652)} = 42.07$, $p < 0.001$). Worthing, Saulnay, and Folkestone had the highest proportions of tail loss. Complete tails were most frequently observed with Felixstowe lizards (67%). Association between tail damage and habitat type (urban/semi urban, quarry, ornamental) was also statistically significant, with urban populations having higher proportion of tail damage than expected values ($X^2_{2, N=652)} = 19.67$, $p < 0.001$) (Fig 2.8).

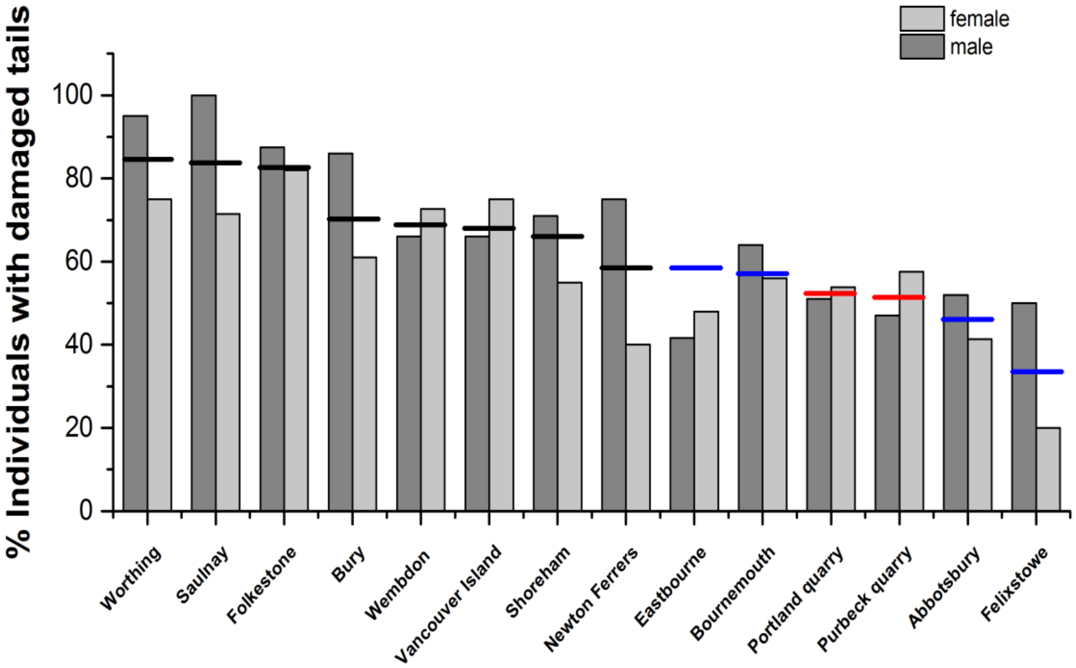


Figure 2-8 Proportion of male, female, and total population (horizontal bars) exhibiting tail damage in 12 introduced populations of *P. muralis* in the UK, the Vancouver Island population, and a native population in Saulnay, France. Horizontal bar colour represents habitat type: black bars = urban/suburban, blue = ornamental garden, red = quarries.

2.4.4 Parasitology

Hemoparasites of the type *Haemogregarina* (Apicomplexa: Adeleiorina) were found in only one (Shoreham) of nine populations tested. Seven of the thirteen individuals sampled from the Shoreham population were infected (54% prevalence), with mean parasitic load in males being 0.838 % (SD ± 0.56, range: 0.34 – 1.33 %), and the mean load in females being 0.885 % (± 0.57, range: 0.09 – 1.67 %). Mean body condition (males) of infected individuals (5.82 ±

0.43) did not differ significantly to that of uninfected lizards (6.21 ± 0.92; t = -0.97, df = 7, *p* = 0.365).

2.5 Discussion

This study is the first to explore the status and health of *P. muralis* populations introduced to the south of England and Vancouver Island. The data presented are also the first estimates of UK *P. muralis* population sizes using CMR surveying techniques. At all five sites, the large numbers of individuals caught and recaptured combined with relatively narrow standard error margins mean that confidence can be placed in the accuracy of the estimates. Although CMR methods for obtaining population estimates have only been achievable at the five sites presented here, they do provide a base line for future census and extrapolation to other populations that appear to be more widely dispersed, once the extent of suitable habitat has been quantified as these other sites. It is important to acknowledge that the comparatively high density estimated for the Bury population is likely reflective of density calculated from lizard occurrence in a very small area of optimum habitat compared to larger sites of contiguous suitable habitat as found at quarry sites.

Podarcis sp can reach high densities of over 1000/ha, particularly in island populations (Barbault and Mou, 1988). My results ranging from 100-400/ha are low in comparison with density ranges in the literature from native locations in France (Barbault and Mou, 1988). Considerably higher estimates of 500-1400/ha have also been reported from native subpopulations in central Italy (Gracceva et al., 2008), and 1500/ha for an introduced population of Italian origin in Ohio, US (Kwiat and Gist, 1987). It is not possible to draw inferences about recent UK wall lizard population trends due to the very limited, and anecdotal, information available on population sizes since introductions took place. However, it is documented that these populations have persisted in an apparently stable state in the UK for between 12 and 50 years (Michaelides et al., 2015). It is worth noting that the non-native population occurring at high densities in Ohio, USA, has been established for longer, having been introduced in 1951 with reportedly just two founding individuals (Hedeen, 1984). Being relatively recent introductions, and following theory and recognition of mechanisms causing temporal lags in the invasion process, it is reasonable to suspect that UK wall lizard populations may currently be demonstrating the ‘expected’ inherent lag in population growth. This lag commonly arises from the classic model of exponential increases seen early in the invasion process, when initial population sizes and area occupied are small (Crooks, 2005). On Vancouver Island the introduced wall lizard population has seemingly broken through a lag phase following introduction in 1970 (Allan et al., 2006) with an apparent population explosion and sudden expansion in range since 2006 (G. Hanke pers comms). Should any of the UK populations experience an abrupt end to such a lag phase it will likely be most apparent for those populations at sites where current habitat is contiguous with exploitable urban habitat (e.g., West Worthing, Eastbourne, Bournemouth, and Shoreham).

Factor analysis was effective in describing the site-specific, non-random habitat use of the UK wall lizard populations studied, but also highlighted the wide breadth of habitats used by the species provided close proximity to refugia, vegetative cover for foraging, and opportunities for thermoregulation are present. The species has been reported to be more generalist in microhabitat preferences when compared to congeners by having greater variation in microhabitat selection (Capula et al., 1993). *P. muralis* is also well documented as being capable of exploiting structural features of human-altered habitats such as stone walls, debris, and railway lines in both native and introduced ranges (Bertram, 2004; Covaciu - Markov et al., 2006; Gherghel et al., 2009), and the importance of human-made structures to UK wall lizards in all but the quarry populations is evident in my analysis.

While population sizes may vary and currently lie below the threshold needed for significant natural range expansion, female body size may directly influence population growth and thus potential for range expansion through its effects on net fecundity (Caswell and Hastings, 1980; Bradshaw and McMahon, 2008). In my study, variation in female size was dependent on lineage and site, with no significant variability observed between habitat types occupied. This variation among lineages suggests any variation is likely a result of inherent genetic variability, or perhaps genetic drift and founder effects resulting from a small population size and few initial founding individuals, rather than post-introduction adaptation to local habitat (Rasner et al., 2004; Kolbe et al., 2012; Michaelides et al., 2018). The small size of the Bury population and the relatively low heterozygosity and allelic richness described for this population compared to other UK populations (Michaelides et al., 2016) goes some way to support this theory.

Clutch size of *P. muralis* has been shown to have a strong positive correlation with female body length (Barbault and Mou, 1988; Capula et al., 1993). The difference between maximum size attained in the population with the smallest individuals (Bury) and the maximum recorded at the population with the largest individuals (Shoreham) was at most only 10%. Based on results observed from a native population in France (Barbault and Mou, 1988), this difference between mean body length would appear unlikely to result in a markedly different clutch size among the UK populations studied. Details of clutch sizes arising from analysis of rates in hatching failure do, however, indicate a degree of variability amongst UK populations, most notably the small average clutch size (based on 3 clutches) of the Bury population compared to several other populations (Michaelides et al., 2016). Disparity in body size even at this magnitude could also have significant bearing on the ability to produce multiple clutches in a year, as even a 3.5 mm difference in SVL has been recorded as the difference between females producing one clutch and those having laid two or three clutches (Ji and Brana, 2000). Indeed, the mean female sizes at three of my UK study sites (Bury, Felixstowe, Portland quarry), and the native French population sampled here, were actually less than (or comparable to) the mean size for females limited to one clutch per year (57.1 ± 0.7 mm) (Ji and Brana, 2000). Recruitment in UK *P. muralis* populations is largely restricted to the first clutch of the season due to the climatic constraints (i.e., cooler, seasonal, climatic conditions compared to native range) placed on embryonic development and juvenile survival (While et al., 2015b). In an adaptive response, females from non-native population produce relatively larger and heavier first seasonal clutches and smaller and lighter second seasonal clutches compared to native females (MacGregor et al., 2017). The combination of climatic and physical (small body size) constraints on fecundity are thus likely to significantly affect the long-term persistence and growth potential of some UK populations, particularly those of French origin. Body size of UK lizards of Italian origin however are well within the range of producing three clutches, which raises interesting questions about potential population growth in response to predicted temperature increases and temporal shifts in seasonality in the UK (Hulme, 2017). Indeed, the rapid range expansion of *P. muralis* in the Mediterranean climate of southern

Vancouver Island (Victoria) may be an indicator of the likely response of UK populations under this scenario.

Studies have shown that *P. muralis* exposed to disturbance and urban environmental stressors (higher concentration of heavy metals and other pollutants, higher temperature, human presence, domestic predators, etc.) exhibit lower mean body condition than those from rural habitats (Amo et al., 2006b; Lazic et al., 2017). Although my results indicate a similar pattern between urban and less disturbed habitats this result was not statistically significant, and neither habitat nor lineage had an effect on the SMI. Variance was only apparent at the local population level, and in further contradiction to the hypothesis of compromised condition in urban habitats, males from the most urban of all my UK study sites (West Worthing) had the largest mass and third highest SMI. A likely explanation for this could be variation in site specific factors, as Lazic et al (2017) provide evidence for a suite of environmental stressors at their urban study sites that may not have influence, or indeed may not even be present, at my Worthing site. Furthermore, Worthing lizards were caught primarily in and around disused railway sidings, a habitat which appears wholly suitable for both *P. muralis* and *Z. vivipara* (Kornacker, 1993; Covaciu - Markov et al., 2006) offering an abundance of refugia and basking sites, and which could be significant in terms of local invertebrate abundance (Strauss and Biedermann, 2006); resources which in turn would influence lizard body condition.

Explanations as to why the Newton Ferrers and Vancouver Island male populations should have particularly low body condition are not forthcoming with the available data. Since I do not have habitat data for these two populations, I cannot examine correlations between body condition and, for example, availability of refugia. The temporal fluctuations in male mass in relation to changes in relative mass of the testes according to the reproductive cycle (Kwiat and Gist, 1987) is likely to be too minor to account for the variance in body mass seen. Furthermore, both the Worthing and Newton Ferrers samples were collected in August (2016-2017 respectively) at presumably similar stages of spermatogenesis. In theory, a number of abiotic factors, biotic interactions, and the influence of density dependence in driving contest for resources (e.g., prey, basking spots, refuge) could be explanations for site variation in body condition, as have been considered as reasons for declining condition of

Anolis lizards experimentally introduced to man-made islands (Campbell and Echternacht, 2003).

The variation in tail damage between urban and more rural populations of wall lizards in the UK is expected due to the likely high densities of mammalian predators in urban areas (Woods et al., 2003), and direct observations (RW) of predation by domestic cats *Felis cattus* at some of the urban sites studied. It is, however, not possible to know the exact cause of tail loss in the populations studied here and although intraspecific contest has also been shown to be a cause of tail loss in lizards, particularly in insular populations (Bateman and Fleming, 2009; Pafilis et al., 2009; Donihue et al., 2016; Itescu et al., 2017), there is little evidence that *P. muralis* suffers tail loss during intraspecific conflict (Brown et al., 1995b).

My results of similar rates of tail loss between the sexes are also in keeping with other studies of several other lacertid species (Pafilis et al., 2017). Although I observed no overall significant association of tail damage with either sex, intra-population variability in tail damage between the sexes (i.e., greater frequency in males) in some populations may indicate that male-male agonistic interactions, or conditions leading to greater susceptibility of males to predatory attack, may influence rates of tail damage at these sites. For example, differences in behaviour between sexes is suspected to be the cause of male biased predation of western green lizards (*Lacerta bilineata*) by the Eurasian kestrels (*Falco tinnunculus*) (Costantini et al., 2007).

Assuming the primary cause of tail damage is attempted predation, my results suggest that this pressure does not adversely affect body condition. Increased refuge use in response to predation pressure has been shown to have a negative impact on body condition in lizards due to reduced food intake; although adaptions in anti-predator behaviour can mediate this so body condition is maintained comparable to lizards from less ‘risky’ habitats (Amo et al., 2007b). For example, *P. muralis* living in an urban habitat have been shown to spend less time in their refuge after predatory attacks and have decreased successive hiding times compared to those of rural lizards (Pellitteri-Rosa et al., 2017), behavioural traits that would mediate losses in time spent foraging in response to predation pressure.

It is important to note that my definition of tail damage includes tails that had regenerated to various degrees, and that the majority of damaged tails (89%) were in fact regrown to over half the predicted length of a complete tail. Deficit in mass due to tail damage is thus generally very small and unlikely to have significantly affected calculations of SMI. Furthermore, some lizards have shown compensatory strategies following autotomy. An increase in mass and subsequent tail regrowth following tail autotomy has been seen in controlled experiments with juvenile skinks (*Eumeces fasciatus*), where lizards that lost most of their tails exhibited compensatory growth for that body part, without sacrificing growth in body mass (Goodman, 2006). Some lizards increase feeding rates to meet increased energetic demands during tail regeneration, particularly those where the tail contains important fat reserves (Sun et al., 2009).

With regard to predation pressure impacts on introduced *P. muralis* populations, it is important to consider that evidence of tail damage is possibly more a reflection of predator inefficiency rather than predation intensity (Jaksic and Greene, 1984). And whilst frequent predation attempts may have adverse impact on individual fitness, the actual losses to the population through predation may be minimal and have little constraint on population growth.

Parasites can have an influential role in invasion success through both direct effects with their host (i.e. effect on host fitness and thus on host population growth and stability), and indirect effects on species with which the host interacts (i.e., density and/or trait mediated effects on host reproduction; survival, and changes to phenotype, behaviour or life history) (Dunn et al., 2012). I found evidence of haemogregarine parasite infection in only the Shoreham population. The absence of parasites in the Vancouver Island sample is consistent with that of previous analysis of other introduced populations of *P. muralis* and *P. sicula* in North America, and suggests an absence of parasites in the founding population or that intermediate hosts/vectors are absent or not encountered (Burke et al., 2007).

We were unable to determine the exact identity of the parasite in the Shoreham sample as it is difficult to determine to species based only on the morphology of gametocytes in erythrocytes. Lacertid lizards are specifically infected by members of the genera *Haemogregarina*, *Hepatozoon* and *Karyolysus* (Telford, 2009). Among these pathogens, *Karyolysus* is particularly prevalent in Palearctic lizards (Hassl, 2012; Haklová - Kočíková et al., 2014) and is found in *Z. vivipara*, *L. agilis* and *P. muralis* (Majlathova et al., 2010; Hassl, 2012). Mites of the genus *Ophionyssus* are the main vector and definitive host of the "Karyolysus" group, with *O. saurarum* commonly parasitic on *P. muralis*, *Z. vivipara* and *L.*

agilis (Fain and Bannert, 2000; Majlathova et al., 2010). There are also records of *O. lacertinus* parasitic on *P. muralis* from Italy and *Lacerta bilineata* introduced to the UK from Italy (Evans and Till, 1966), indicating the possibility of either mite species being a potential vector in the Shoreham population. Why this particular population should be infected and not others could be due to a historical prevalence of the parasite and its mite vector in the original captive population prior to release. *Z. vivipara* is not known to occur in sympatry with *P. muralis* at this location so the transmission of mites from a native host seems unlikely. Alternatively, *Podarcis* spp. are also frequently host to *Hepatozoon* parasites (Roca and Galdon, 2010; Maia et al., 2011; Harris et al., 2012). Unlike the mite vector of *Karolysus*, *Hepatozoon* is transmitted via ingestion of a wide spectrum of invertebrates (ixodid and argasid ticks, triatomid bugs, leeches, flies, sucking lice, fleas, sandflies and mosquitoes) (Haklová - Kočíková et al., 2014). In this case, the localised infection of the Shoreham lizards might be on account of predation of a specific invertebrate vector associated with the rather unique habitat (vegetated shingle beach) in which the lizards forage. This theory is in keeping with suggestions that haemogregarines are more host-specific to their invertebrate hosts than they are to their vertebrate hosts (Tome et al., 2018).

Severe haemogregarine infections can cause a depression of hematocrit levels and subsequent anemia, with potential to significantly affect lizard physiology and behavior, such as foraging efficiency or sprint speed (Oppliger et al., 1996; Damas Moreira et al., 2014). Compromised activity levels should therefore ultimately affect body condition. The Shoreham population shows no apparent adverse effects of infection on condition. This could be due to the low infection prevalence and parasitic loads observed, that are generally comparable to those recorded for field populations of *Podarcis* spp. in the literature: *P. bocagei* and *P. carbonelli* (Roca and Galdon, 2010); *P. vaucheri* (Damas Moreira et al., 2014); *P. muralis* (Amo et al., 2005b; Martin et al., 2008) (Table 2.4). Should infection be reducing survival in the Shoreham lizards, the lack of effect on body condition recorded in the population may reflect a sample bias wherein only uninfected, and individuals in good condition surviving the demands of allocation of resources to the immune system to fight infection were caught (Amo et al., 2005b). This is somewhat supported by the fact that infected lizards had similar mean condition to those uninfected.

Conversely, the absence of parasites in the other introduced populations could reflect a release from this particular parasite. This could have important implications for invasive success, particularly if there is a differential in the presence/effects of parasites between the introduced species and native competitors (Dunn, 2009; Dunn et al., 2012). Haemogregarine infections are common in the two lizard species (*Z. vivipara* and *L. agilis*) (Majlathova et al., 2010) with which *P. muralis* is likely to interact with in the UK. Screening of native species in areas of sympatry with introduced *P. muralis* in the UK, and further investigation into the identity and prevalence of invertebrate vectors within the community, would therefore be very useful to provide insights into the interaction between parasites, their native hosts, and a non-native intruder.

Table 2-4 Prevalence and intensity of infection by hemogregarine parasites in *Podarcis* spp.

Species	**Origin**	**Prevalence (%)**	**Intensity (%)**	**Source**
Podarcis muralis	Introduced, UK (Shoreham)	54%	0.8	This study
Podarcis muralis	Spain	79%	0.4	(Martin et al., 2008)
Podarcis lilfordi	Menorca, Spain	95%	0.9	(Garrido and Pérez-Mellado, 2013)
Podarcis muralis	Spain	58%	0.1	(Amo et al., 2005b)
Podarcis bocagei	Portugal	75%	-	(Roca and Galdon, 2010)
Podarcis carboneli	Portugal	70%	-	(Roca and Galdon, 2010)
Podarcis vaucheri	Morocco	96%	1.8	(Damas Moreira et al., 2014)

Based on the aspects of individual and population fitness studied here, there does not appear to be any constraints significantly affecting the persistence and potential long-term growth of introduced populations of *P. muralis* in the UK and Vancouver Island. Being highly adaptable to exploiting various habitat types, particularly those with high levels of anthropogenic disturbance, climatic constraints on physiological process are likely to restrain the species range most of all (Michaelides et al., 2015).

Some populations, particularly those most isolated by unsuitable habitat have remained relatively small since introduction, with densities well below those potentially attainable. This raises the question of whether control or elimination of populations should be considered whilst numbers are potentially at their most manageable.

Any decision on eradication, control or mitigation of UK *P. muralis* populations would need to take into account a range of considerations such as feasibility and non-target impacts (Foster, 2015). My CMR data provides some insight into the feasibility of management options. The estimate of the Bury population at 35 implied that 83% of the population was captured at the survey site during the sampling. At Abbotsbury, an estimated 90% of the population was captured, at Purbeck an estimated 72% and at Portland an estimated 65%. These estimations appear realistic given the relative times spent sampling and the area of each site. Capture rates based on the effort and capture method used indicate that control, and perhaps even eradication, could be feasibly attained at certain sites. Furthermore, if UK populations are indeed currently experiencing a lag phase there is argument to suggest that such methods should be employed as a timely intervention before a possibly abrupt end to the lag phase occurs.

Chapter 3: End of the line? Climate and habitat configuration limit range expansion and patterns of dispersal in a non-native lizard

3.1 Abstract

The impact of invasive species is one of the main causes of biodiversity loss world-wide. As introduced populations increase in abundance and geographical range, so does the potential for negative impacts on native species and communities. As such, there is much interest in understanding the patterns of demography, dispersal, and rate of expansion of species once they have become established in recipient landscapes. Here, I characterize the potential for population growth and range expansion of the Common wall lizard (*Podarcis muralis*), introduced to the south of England, considering both capacity for natural dispersal at the local scale and wider range expansion through secondary human assisted movement. I collated and used records of *P. muralis* presence through field surveys and a citizen science campaign to determine the current extent of introduced populations. Presence-only models built in MaxEnt were then used to predict national climatic suitability and fine scale habitat suitability at the local level. The local model was then integrated into the individual-based modelling platform, RangeShifter, to simulate projected population dynamics and range expansion of 10 populations across various landscapes (i.e., urban, semi-urban, rural) to better understand patterns of natural dispersal and invasion potential. National-scale models showed that climate suitability for *P. muralis* is largely restricted to the southern coasts of England and Wales, with limits associated with increasingly harsh over wintering conditions further north. Urban heat island (UHI) effects may however facilitate establishment in some areas otherwise unsuitable. Local-scale models suggested that local population growth rates, dispersal patterns, and rates of expansion varied both spatially and temporally and were related to landscape configuration and heterogeneity, and time since introduction. Landscapes of highly clustered fragments of suitable habitat, such as those found in urban areas, and features of contiguous habitat (cliff faces, rail lines) promoted greater dispersal distances. Population growth curves suggest all the populations studied could be in the early stages of exponential growth, but that annual natural dispersal distances are generally low (5-16 m) due to abundance of suitable habitat allowing populations to increase locally without the need for longer distance movements. I conclude that natural range expansion of *P. muralis* populations is likely to remain small, but that exponential increases in population size, particularly in areas with many transport pathways

may facilitate greater incidence of assisted secondary translocation, both locally and further afield.

3.2 Introduction

The global rise in the number of species introduced to regions beyond their native range via human-mediated translocation shows no sign of reaching saturation point (Seebens et al., 2017). And whist many species fail to establish or have little negative effect following introduction, a subset of these do spread and can have significant impact on economies, human health, native biodiversity and ecosystem services (Kolar and Lodge, 2001; Vila et al., 2010; Keller et al., 2011). The severity of potential negative impacts (e.g., extirpation and extinction of native species) are such that invasive non-native species (INNS) are justifiably regarded as one of the most significant threats to biodiversity worldwide (Genovesi, 2009; Simberloff et al., 2013).

For non-native species to become widespread and potentially damaging following introduction to new regions, introduced populations must negotiate the three stages of an introduction–establishment–invasion continuum (Blackburn et al., 2011). Evaluation of the likelihood of a species to be transported, to establish and to spread, as well as the potential for having ecological, economical, and health impacts, forms the basis of ‘invasive’ risk assessment for alien species (Bacher et al., 2018; Roy et al., 2019). Although it has been argued that the term ‘invasive’ doesn’t always necessarily equate with a species’ negative impact (Ricciardi and Cohen, 2007), the potential for damaging effects inherently increases as introduced species increase in population size and spread across novel landscapes thus affecting broader areas and more ecological communities (Crooks, 2005). As such, the ability to predict the potential of introduced species geographical spread and understand the environmental factors which limit their distributions is key in formulating management strategies if control is desirable (Gallien et al., 2010; Roy et al., 2014; Roy et al., 2018; Roy et al., 2019).

Following introduction and successful establishment beyond native ranges, introduced species can further expand their range through natural dispersal processes and/or by jump dispersal events – often by human-mediated transport but also possible depending on natural dispersal ability (i.e., long distance flight in birds) (Suarez et al., 2001; Ingenloff et al., 2017; Cesari et al., 2018). Invading species typically exhibit several phases in the pattern of spread that are influenced by a range of traits: propagule size, dispersal mode, vital rates (births and deaths), and matching of habitat conditions at the receptor site with the introduced species' physiological and ecological traits (Sakai et al., 2001; Arim et al., 2006; Mahoney et al., 2015). Firstly, there is an initial establishment phase with low rates of spread. Secondly, an expansion phase typified by increasing rates of spread, and finally, a saturation phase when available space is occupied and spread rates reach a plateau (Arim et al., 2006). In spite of these well understood temporal dynamics of biological invasions, our ability to predict and manage the geographical spread of invasive species is often complicated by the phenomenon of lag phases, wherein an introduced species remains at low population levels in the early stages of establishment for a long period of time before the sudden onset of rapid range expansion (see Crooks (2005) for review of temporal lags at all stages in the invasion process). For example, introduced populations of the northern Racoon (*Procyon lotor*) remained small for a number of years following introduction to Europe before a population explosion in the mid 1990's (Salgado, 2018). Furthermore, lag periods may range from a few years to several centuries (Essl et al., 2012), and are well documented for plants (Essl et al., 2012; Larkin, 2012), invertebrates (Suarez et al., 2001; Rilov et al., 2004; Grayson and Johnson, 2018), and vertebrates (Aagaard and Lockwood, 2014; Azzurro et al., 2016; Vimercati et al., 2017).

Lag phase in growth and spread of introduced populations may be explained by ecological factors (inherent lags), such as when the population is exhibiting exponential growth in the initial low-density phase of establishment and circular expansion from small areas of introduction (Crooks, 2005). Negative density dependence (e.g., Allee effects) may also constrain population growth and geographic spread when founder populations are at low density (Marsico et al., 2010; Kramer et al., 2018). Other biological constraints can have a regulatory effect on range expansion before the saturation phase is approached, i.e., individuals must grow to reproductive maturity at newly invaded sites before generating propagules for further dispersal and colonisation (Arim et al., 2006). Genetic constraints (intrinsically linked to propagule size) can also influence rate of spread and are a potential cause of early lag phases preceding rapid population increases. For example, if novel selective regimes are encountered during the initial establishment phase and range expansion, the rate and extent of range expansion will be influenced by the adaptive response of individuals to the selection pressures imposed by the new environment (Lockwood et al., 2005; Blackburn et al., 2015; Michaelides et al., 2018). This is particularly likely when species are introduced to areas at the extremes of climatic tolerance (Sax, 2001; Guo et al., 2012; While et al., 2015b).

Our understanding of the factors that underlie the distributions of species – whether invasive or native – often relies on statistical associations between environmental conditions and species presence/absence. Numerous studies have employed principles of species distribution modelling (SDMs) in predicting range expansion of introduced species (Elith and Leathwick, 2009; Merow et al., 2013; Guisan et al., 2014). Such models are often used to make predictions of the extent of available area open to invasion based on matching climatic conditions in native ranges to those in invaded regions (i.e., predicting the invaded distribution with the model fitted in the native range, and vice versa) and have been used across taxa; birds (Sullivan et al., 2012; Su et al., 2017); invertebrates (Zeng et al., 2016), mammals (Fraser et al., 2015) ; plants (Padalia et al., 2014; West et al., 2016); reptiles and amphibians (Wirga and Majtyka, 2015; Lopez et al., 2017; Suzuki-Ohno et al., 2017); and fish (Moore et al., 2018). These models can reveal much about ecological processes in invasion dynamics, particularly species' adaptive responses to novel climates (Elith et al., 2010). For example, SDMs reciprocally projected between native and invasive range of the red-legged earth mite (*Halotydeus destructor*) showed the species has expanded in its invasive range beyond what is predicted from the native distribution, supporting theories of adaptive niche shift (Hill et al., 2012). SDMs have also assessed niche shift in introduced population of the sea-slug *Pleurobranchaea maculata* (Battini et al., 2019). In contrast, 'niche unfilling' (i.e., invaded area is only a sub-space of the niche of the native area) has been predicted by range expansion models of the introduced population of a solitary wasp (*Isodontia mexicana*) in Europe (Polidori et al., 2018).

Dispersal is one of the key determinants of species spatial dynamics, and accurately simulating dispersal of species undergoing range expansion process is central to predicting species spread (Hastings et al., 2005; Arim et al., 2006; Bocedi et al., 2014b). Increased understanding of dispersal dynamics (Travis et al., 2011; Grayson and Johnson, 2018) along with development of platforms for individual based modelling of range expansion (Bocedi et al., 2014a; Bocedi et al., 2014b; Samson et al., 2017), have therefore allowed the influences of dispersal processes to be incorporated as a fundamental consideration in range expansion models (Andrew and Ustin, 2010; Sullivan et al., 2012; Ferrari et al., 2014; Mang et al., 2018). Intrinsically linked to dispersal processes are the structural characteristics of the landscape that determine the ease at which animals can move through the landscape matrix (Bonte et al., 2012). Structural landscape connectivity (i.e. the physical relationships between habitat patches), and functional connectivity (i.e. an organism's behavioural response to both the landscape structure and the landscape matrix) (Baguette et al., 2013) are considered to be of vital importance in maintaining demography, evolutionary processes and long-term population viability in heterogeneous landscapes (Taylor et al., 1993; Villard et al., 2014). And whilst there is a huge body of work detailing the effects of landscape structure in relation to biodiversity conservation (Fahrig, 2003; Gagne et al., 2015; Kormann et al., 2015; Rosch et al., 2015), it is only relatively recently that these same landscape processes have been incorporated into models of establishment and spread of introduced species (With, 2002; Pitt et al., 2009; Fraser et al., 2015; Ingenloff et al., 2017; Lustig et al., 2017).

The common wall lizard (*Podarcis muralis*) has a long history of introductions beyond its native range which covers most of Western and Southern Europe (Gassert et al., 2013). Many of these introductions have extended its range throughout the continent (e.g., Germany (Schulte et al., 2012a); Czech Republic (Šandera, 2017); Poland (Wirga and Majtyka, 2015); Iberian Peninsula/Balearic Islands (Silva-Rocha et al., 2012)), but also across the English Channel into southern England (Michaelides et al., 2015). The species also has several populations established in the New World, both in the United States (Hedeen, 1984; Brown et al., 1995a) and Canada (Bertram, 2004; Allan et al., 2006). Introduced to Vancouver Island, British Columbia, in 1970 (Allan et al., 2006), the species persisted in isolated populations until 2006, but has since spread with alarming speed due to jump dispersal (human mediated) and natural radial dispersal of 40-70 meters a year in urban areas (G. Hanke pers. comm.).

To date there is no empirical evidence of negative ecological impacts of *P. muralis* introductions in the UK, and there is mixed social perception and opinion towards the species' presence (Williams et al., 2019). However, suspected declines in native lizards through interference and/or exploitation contest have been reported following introductions of *P. muralis*, to both Germany (Münch, 2001; Kühnis and Schmocker, 2008; Schulte et al., 2008; Schulte, 2009) and the UK (Mole, 2010) – the latter reporting a 75% decline in the native common lizard (*Zootoca vivipara*) population, and increasingly marginalised distribution to the fringes of suitable habitat, coincident with a 40% increase in the *P. muralis* population. Range overlap with the native sand lizard *Lacerta agilis,* one of the UK's rarest reptiles, is currently limited, but could increase with further range expansion of *P. muralis.* Disruption to food webs and community structure are also highlighted as cause for concern, whereby high density *P. muralis* populations may reduce invertebrate diversity and density, and supplement predators (Foster, 2015).

There have been multiple introduction events of *P. muralis* to the UK both as deliberate releases of captive animals and as cargo stowaways, with some extant populations having been established on the UK mainland as early as the 1970s (Michaelides et al., 2013). More recent introductions (1980s onwards) have mostly arisen from movement of individuals from already established populations (secondary introduction) or captive-bred animals, rather than directly sourced from the native range (Michaelides et al., 2015). The UK populations represent the species at the northern extent of its range, with sites having markedly different climatic conditions compared with the native range. For example, air temperatures during the main activity season in populations in England are 5–10°C lower than their source regions in Tuscany and western France (While et al., 2015b).

The main aim of this study was to determine the potential for range expansion of *P. muralis* in the UK at both the national and local scale. Since long distance jump dispersal via translocation is important in facilitating spread of this species, I predict the national extent of the area potentially available for further colonisation by running species distribution models (SDM) based on climatic suitability at these northern extremes. To make predictions of population growth and identify environmental features important to future range expansion at a local level, I combined SDMs informed by variables characterising 10 local landscapes (i.e., microclimate, proximity to geographic features, and habitat type), with a high resolution (2x2 m) spatiotemporal individual based model (IBM) simulating local population dynamics and spatial patterns of spread.

I hypothesised that variability in introduction history (i.e., time since establishment) and landscape characteristics at introduction sites would result in differences in predicted patterns of population growth and range expansion for 10 introduced *P. muralis* populations.

3.3 Methods

For the purposes of this study, efforts were made to determine the current geographic extent of as many of the UK wall lizard populations as logistically possible. The locations of established *P. muralis* populations were obtained from the Surry Amphibian and Reptile Group website (Langham, 2019). Of the 30 extant populations recorded on the UK mainland, 21 were visited between three field seasons (April-September) of 2016, 2017, and 2018. Site visits were not carried out at the remaining nine locations because the lizard population were either known to be very small, access was restricted, and/or site locations were otherwise logistically challenging (i.e. distance from other populations). Wall lizard location data were also gathered from populations at two additional sites, Eastbourne (50.768° N, 0.291° E) and Kingswear (50.349° N, 3.568° W). The former was confirmed to be an established colony through an ad hoc site visit and the latter was reported to RW by a member of the public responding to a citizen science campaign in regional media designed to generate new recorders of wall lizard sightings (see below).

The current extent of populations was determined using a combination of visual surveys, canvassing of the local public at sites of interest, and press releases in local and regional media encouraging members of the public to report their wall lizard sightings.

3.3.1 Visual surveys

Surveys took place between 07.30 and 18.00 on days with at least periods of sun, as this weather is considered most productive for lizard surveys (Gent and Gibson, 1998). Sites were walked by 1-4 surveyors paying particular attention to habitat features that provided opportunities for basking and refuge, as lizards aggregate around such features. Locations of lizards were recorded to within ± 1 metre accuracy on handheld GPS (Garmin *etrex* 10™) or manually recorded by annotating aerial photographs using the Aerial Roam service at https://digimap.edina.ac.uk. As wall lizards are abundant in localised areas and very conspicuous wherever they are present, it was feasible to identify the current extent of most populations by simply walking the area until lizards were no longer encountered. Lizard locations collected from GPS were overlaid onto aerial images and adjusted for precision.

Specific attention was given to assessing the extent of *P. muralis* presence along railway habitat at West Worthing, Sussex (50.818° N, 0.390° W) during a five-week period in June-July 2018. The railway acted as a linear transect, along which 21 visual survey points and 11 artificial refugia locations were set, providing survey coverage of a transect ~ 9.5 km long running from Angmering station to East Worthing station (Appendix 3.1). The location of these survey points was determined by limitations to access and therefore it was not possible for the survey effort to be evenly distributed along the transect. Direct access to the railway track was granted by Network Rail, which provided the opportunity for visual surveys and placement of 70 artificial refugia in trackside habitat. Three or four visual survey points were visited per day and searched for 20 minutes at each site. The visual survey points requiring Network Rail access were surveyed four times each, whereas the visual survey points that were accessible to the public were surveyed five times each. Artificial refugia were left undisturbed for one week prior to beginning surveys, to allow them to 'bed down'. Although it is recommended to leave the refugia to establish for several weeks (Gent and Gibson, 1998) this was not possible due to time constraints. Refugia on public land were surveyed once per week for five weeks, and those on land owned by Network Rail were surveyed once per week for three weeks due to the constraints to access.

3.3.2 Community engagement

Surveyors took opportunities to engage with the local public during site visits to gain further information into the extent of local lizard populations. When new information was provided surveyors would extend their search accordingly. Door to door canvasing (at suburban/urban sites) was employed in 2017-2018 to confirm absence of lizards from residential gardens beyond the limits of the population extent observed through visual surveys. Home visits were conducted to investigate presence of lizards within 200 m of known locations through random sampling of households. During canvassing, householders' were either spoken to directly and shown images of wall lizards for identification purposes and asked if they had lizards on their property or seen them locally, or a freepost postcard (coded with street and house number) showing clear pictures of male and female wall lizards was posted through the door asking the same questions and requesting details of where lizards had been seen. Five hundred postcards were delivered, with a return of 76 (15%). Of these returns, 52 reported confirmed lizard locations. In addition to requesting the return of the postcards regardless of response (confirmation of lizard absence was welcomed), postcards also invited recipients to record their sightings via an online Participatory GIS (PPGIS) hosted through map-me.org (Huck et al., 2014) where they were given instruction on how to record their sightings on a satellite image of the local area (bit.ly/lizarduk). The PPGIS not only records sightings as locations that can be visualised in GIS software, but also allows researchers to ask questions of participants, the responses to which are stored as attributes linked to these spatial points. In this instance, I asked participants questions that would aid in assessing the veracity of the sightings recorded. Specifically, I asked, 1) Where was the lizard (e.g., on a garden wall, on patio steps)? Such supporting information could describe behaviour indicative of wall lizards, and 2) How confident on a scale of 1-5 (5 being very confident) are you in the accuracy of your identification of wall lizard? Spatial points were reviewed periodically throughout 2017-2018 by overlaying point features onto aerial photographs. Records were validated based on their location, photographic evidence (when provided), and proximity to known populations, in conjunction with question responses attributed to the spatial data. Records were then either rejected outright or retained for confirmation through a site visit. Any points extending the known spatial extent of populations were ground-truthed through additional site visits and widened visual survey in the vicinity of the new sighting records. 114 users engaged with the online portal, of which, 76 generated credible sighting records.

3.3.3 Press release

Wall lizard sightings were also generated through a 2017 press release in local news outlets covering the wider distribution of wall lizards in the UK, and where possible, parish magazines covering the 23 study populations. These releases provided information on the wall lizard introduction, pictures to aid identification, and invitation for readers to record sightings at bit.ly/lizarduk or to contact the lead researcher with information directly.

Sightings were confirmed for eight new locations as a result of the citizen science campaign (Fig 3.1). Sites and variables for national habitat suitability

A total of 1331 lizard sightings (presence) data (76 from online portal, 52 from postcard returns, 1203 from survey effort) were used to develop relative habitat suitability maps at the UK national extent using MaxEnt v3.3.3k software (Phillips et al., 2006) to estimate areas that could be potentially occupied by the species. At the national level I focused on seasonal averages of six climatic variables (predictors) at 5 km resolution (Met Met Office, 2017) that have most relevance to wall lizard biology and therefore likely to influence distribution (Wirga and Majtyka, 2015) (Table 3.1). These six variables were refined from an initial input of 13 climate variables through an iterative process of removal/retention to limit variable correlation and maximise model performance (Glover-Kapfer, 2015).

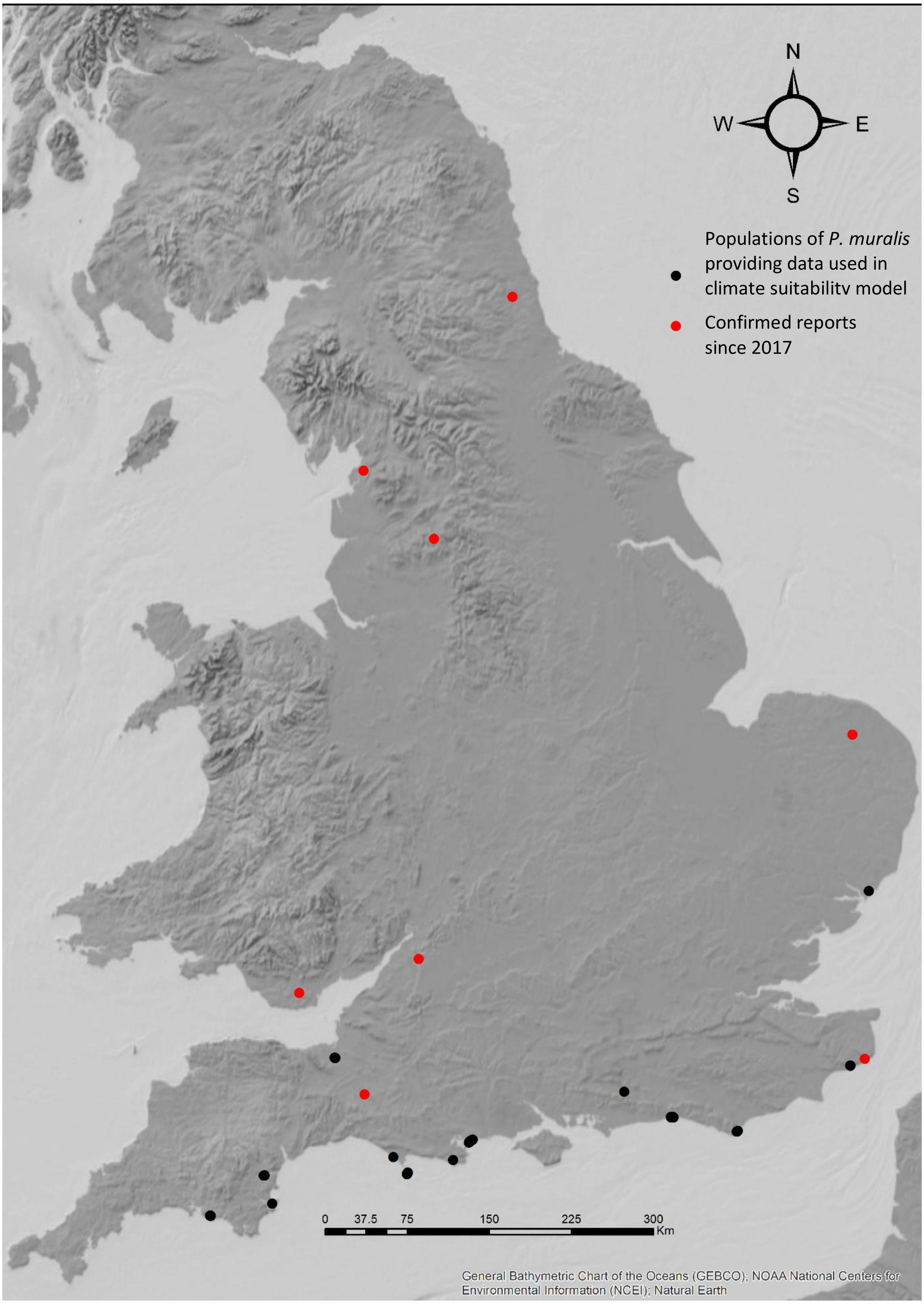


Figure 3-1 Locations of UK breeding populations of *P. muralis* from which presence data informed models of climatic suitability and locations of confirmed sightings arising from a citizen science campaign 2017-2019.

3.3.4 Sites and variables for local habitat suitability and IBM

A total of 1083 presence records (all from direct observation during survey effort) across 10 study locations representing the range of habitats used by *P. muralis* in the UK (urban, suburban, rural) were selected for use in producing relative habitat suitability maps and predictive models of range expansion at a local level. These study sites were surrounded by heterogeneous land use that would provide the most insight into variables affecting local habitat suitability and features that might confer important corridors for range expansion. Data for six environmental variables at 2 m resolution were used for the MaxEnt input and are summarised in Table 3.1. All variables were calculated and prepared in ArcGIS® (Esri 2017).

Fine scale habitat type data layers were created for each study site using the Phase One Habitat Survey Toolkit (Centre for Ecology Environment and Conservation, 2018). This involved drawing polygons around discrete land parcels, as viewed on high resolution satellite imagery and observed in the field, and categorising the habitat according to JNNC classifications (JNNC, 2016). Effort was made to be as detailed as practically possible when creating habitat layers.

3.3.5 MaxEnt modelling

Parameter settings in MaxEnt were kept the same for modelling at the national and local levels and are summarised in Table 3.2. To prevent model over-fitting and assist in the interpretation of outputs I minimised model complexity by restricting the functional form of transformations to linear features and increased the regularisation multiplier to two (Merow et al., 2013; Syfert et al., 2013; Merow et al., 2014). All other settings were kept at default values (Phillips and Dudik, 2008). A jackknife test was used in MaxEnt for assessing the effects of individual environmental variables on the prediction accuracy. Area under the receiver operating characteristic curve (test AUC) was used to evaluate models, where test AUC is as a measure of the model’s ability to accurately predict the habitat suitability of a random sample of presence locations that were not used to develop the model (Elith et al., 2010).

Table 3-1 Details of variables and their data source used in MaxEnt models *of P. muralis* probability of occurrence. Asterisk denotes variables used in local scale models only.

Environmental variable	description	resolution	source
Spring max temp	Average of monthly mean max temp °C (Mar, Apr, May) 1981-2010	5 km	UKCP09 gridded observation datasets (Met Office)
Summer max temp	Average of monthly mean max temp °C (Jun, Jul, Aug) 1981-2010	5 km	UKCP09 gridded observation datasets (Met Office)
Autumn max temp	Average of monthly mean max temp °C (Sep, Oct, Nov) 1981-2010	5 km	UKCP09 gridded observation datasets (Met Office)
Winter max temp	Average of monthly mean max temp °C (Dec, Jan, Feb) 1981-2010	5 km	UKCP09 gridded observation datasets (Met Office)
Frost days	Mean number of frost days in the year (minimum grass temperature below 0°C) 1981-2010	5 km	UKCP09 gridded observation datasets (Met Office)
Annual sunshine	Annual total hours of sunshine duration	5 km	UKCP09 gridded observation datasets (Met Office)
NDVI*	Normalised difference vegetation index	2 m	Calculated from Landsat 8 OLI/TIRS (USGS)
Distance to buildings*	Euclidian distance to buildings	2 m	Calculated from OS Open Map (1:10000) (Digimap®)
Distance to roads*	Euclidian distance to all roads	2 m	Calculated from OS Open Map (1:10000) (Digimap®)
Distance to rail*	Euclidian distance to railway tracks	2 m	Calculated from OS Open Map (1:10000) (Digimap®)
Spring insolation*	Mean incoming solar insolation for months Mar,Apr,May 1981-2017	2 m	Calculated in ArcGIS ®from Lidar DSM 2m (Environment Agency)
Phase 1 habitat*	Habitat classification	2 m	Created using Phase 1 Habitat Survey Toolkit (CEEC, 2018)

Table 3-2 Settings for MaxEnt modelling of *P. muralis* probability of occurrence

Features used	Linear
Output format	logistic
Random Test %	20
Regularization Multiplier	2
Max number of background points	10000
Replicates	5
Replicated run type	Crossvalidate

3.3.6 RangeShifter method

Habitat suitability maps from my local scale MaxEnt models were prepared as habitat quality landscape layers by linear transformation of the MaxEnt logistic values (estimates between 0 and 1 of probability of presence) above the maximum test sensitivity plus specificity logistic threshold. This is the threshold at which the MaxEnt models maximize their discrimination of presences from background data (Jimenez-Valverde and Lobo, 2007; Glover-Kapfer, 2015). The resulting habitat quality landscape (scaled 0-100 and where cell values scale with cell carrying capacity in RangeShifter), in addition to a cost layer to movement created by reclassifying (inverting) the habitat quality landscape layer, provided the input for RangeShifter v1.1 software (Bocedi et al., 2014a). A single cell in each landscape was identified as the initial species distribution (i.e., point of introduction for each population respectively) based on knowledge of the location of introduction when known or by using the centre point of the current extent of sighting records for the population. All inputs were resampled using bilinear interpolation to 15 m x 15 m cell size to reduce demands on computational memory whilst retaining biological relevance to wall lizard movement capabilities.

3.3.7 Model description and parameterisation

This was a complex, polygynous, sexual system with overlapping generations in a three stage population model. Fecundity was set at a maximum of 12 offspring (assuming two clutches per year) with hatchling failure accounted for in survival probability at the juvenile stage. Dispersal probability (*D* in Appendix 3.2) was sex and stage dependent in relation to the effects of density, and was skewed to reflect dispersal predominantly at the natal stage, increasing site fidelity into adulthood (both sexes), and male territory holding (i.e., greater propensity to disperse with increasing density). Movement processes were modelled as stochastic movement simulations (SMS) using cost maps (derived from habitat suitability maps created in MaxEnt) where a relative cost to movement is assigned to each cell. During emigration, movement is away from the natal cell and each individual evaluates their current cell for the possibility of settling, stopping if there is suitable habitat. Settlement rules were further defined to assume settlement to be also under density dependence (i.e., find a suitable cell + density dependence).

Model parameters for demography, fecundity, survival at each life stage, dispersal capabilities, and behavioural attributes were based on estimated values in the literature (Appendix 3.2). Where published empirical data were not available, reasonable judgements and/or simplifying assumptions were made. Parameterisation was further refined through an iterative process, where simulations were repeated across all study sites with fine parameter adjustments within biologically meaningful limits until a single set of parameters was found where simulations modelled as closely as possible the currently observed spatial extent of each study population (Fraser et al., 2015) (Appendix 3.3). The final parameter values used were biologically realistic and justifiably reflect the functional biology of *P. muralis* (Appendix 3.2).

3.3.8 Initialisation

Simulations were initialised using known founder size where documented (Michaelides et al., 2015; Langham, 2019). Where founder size was unknown I used a minimal founder size that resulted in reasonable simulation outputs as per the iterative process mentioned above. I assumed adult age class for all founders. Local extinction probability (i.e., probability that each cell population (independently) goes extinct at each year) was set at a constant of 0.003 across sites to include an element of environmental stochasticity. Simulations (100 replicates) of population range expansion for the 10 study populations were then run for the period of time since introduction (which varies among sites) up to the year 2040.

3.4 Analysis

To investigate how landscape characteristics at each location might influence population size, rate of population growth and range expansion, I first obtained standard population growth metrics: carrying capacity (*K*), and intrinsic rate of increase (*r*), by taking mean yearly population size values from across all simulation iterations and applying linear growth curves in R Studio (R Core Team, 2017) using the package Growthcurver (Sprouffske, 2018). Binary habitat suitability layers from my MaxEnt outputs were then created for a radius of 200 m around introduction points and used as input for the programme FRAGSTATS v4 (McGarigal et al., 2002). I then ran linear regression models with two FRAGSTAT metrics describing heterogeneity of suitable habitat patches within the landscape (Normalised Landscape Shape Index, Connectance) and average habitat quality as explanatory variables, and the growth rate parameters (*k, r*) and annual dispersal distance as response variables.

The Normalised Landscape Shape Index (NLSI) provides a simple measure of class aggregation or clumpiness. NLSI = 0 when the landscape consists of a maximally compact patch of the corresponding type; NLSI increases as the patch type becomes increasingly disaggregated and is 1 when the patch type is maximally disaggregated (i.e., a checkerboard configuration), whereas Connectance is defined on the number of functional joinings between patches of the corresponding patch type, where each pair of patches is either connected or not (McGarigal et al., 2002). The threshold distance within which patches are deemed "connected" was set to an arbitrary 100 m.

3.5 Results

National scale climatic suitability

The MaxEnt model fit at the national scale had an average test AUC score of 0.98 (SD <0.01). The most important variable to the model was ‘number of frost days’ which made the highest relative percent contribution to the model (38.1%). The jackknife test of variable importance also indicated that ‘number of frost days’ had the highest gain when modelled in isolation and decreases the gain the most when it is omitted. ‘Number of frost days’ therefore appears to have the most useful information that isn't present in the other variables. ‘Annual total hours of sun’ had the second highest percent contribution to the model (26.2%), whereas ‘autumn max temperature’ had the lowest (2.9%). The model indicates suitable climatic conditions for *P. muralis* all along the south coast of the UK – from Norfolk in the southeast, to the south coast of Wales. Favourable conditions inland diminish towards a latitude of ~52°N, but are particularly evident in the Greater London Metropolitan area (Fig 3.2).

Podarcis muralis probability of presence responded positively to increasing total hours of sunlight and mean maximum Spring, Summer, Autumn and Winter temperature, although probability of presence diminished past a peak of 3°C with the latter. Probability of presence declined with increasing number of frost days (Fig 3.3)

Local habitat scale suitability

The model fit to the local study areas had an average test AUC of 0.88 (SD = 0.01) over the 10 areas and 50 replicated runs. The most important variable to the model was ‘habitat type’, which made the highest relative contribution to the model (66%). The jackknife test of variable importance also indicated that ‘habitat type’ had the highest gain when modelled in isolation and decreases the gain the most when it is omitted. ‘Habitat type’ therefore appears to have the most useful information that isn't present in the other variables. Ten habitat classes out of 44 stood out as being influential to increased probability of *P. muralis* presence; bare ground (1), residential garden (2), dense scrub (5), scattered scrub (6), rail track (17), road (18), introduced shrub (22), dry dwarf shrub (25), hard cliff (28), and quarry (37) (Fig 3.4). Spring radiance had the second highest percent contribution to the model (15%), where the amount of spring solar insolation had a positive influence on probability of presence (Fig 3.4). Probability of occurrence was also negatively correlated with increasing distance from buildings, rail track, and roads. The response to NDVI is one of increasing probability of presence with an increase in vegetation from bare ground followed by a rapid negative response past NDVI = 0.25. Maps indicating configuration of suitable habitat within local landscapes are presented in Figure 3.5 and Appendix 3.4).

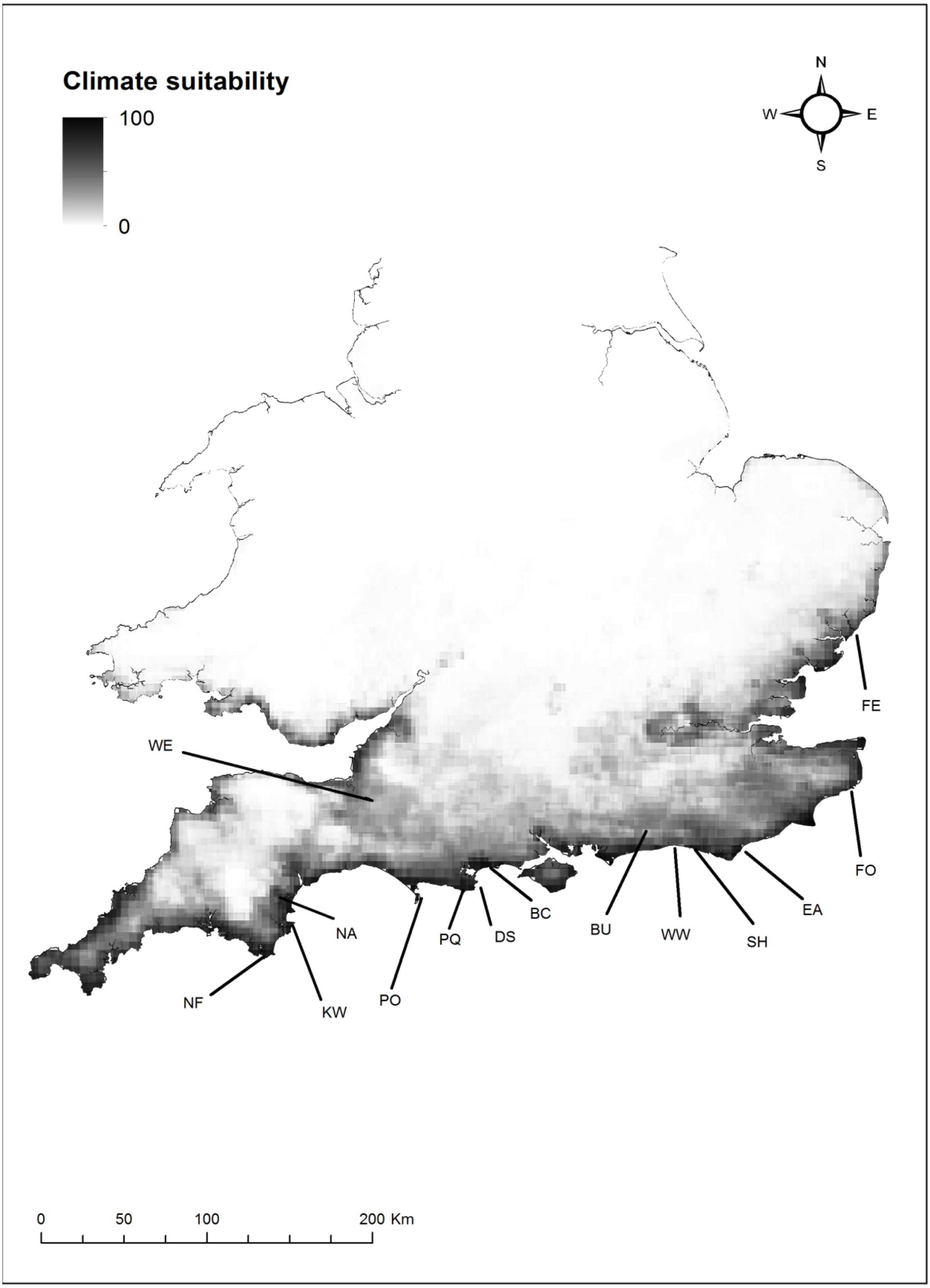


Figure 3-2 Regions of climatic suitability for *P. muralis* in the UK as predicted by MaxEnt models considering seasonal averages of six climatic variables. Locations of major populations from which presence data informed model output: WE, Wembdon; NF, Newton Ferrers; KW, Kingswear; NA, Newton Abbot; PO, Portland; PQ, Purbeck quarries; DS, Durleston Head; BC, Bournemouth coast; BU, Bury; WW, West Worthing; SH, Shoreham; EA; Eastbourne; FO, Folkestone; FE, Felixstowe.

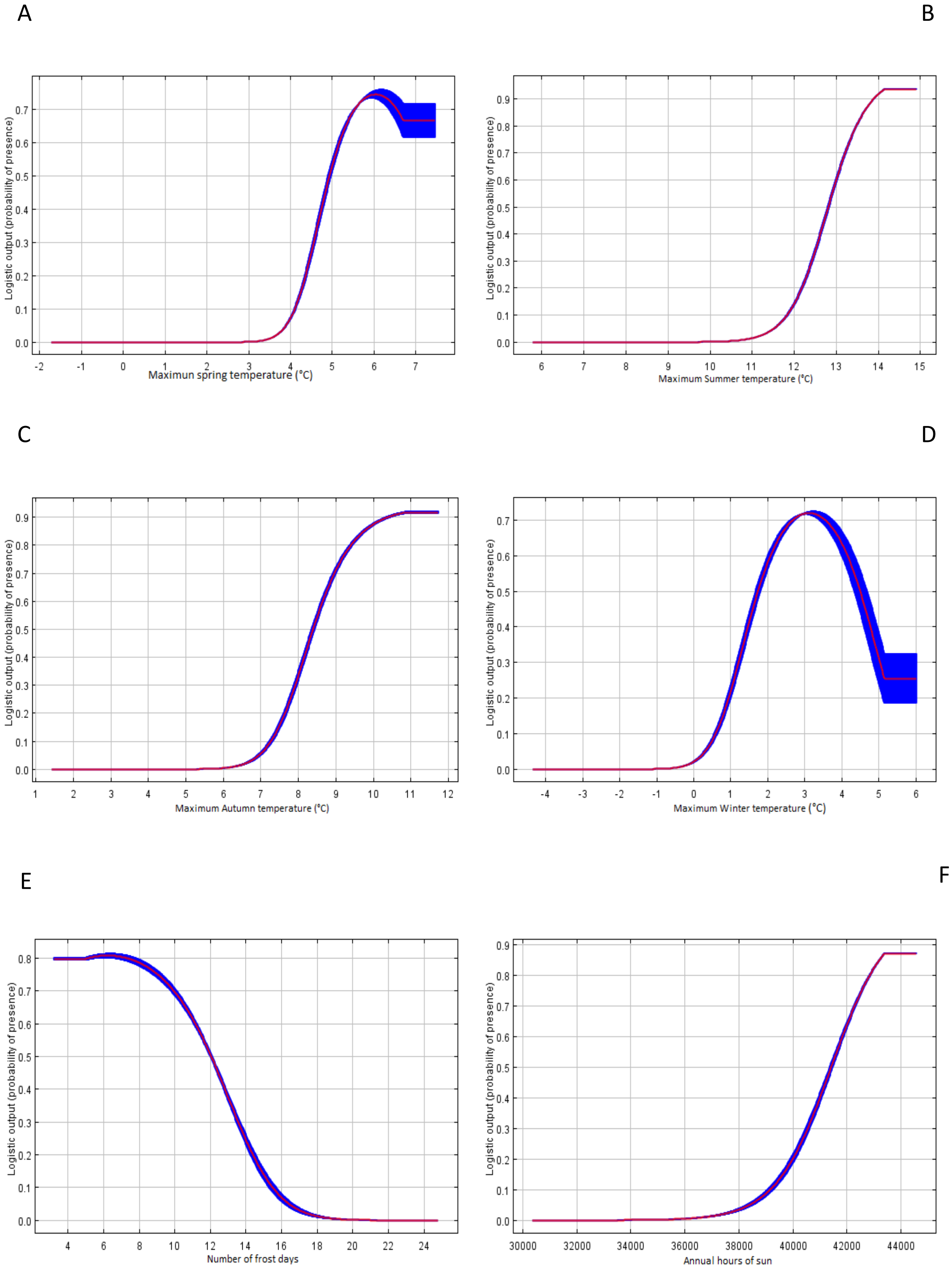


Figure 3-3 Response of *P. muralis* (probability of presence) to six climate variables as modelled in MaxEnt at the UK national scale: A) Maximum Spring temperature, B) Maximum Summer temperature, C) Maximum Autumn temperature, D) Maximum Winter temperature, E) Number of frost days, F) Annual duration (hours) of bright sun shine.

Individual-based models results

Patterns of range expansion from time since introduction to 2040, as determined by population dynamics and local landscape character, are presented in Figure 3.5 and in Appendix 3.3. Growth curves for the 10 study populations are presented in supplementary information (Appendix 3.4). Growth rates ranged from 0.07 (Shoreham) to 0.15 (Eastbourne). Following simple stepwise linear regression analysis (Table 3.3), growth rate (*r*) was positively related to the NLSI ($F_{(1, 9)}$ = 8.39, p = 0.02, R^2 = 51.13), and negatively related to time since introduction ($F_{(1, 9)}$ = 5.80, p = 0.04, R^2 = 42.22) (Fig 3.6 A, B). Branksome and Canford – two populations on the Bournemouth coast – had the highest carrying capacity (10443 and 10315 individuals, respectively). Eastbourne had the lowest carrying capacity (1447). A positive relationship between habitat quality and carrying capacity ($F_{(1,9)}$ = 6.22, p = 0.03, R^2 = 43.74) was the only relationship observed between this growth parameter and the explanatory variables (Table 3.3). Annual dispersal distance was best explained by combined increases in NLSI and habitat quality ($F_{(2,9)}$= 29.65, p <0.001, R^2 = 89.44) (Fig 3.6 C), although habitat quality was not a significant predictor of annual dispersal distance on its own ($F_{(1, 9)}$ = 1.21, p = 0.34, R^2 = 13.14). Greatest annual dispersal was predicted for the Eastbourne population (16 m), whilst the Shoreham, Wembdon, and Newton Ferrers populations had similar low dispersal of ~4 m per year. Connectance between suitable habitat patches had no relationship with any of the dependent variables.

Table 3-3 Summary of separate stepwise regression analysis showing significant variables predicting growth rate (*r*), carrying capacity (K), and annual dispersal distance of introduced *P. muralis* populations in the UK (N = 10)

	Predictors	β	SE	p	R^2
Population growth rate (r)	NLSI	0.30	0.10	<0.01	0.522
	Time since introduction	<-0.01	<0.01	0.04	
Carrying capacity (K)	Habitat quality	218.8	87.8	0.03	0.437
Annual dispersal distance	Habitat quality	0.29	0.05	<0.01	0.894
	NLSI	68.18	9.59	<0.01	

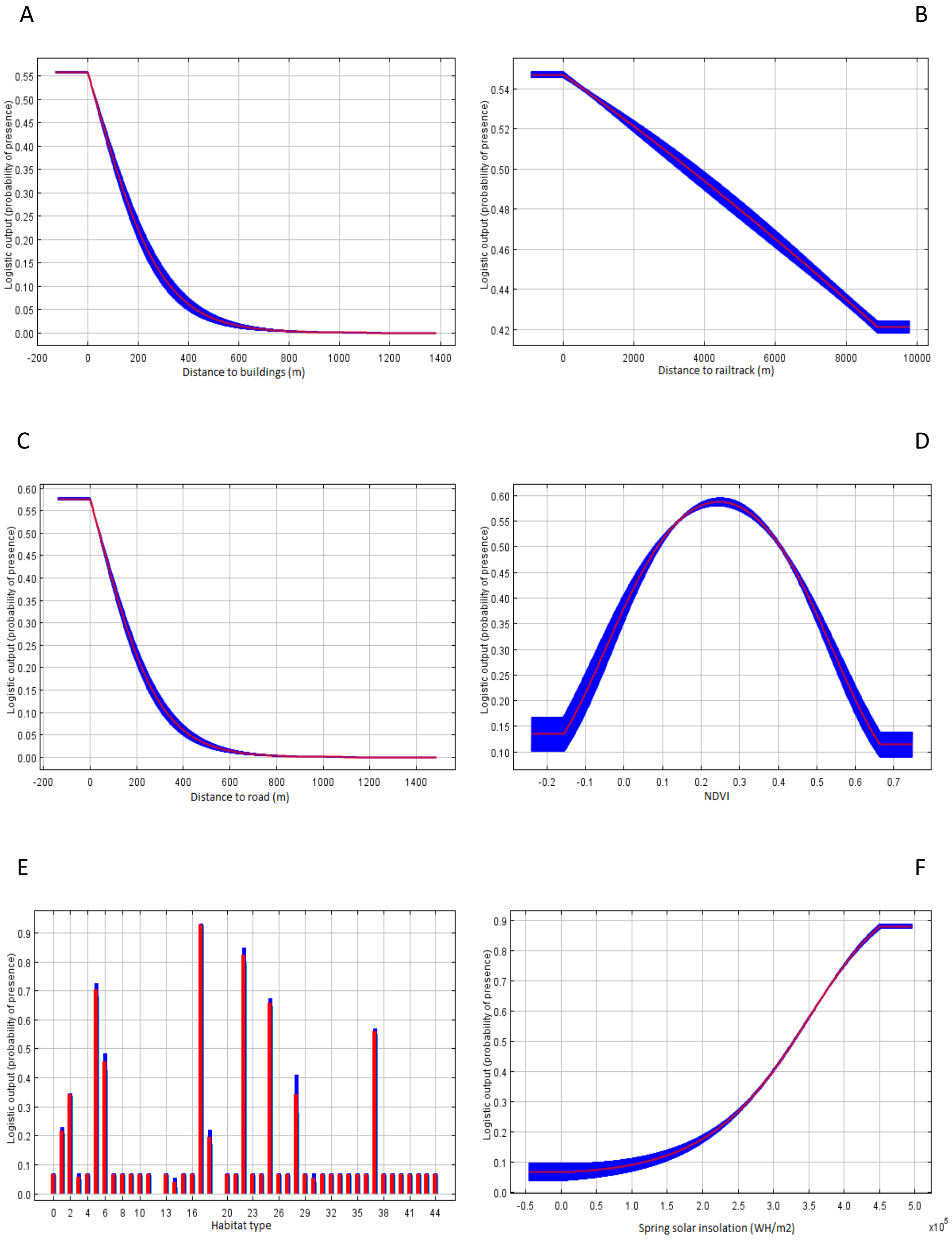


Figure 3-4 Response of *P. muralis* (probability of presence) to six environmental variables as modelled in MaxEnt at the UK local scale: A) Distance to buildings, B) Distance to rail, C) Distance to roads, D) NDVI, E) Habitat type, F) Spring solar insolation

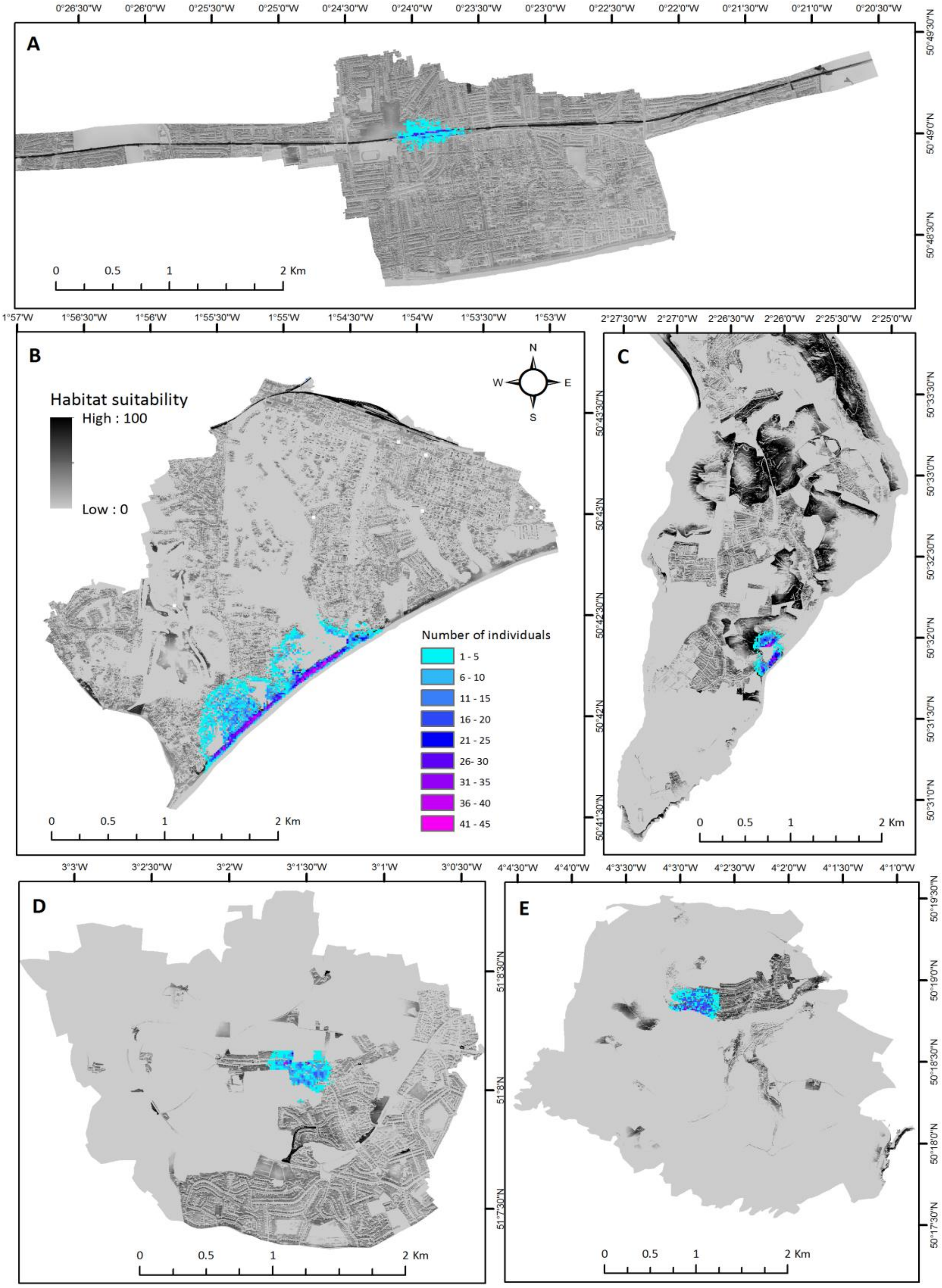


Figure 3-5 MaxEnt outputs showing local extent and configuration of suitable habitat for *P. muralis* populations in the UK. Order demonstrates the range of variance in patch fragmentation, patch isolation, and linear features of suitable habitat across local landscapes: A) West Worthing, B) Bournemouth (including Boscombe and Canford populations), C) Portland, D) Wembdon, E) Newton Ferrers. Outputs from RangeShifter models are overlain, indicating patterns of population dispersal projected from year of introduction to 2040 and number of lizards per occupied 225m^2.cell

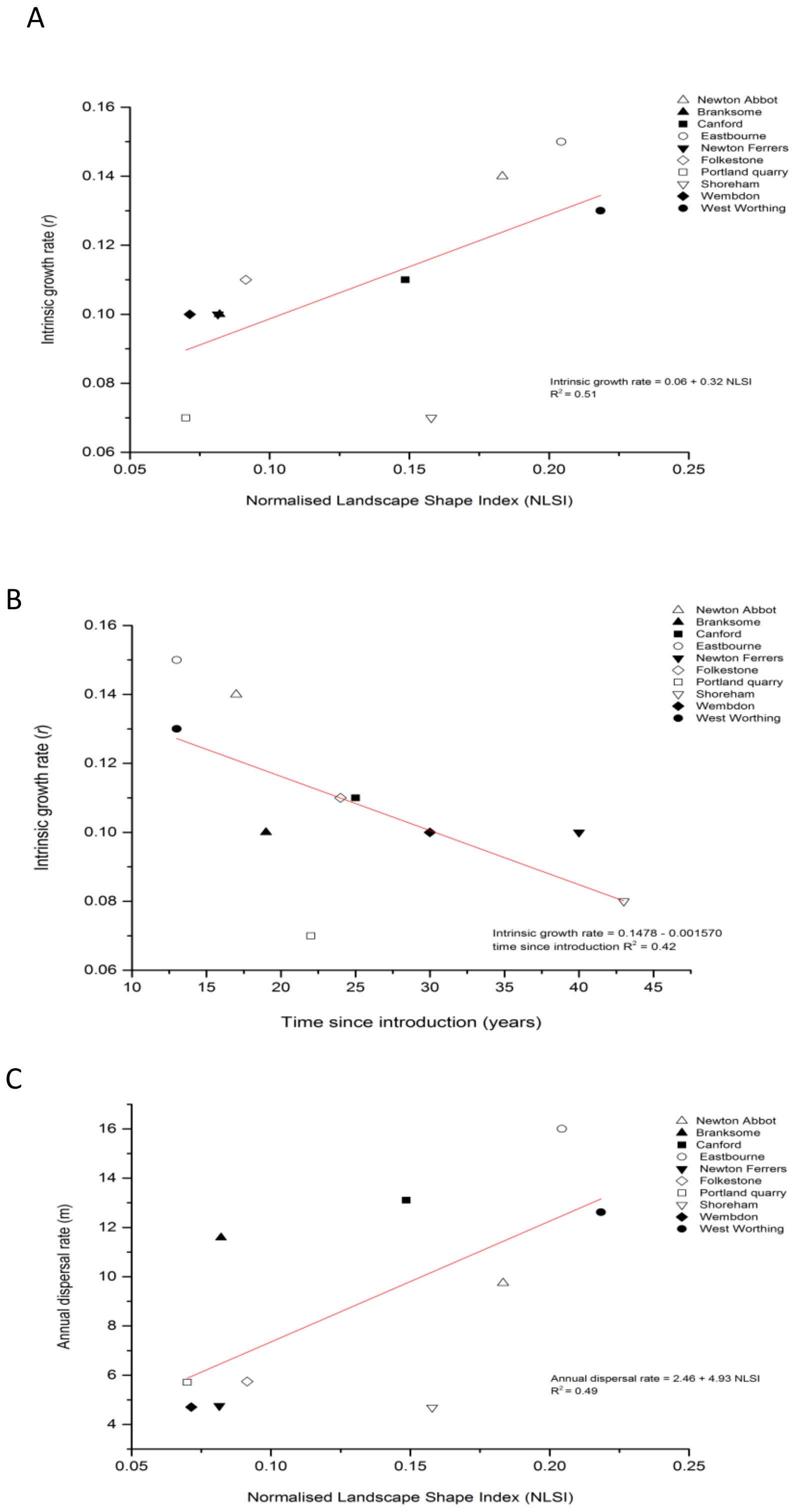


Figure 3-6 Relationship between growth rate (*r*) and A) aggregation of suitable habitat (NLSI), time since introduction B), and C), relationship between NLSI and annual dispersal distance in non-native population of *P. muralis* in the UK

3.6 Discussion

The predicted suitable climate for *P. muralis* in the UK is contiguous along the south east coast, the entire south coast, and through to the south coast of Wales; a latitudinal range likely to reflect climatic conditions most akin to those found in the introduced populations' native origins. My model also accurately predicted the Isle of Wight (where *P. muralis* has been present since the 1920's) to be climatically suitable, despite not including presence data from this locality. This southern limit is in keeping with climate matching being an important limiting factor in determining establishment success and range expansion of introduced species, and particularly significant for reptiles (Bomford et al., 2009; Pysek et al., 2010b; Mahoney et al., 2015). A previous SDM of *P. muralis* using similar methods to mine also highlighted the southern coast of the UK having most favourable climate for *P. muralis,* but differed by indicating a much larger extent of suitable conditions comprising all of southern UK (Wirga and Majtyka, 2015). However, direct comparison between the two models is not possible due to a differing suite of climatic variables and species presence data informing the models. The species has demonstrated prolonged embryo retention and faster embryonic growth at low temperatures - compared to ancestral states - in a rapid adaptive response to introduction to a cool climate in the UK (While et al., 2015b). For this reason, only *P. muralis* presence records from the introduced UK range were used in my MaxEnt model as they best reflect the current climatic tolerance of the species and secondary introductions from established populations are the primary concern for the species extending its range in the UK.

My model shows that number of frost days and amount of annual sunshine were most informative in predicting probability of occurrence. As mentioned above, *Podarcis* spp. have shown remarkable adaptive potential and rapid response to novel climatic conditions in introduced regions (While et al., 2015b). Even so, as has been speculated elsewhere, the ability to survive cold winters is likely limiting to spread of introduced *Podarcis* populations (Burke et al., 2002), as sudden or prolonged freezing in wet conditions, that would likely be encountered under shallow hibernation refuge, is beyond even the species' capacities for supercooling (Claussen et al., 1990). Hibernation period is short in *P. muralis* and individuals are often active in mid-winter during sunny mild spells, even in the northern extremes of their range, making them vulnerable to sudden changes in the weather (Claussen et al., 1990). Measurements of critical thermal minimum temperature in an introduced population of *P. sicula* have been shown to be above temperatures likely experienced by some non-native populations in winter, suggesting individuals may need to find urban thermal retreats to survive winter conditions, or hibernate at a depth below soil freezing to survive (Burke et al., 2002; Liwanag et al., 2018). Interestingly, my model accurately predicted the Greater London Urban Area as having relatively high habitat suitability, likely arising from matching to thermal characteristics associated with the "urban heat island" (UHI) effect (Trajer et al., 2014; Villalobos-Jimenez and Hassall, 2017). There are historic records of small, established *P. muralis* populations persisting in this area (Langton et al., 2011; Langham, 2019), and since I did not include these records in the input for the model (due to no recent confirmed sightings and no accurate location data), the predicted suitability in this area gives credence to the validity of the model and the theory of UHI in built environments facilitating overwintering for the species.

Extensive nationwide range expansion through secondary introduction is therefore likely to be restricted by currently unsuitable climate beyond the most southerly regions of the UK. However, growth of local populations in habitats providing transport pathways (i.e., movement of aggregates, timber, plants) is likely to increase opportunities for regional expansion.

The fine scale modelling of probability of occurrence has provided a detailed insight into local landscape structure and spatial pattern of suitable habitat availability. To generalise, the contribution of habitat classification and Spring solar insolation to the model, and the overall response to environmental variables, particularly the unimodal response observed toward vegetation cover (NDVI), is indicative of the species' affinities to disturbed habitats that provide resource for refugia (thermal and safety), egg deposition sites, and basking sites necessary for heliothermic temperature regulation (Bertram, 2004; Gherghel et al., 2009). It is possible that even though great effort was applied to assign habitat type in as much detail as practical, generalisations made during the construction of the habitat classification layer could possibly lead to overestimation of the extent of suitable habitat (e.g., not all habitat classed as residential garden would in reality be suitable to *P. muralis*). However, the combined effect of the NDVI variable would go some way to enhance fine-scale delineation between suitable and unsuitable habitat type.

The relative importance of railway line and introduced shrub habitat in the model can be explained by the number of presence records associated with those habitats in relation to the relative scarcity of those habitats in the landscape. Habitat associated with railway lines has been documented elsewhere as providing important habitat for *P. muralis*, facilitating both natural dispersal and accidental human movement of animals (Covaciu - Markov et al., 2006; Kühnis and Schmocker, 2008; Strugariu et al., 2008; Gherghel et al., 2009). Dispersal of the introduced population in Ohio, Cincinnati, has been reported to be more rapid along the continuous hospitable terrain of rail embankments compared to the relatively slow spread through highly fragmented residential and commercial areas (Hedeen and Hedeen, 1999). Although my simulations of the West Worthing population did have relatively higher dispersal distance than most other populations, the pattern of spread did not indicate extensive natural dispersal along the railway, despite the core population being centred on and around disused sidings and associated habitat. Instead, the simulated dispersal pattern is one of predominantly radial diffusion out into adjacent residential and commercial areas, where, although highly fragmented, the habitat was of suitable quality to facilitate this pattern of spread. Such corridors may therefore only become important to natural dispersal when adjacent habitat is of low quality or is less preferred, as is the case of invasive cane toads (*Bufo marinus*) selecting to use open roads for dispersal through less favourable vegetated habitat (Brown et al., 2006). The presence of other contiguous, linear habitat features in my landscape models also increased rates of annual range expansion (e.g., vegetated cliff faces at Branksome and Canford; sea front garden along the promenade at Eastbourne), but this is likely a result of there being restrictions to radial dispersal as suitable habitat is bordered by inferior inland habitat and the shore line. These findings are congruent with the theory that corridors may be most effective when they actively influence, direct, and channel dispersal rather than simply provide additional suitable habitat (Andrew and Ustin, 2010).

The potential role of the railway in facilitating secondary dispersal is arguably more important rather than it functioning as a corridor to natural spread, particularly at the West Worthing site. Secondary dispersal is indicated by the fact that the simulated natural dispersal pattern for the West Worthing population does not account for my observations of a small number of individuals recorded at a rail station some 820 m west from the core population, despite ample dispersal capability being included in the model (max number of steps yr. = 45, therefore maximum dispersal distance (at 15 m steps) per year is 675 m min straight line distance) (movement distances of *P. muralis* inferred from mark-recapture studies range from 50 m/h to 500 m/1–3 years (Schulte et al., 2013)). And since no sightings were recorded along the intermediate length of rail track, this suggests assisted jump dispersal may be an explanation in this case.

The shape of predicted growth curves was similar across all the study populations and clearly shows the populations to be in the early stages of exponential growth, with no obvious protracted periods of slow growth (lags) apparent – beyond that expected from the exponential growth function – between the time since introduction and the 2040 projection. The negative correlation between intrinsic growth rate and time since introduction is to be expected as a function of logistic growth, where the longer-established populations approach local carrying capacity and density dependence constrains growth (Sibly and Hone, 2002).

My simulations suggest that natural dispersal of *P. muralis* from points of introductions in the UK is likely to be slow (Foster, 2015), with annual population range expansion of between 5 -16 meters. Spread distances were particularly small for populations in areas of relatively contiguous suitable habitat which allows for radial dispersal into suitable neighbouring habitat with limited search effort (i.e., rural villages with interconnected gardens, quarries) (Bonte et al., 2012; Baguette et al., 2013). In such instances it would appear that populations with limited opportunities/need for long distance dispersal are increasing their populations locally, but will be limited for establishing a population over a large area (Lustig et al., 2017).

Increasing disaggregation of suitable habitat had a joint positive influence on dispersal rate and growth rate in my models. This suggests that increasing abundance of discrete local patches of suitable habitat provides opportunity for individuals to disperse more widely in the landscape and thus release density dependent constraints on population growth that would be in effect when suitable habitat is more aggregated and compact. These findings are most apparent in the urban population of West Worthing, and highlights the ability of the species to exploit areas of human disturbance that may facilitate overall invasion success (Marvier et al., 2004). This pattern is in line with the theories of a percolation threshold where invasive spread may occur most rapidly and extensively above a threshold level of disturbance (i.e., amount of habitat fragmentation) (With, 2002). In addition, functional connectedness of suitable habitat patches had no relation to any of the growth parameters or rate of spread, indicating that localised habitat fragments are acting as stepping stones to dispersal (Alharbi and Petrovskii, 2019). Similar effects of landscape heterogeneity on range expansion have been observed in introduced populations of whistling frog (*Eleutherodactylus johnstonei*) (Ernst et al., 2011), American mink (*Neovison vison*) (Fraser et al., 2015), Eurasian collared dove (*Streptopelia decaocto*) (Ingenloff et al., 2017), and invasive weeds (Bergelson et al., 1993).

Despite the fundamental physiological importance of sun exposure to diurnal reptiles, to the best of my knowledge the models presented here are the first to incorporate estimates of solar insolation into models of probability of occurrence at this fine scale (but see Bennie et al. (2008) for a detailed discussion on use of solar influx as a variable in modelling fine scale topographic microclimate). My results suggest the inclusion of the variable at this scale, and indeed my entire approach to developing a fine scale SDM, could be very useful in other applications relating to reptile ecology (e.g., in developing habitat suitability indices, directing habitat management, guiding survey effort for conservation purposes/cryptic invasives). Furthermore, whilst the use of SDM and IBMs have become a widely used to further understanding of mechanisms driving invasion dynamics (Kadoya and Washitani, 2010; Fraser et al., 2015; Suzuki-Ohno et al., 2017), the benefits of incorporating spatially explicit individual based models into management plans for the control of invasive species has only recently been recognised (Day et al., 2018). In this regard, my models provide a best estimate for future expansion of *P. muralis* at both the UK national and local scale, and essential information (i.e., dispersal patterns, key habitat, current and projected population size) on which management decisions could be made.

Chapter 4: Morphological divergence and bite performance as indicators of invasion potential in introduced wall lizard (*Podarcis muralis*) populations

4.1 Abstract

Adaptive morphological plasticity can play a beneficial role when species become established in a novel environment, allowing organisms to maximise fitness and survival in prevailing conditions. Morphological adaptations are subsequently expected to be associated with optimisation of ecological performance for a particular niche. The capacity for rapid adaptive phenotypic evolution, which can arise as a result of both random genetic drift and natural selection is regarded as an important trait influencing species establishment in novel environments and invasion success. I investigated levels of divergence in body size, head dimensions, bite force and diet between 12 introduced populations of the Common wall lizard (*Podarcis muralis*) at the northern extent of its range in the UK, and the introduced population on Vancouver Island, Canada, to understand how an adaptive response may contribute to the invasion potential and impact of an introduced species. In addition, I considered how these traits compare with those of native lizards (*Lacerta agilis*, *Zootoca vivipara*, and *Elgaria coerulea*) with which *P. muralis* may be in direct/indirect contest and the implications for niche overlap, interaction outcomes, and invasion success. I found significant variation in body size and head morphology between introduced populations, although this variation may be largely explained by ancestral divergence in morphology between animals of French and Italian lineage rather than being reflective of adaptive response post-introduction. The form-function relationship between head morphology and bite force was generally maintained within populations of shared lineage, although variation in relative influence of head components on allometric scaling of bite force with body size suggest this system is highly flexible and susceptible to natural and sexual selective forces. Comparison of morphological and form-function traits between introduced *P. muralis* and native lizards suggest considerable niche overlap and thus high potential for competitive interaction.

4.2 Introduction

Exposure to novel structural, biotic and climatic characteristics of the environment can exert ecological pressures on organisms, and shape phenotypic adaptation and morphological diversification to maximise fitness and survival in prevailing conditions (Gomes et al., 2016; Haenel, 2018; Fox et al., 2019). Such divergence can be apparent in local adaptations of widespread species that occupy a diverse range of habitats imposing different selective pressures (Diamond et al., 2018; Pepino et al., 2018; Taylor et al., 2018; Bodensteiner et al., 2019). These morphological adaptations can be driven by response to abrupt environmental shifts such as changes in habitat structure (Vitt et al., 1997; Winchell et al., 2016), response to interactions with predators, prey and competitors (Roughgarden, 1976; Herrel et al., 2008; Losos, 2011; Jaffe et al., 2016; Barquero and Bolanos, 2018), and can occur over clines in environmental gradients (i.e., salinity, temperature) (Gomes and Monteiro, 2008; Campbell-Staton et al., 2016; Dudaniec et al., 2018). The evolutionary significance of such morphological variation is measured by the degree to which specific adaptive traits relate to increased functional performance of an organism to carry out key tasks (Wainwright, 1991; Irschick, 2003; Kingsolver and Huey, 2003). As such, morphological adaptations are expected to be associated with variance in function, for example, cranial structure and bite force (Herrel and Holanova, 2008; Da Silva et al., 2016), limb morphology and locomotor performance (Colombo et al., 2016; Donihue, 2016a). These adaptations, in turn, translate into variation in fitness among individuals/populations for a specific environment (Arnold, 1983; Irschick et al., 2008; see also Lailvaux and Husak, 2014). This ecomorphological paradigm is an underlying framework within which interactions between species and their environment shape morphology and functional capability to promote the exploitation of different ecological resources and coexistence within guilds of ecologically similar, syntopic species (Losos, 1990; Simberloff and Dayan, 1991; Losos, 2009).

Adaptive phenotypic change can occur rapidly in populations experiencing abrupt environmental shifts and divergent regimes of natural selection (Reznick and Ghalambor, 2001; Salamin et al., 2010; Shimada et al., 2010; Fox et al., 2019), as demonstrated in the extreme by the phenotypic shift in limb and toepad morphology of Anolis lizards (*Anolis scriptus*) surviving hurricane events (Donihue et al., 2018). The rapid rate at which divergence between populations can occur can also be evidenced in real time following the introduction of species beyond their natural range and examination of the subsequent adaptive response to new environments (Westley, 2011; Franks and Munshi-South, 2014; Colautti and Lau, 2015). Indeed, the capacity for rapid adaptive phenotypic evolution, which can arise as a result of both random genetic drift and natural selection (Kolbe et al., 2007; Lande, 2015), is regarded as an important trait influencing species establishment in novel environments and invasion success (Sax et al., 2007; Flores-Moreno et al., 2015; Wang and Althoff, 2019). This is particularly true in cases where a species is introduced to regions at the latitudinal limits (or beyond) of their native range, and perhaps climatic tolerance, where rapid adaptation in a way akin to niche evolution is necessary in order to persist and further expand their range (Sexton et al., 2009; While et al., 2015b). Furthermore, phenotypic shifts during the range expansion of invasive species may be sex-specific, and are potentially related to the degree of realized niche shift that has occurred between the source and introduced range (Miller et al., 2017).

Phenotypic plasticity can allow for introduced populations to persist in novel environments, increasing the opportunity for directional selection to act on genetic variation and thus facilitating local adaptation (Rasner et al., 2004; Fischer et al., 2016; Mittan and Zamudio, 2019; Westrick et al., 2019). For example, introduced populations of Burmese pythons (*Python molurus bivittatus*) in Florida, USA, show directional selection in genomic regions enriched for genes associated with thermosensitivity, behaviour and physiology in an adaptive response to freeze events, a key factor in the species' invasive success (Card et al., 2018). Furthermore, multiple introductions and/or hybridizations between individuals from different source populations may increase genetic heterogeneity and promote local adaptation, causing non-native populations to differ from their native-range counterparts and from each other, with potentially significant bearing on invasive potential and range expansion (Kolbe et al., 2004; Kolbe et al., 2007; Rius and Darling, 2014; Le Gros et al., 2016; Michaelides et al., 2018).

Although capacity for adaptation is an important trait for invasive potential, a degree of preadaptation to local environments is a prerequisite to the successful establishment of species following introduction (Hayes and Barry, 2008; Ferreira et al., 2012a; Mahoney et al., 2015). As such, there is often a high degree of niche overlap between closely related native and invasive species, increasing the likelihood of resource contest and interference interactions, the outcomes of which can have significant implications for native species and the invasion process (Short and Petren, 2012; Stroud et al., 2017; Hernandez-Brito et al., 2018). Competitive interactions are generally categorised as either direct interference, with one species aggressively displacing the other from a shared resource during agonistic encounters where the species with greater fighting ability is expected to dominate (Peiman and Robinson, 2010; Lailvaux et al., 2012; Dufour et al., 2018b), or indirect as in exploitative competition where the ability of a competitor to acquire a key resource excludes or reduces the other species from obtaining the same resource (e.g., prey, refuge, basking space) (Petren and Case, 1996; Cadi and Joly, 2003; Cole and Harris, 2011). Outcomes of conflict arising from such overlap are often asymmetrical, most demonstrably in relation to body size (Smith and Brown, 1986; but see Langkilde and Shine, 2007; Eichenberger et al., 2009; Chock et al., 2018), which in time can lead to niche segregation, character displacement, exclusion of inferior competitors from a particular niche, and ultimately local extinction (Schoener, 1983; Cadi and Joly, 2003; Cole and Harris, 2011; Williams et al., 2016; Dufour et al., 2018a). Understanding the extent of local adaptation is therefore crucial to predicting the spread of invasive species and their interaction with native species (Phillips et al., 2010; Colautti and Lau, 2015).

Large-scale macroecological patterns, such as Bergmann clines in body size, may also interact with invasion through the mediation of traits that determine competitive outcomes. Rapid range expansions that involve the extension of latitude-size patterns (e.g. Hassall et al. 2014) may have concomitant impacts on traits such as body size and head morphology and their associated functionalities (i.e., bite force, prey handling, diet breadth, and fighting ability). Whereas phylogenetic evidence reveals that endotherms follow Bergmann's rule, the degree to which ectothermic species might follow latitude-size patterns is debateable owing to their specific physiological and behavioural mechanisms for regulating body temperature (Pincheira-Donoso et al., 2008). Some studies on amphibians and squamate reptiles suggest that a smaller body size might enable more efficient thermoregulation in colder climates in a reversal of Bergmann´s cline and that different trends can be found within a genus or even within the same species (Ashton and Feldman, 2003; Ortega et al., 2019).

Lizards are model organisms in ecomorphological studies that have investigated the relationships between whole-organism performance and functional morphology in various contexts: interspecific scaling of jumping ability (Toro et al., 2003), relationship between secondary sexual characters and bite performance (Vanhooydonck et al., 2005; Baeckens et al., 2018), limb morphology, locomotion, and habitat use (Donihue, 2016a; Haenel, 2018; Lowie et al., 2019), and the link between agonistic interaction and morphology (Barquero and Bolanos, 2018). For example, head morphology of lizards and its relation to bite performance has received much attention owing to the repercussions for multiple and highly relevant ecological and social interactions, such as feeding (Sagonas et al., 2014; Dollion et al., 2017), mating success (Herrel et al., 2010), and aggressive interactions (Donihue et al., 2016; Baxter-Gilbert and Whiting, 2019). In addition, lizard species have long been an important model for research on the occurrence of competition in nature and investigations into its role in shaping ecological communities (Pianka and Huey, 1978; Ricklefs et al., 1981; Schoener, 1983; Losos, 2000).

The introduction history of the common wall lizard (*Podarcis muralis*) beyond its native European range features several characteristics conducive for local adaptation to arise (Reznick and Ghalambor, 2001; Colautti and Lau, 2015), thus making it an excellent study model for investigating contemporary evolution following colonisation into new regions. Numerous separate introductions of generally small founder size have resulted in an extensive introduced range not only in continental Europe, but also established populations across southern England and in North America (Hedeen and Hedeen, 1999; Münch, 2001; Allan et al., 2006; Lescano, 2010; Schulte et al., 2011; Sas-Kovacs and Sas-Kovacs, 2014; Michaelides et al., 2015; Šandera, 2017). In many instances the species persists in isolated populations, but appears to inhabit a broad variety of habitat types (Foster, 2015). In several cases, as in the UK, these introduced populations have also extended the species' range northwards to the limits of climate suitability (Strijbosch et al., 1980; Gassert et al., 2013; While et al., 2015b). Furthermore, the introduction history (particularly in the UK) has involved multiple release events of animals from multiple source populations of Italian and French origin (Michaelides et al., 2015), resulting in some populations having genetic admixture through interbreeding of individuals from multiple source locations (Michaelides et al., 2013).

Within the introduced range of *P. muralis* potential exists for novel competitive interaction with native lizards. In the UK, the range of *P. muralis* populations overlap that of the widespread common lizard (*Zootoca vivipara*), and in some areas that of the nationally endangered (Woodfine et al., 2017) sand lizard (*Lacerta agilis*) (Mole, 2010; Foster, 2015). On Vancouver Island, *Podarcis muralis* is becoming ubiquitous around the suburbs of Victoria where it is found in sympatry with the Northern alligator lizard (*E. coerulea*), a species of provincial conservation concern in British Columbia (B.C. Conservation Data Centre, 2003).

In this study, I investigated aspects of morphology, bite performance and diet in introduced populations of *P. muralis* from the UK and Vancouver Island, Canada. My aims were three-fold: firstly, in consideration of the potential for rapid local adaptation within this model system, I sought to determine if there is divergence in body size, head dimensions, bite force and diet among introduced populations. Secondly, I considered how these traits might compare with those of native lizards with which *P. muralis* may be in direct/indirect competition and the implications for interaction outcomes. Bite force serves a good functional indicator regarding these two aspects of competition as it has a direct influence on the size and hardness of prey that can be acquired (Herrel et al., 2001; Verwaijen et al., 2002; Kaliontzopoulou et al., 2012), and the outcome of fighting/territoriality in lizards (Husak et al., 2006; Herrel et al., 2007; Herrel et al., 2010; Donihue et al., 2016; Dufour et al., 2018b). Furthermore, as bite force and related head morphology in lizards are also under sexual selection due to male–male competition and mating behaviour – often leading to male biased dimorphism in these traits – the ecomorphological and functional differentiation between sexes is also relevant in species interactions (Zagar et al., 2017). Finally, I examine patterns of allometry across native and invasive lizards that may infer changes in competitive ability due to latitudinal body size clines accompanying the poleward invasion.

4.3 Methods

To quantify variation in morphological characters relevant to bite force and prey consumption between populations and species I measured snout-vent length (SVL) as a measure of body size, and four head characters: head length (HL) from the tip of the snout to the posterior border of the collar, head width (HW) at the widest point of the head, head height (HH) at the tallest point of the head (Fig 4.1). I also determined an additional measure of head size (HS) using the geometric mean approach as calculated from the third root of the product of head length, head width and head height (Mosimann, 1970; Kaliontzopoulou et al., 2012). All measurements were taken to the closest 0.01 mm using electronic callipers.

Morphometric data were obtained from a total of 652 *P. muralis* across 12 introduced populations in the UK (n= 548), the introduced population on Vancouver Island from locations around the Fairfield district of Victoria (48.24 °N, -123.20 °E, n= 79), and a native population from Saulnay, France (46.86 °N, 1.26 °E, n= 25) (Chapter 2, Fig 2.1). UK populations were sampled between May-August from 2016-2018; the France population in August 2017; and the Vancouver Island population in July 2018.

For comparison with native lizard species I also sampled *Z. vivipara* (11 females, 7 male) and *L. agilis* (11 female, 19 male), caught as part of active mitigation translocations at three UK sites: High Wycombe, Buckinghamshire (51.61 °N, - 0.71 °E) and West Malling, Kent (51. 28 °N, 0.32 °E) in August 2018 (*Z. vivipara*); and East Stoke, Dorset (50.69 °N, -2.19 °W), in June 2018 (*L. agilis*). Native *E. coerulea* (11 female, 7 male) were caught at Kingzett Lake quarry (48.67 °N, -123.63 °E) and Mt. Douglas, VI (48.49 °N, -123.34 °E), during July 2018. All individuals were caught either by hand or through noosing, and in the case of native lizards, returned to point of capture or respective receptor sites. Non-native *P. muralis* were euthanized (pithing and decapitation) following anaesthesia with 25% Benzocaine gel via oral administration (G.Hanke, pers comm.) and stored in 90% ethanol (the abdominal wall being slit to ensure rapid fixation of the viscera) for further study.

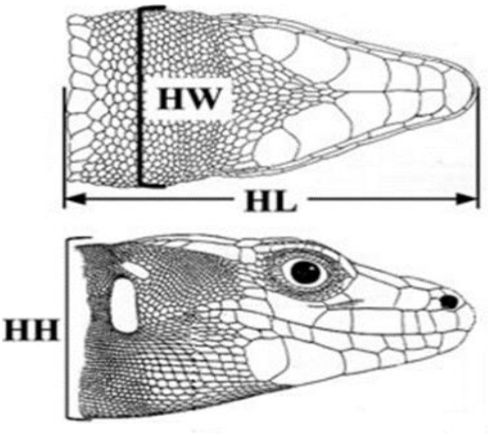


Figure 4-1 Linear head measurements taken from all lizards. HW = head width, HL = head length, HH = head height (after Kaliontzopoulou et al., 2012).

Bite force was measured *in vivo* for eleven introduced populations of *P. muralis* in the UK, the Vancouver Island *P. muralis*, and the native species (*Z. vivipara, L. agilis. E. coerulea*) using an isometric Kistler force transducer (type 9203, Kistler Inc., Wintherthur, Switzerland) mounted on a purpose-built holder (see Herrel et al., 2001 for detailed description). The natural defensive behaviour of lizards was provoked during handling to entice bites onto a pair of thin metal plates (connected to the transducer). The position at which bite force is exerted onto the plates and the vertical distance between plates can significantly affect bite force measurements (Herrel et al., 2001; Lappin and Jones, 2014). The procedure was therefore standardised by having lizards bite the plates head on, such that the lizards consistently bit with the front of the mouth, and by maintaining the distance between the bite plates to 3.5 mm (Donihue et al., 2016). Each lizard was tested five times with the maximum bite force attained during repeats being retained for analyses. Bite force was measured in the field and before performing bite tests lizards were acclimated in a temporary vivarium (L20 × W12 × H16 cm) to an ambient temperature of 22 °C ± 1.5°C by positioning the vivarium in shade/sunlight accordingly.

Diet composition was investigated for adult *P. muralis* from four UK populations; Purbeck Quarries (PU) (n= 12), Portland Quarry (PQ) (n = 7), Wembdon (WE) (n = 12), West Worthing (WW) (n= 5) and VI (n = 21). Invertebrate remains in the stomach were examined under a dissecting microscope following dissection of the alimentary canal and prey items were identified and classified to Operational Taxonomy Units (OTU), which in this case was defined by taxonomic order or infraorder (except for Formicidae due to their ecological differentiation from other Hymenoptera). Prey counts were based on cephalic capsules, wings and legs, following the minimum numbers criterion per sample (Carretero, 2004; Mella et al., 2010). Invertebrate prey were also categorised in terms of hardness (soft and hard) according to classifications made in previous works (Herrel et al., 2001; Verwaijen et al., 2002; Kaliontzopoulou et al., 2012). Adults of Isoptera, Diptera, Hymenoptera, Annelida, Aphidomorpha, Microlepidoptera, Lepidoptera, Psocoptera, Geophilomorpha, Neuroptera, and all larvae were classed as soft prey; adults of Formicidae, Coleoptera, Hemiptera, Gastropoda, Dermaptera and Isopoda were considered hard prey.

4.3.1 Statistical analysis

The data were analysed using two complementary model structures to test (i) intraspecific differences and (ii) interspecific differences. For introduced UK and Vancouver Island, and native (France) *P. muralis* populations I tested for intraspecific differentiation in the quantified morphological traits, lineage, and bite force using factorial univariate and multivariate analysis of variance ((M)ANOVA), with population (site), sex, and their interaction (site*sex) as model effects. To test for interspecific variation between introduced UK populations of *P. muralis* and native *Z. vivipara* and *L. agilis*, and between introduced *P. muralis* on Vancouver Island with *E. coerulea*, the same models were used but with species as a factor in place of site.

Determinants of bite force were explored with ANCOVA tests on bite force with site or species (as appropriate) and sex as factors, and with each of the linear morphological traits (SVL, HS, head dimensions) treated separately as covariates. All interaction effects were also included. Analysis was applied to UK *P. muralis* populations to test for intraspecific variation, and to UK lizards and Vancouver Island lizards separately to evaluate interspecific patterns.

Diet composition was described for the five populations by the following indices: percentage occurrence (%P) (i.e., percentage of samples containing each prey item), percentage of numerical abundance of each item (%N), and the resource use index (IU), which is calculated by multiplying the numerical abundance by the diversity of each OTU throughout all the individual gut samples (Eq 1), where E = Brillouin’s index of relative diversity (Carretero, 2004; Mella et al., 2010).

$$\mathrm{IU_J} = \mathrm{E_J} \,.\, \%\mathrm{N_J} \qquad \text{Equation 1}$$

$$\left[\mathrm{E_J} = \frac{\mathrm{H_J}}{\mathrm{H_{max}}}\right]$$

Levin's standardised measure of niche breadth was also calculated for each population (Krebs, 1999), and a quantitative measure of shared resource use between pairwise groups was estimated using Pianka's overlap index (Pianka and Huey, 1978) in the R package EcoSimR (Gotelli et al., 2015). In addition, I tested for independence in diet composition between population groups using a Chi-squared test of frequencies of soft and hard prey items found in stomach analysis.

4.4 Results

4.4.1 Morphological Results

P. muralis *populations*- Analyses of morphology using ANOVA and Tukey *post-hoc* comparisons indicated significant morphological differences between populations, lineage, sexes, and in some cases significant interactions between factors (Table 4.1, additional descriptive results are presented in Appendix 4.1).

Sexual size dimorphism was present (P = 0.03), with males (mean = 60.67, SE = 0.31 mm) being significantly larger than females (58.91 ± 0.33 mm). This size dimorphism did not change across populations (sex*site, P = 0.15), although was less pronounced in the French lineage (males = 58.55 ± 0.51, females = 57.11 ± 0.51) (P =0.23). Body size varied significantly between populations (P <0.001), with the smallest sizes at Bury (55.01 ± 0.70 mm) and France (55.5 ± 0.61 mm), compared to the largest individuals at Worthing (63.02± 0.82 mm). There was a significant difference in SVL between lizards of Italian origin (60.81 ± 0.25 mm) and those of French origins (58.20 ± 0.40 mm) (P <0.001) (Table 4.1, Fig 4.2 A, B).

Head size differed significantly between sites, sexes, and lineages (P <0.05 in all cases) (Table 4.1). France (8.50 ± 0.10 mm), Bury (8.60 ± 0.10 mm), and Folkestone (8.51 ± 0.10 mm) had the smallest head size, while Purbeck (10.0 ± 0.14 mm) and Vancouver Island (9.90

± 0.12 mm) had the largest. Lizards of Italian origin had significantly greater head size (9.73 ± 0.06 mm) than those of French origins (9.21 ± 0.08 mm) (P<0.001) (Table 4.1).

Raw head dimensions also differed significantly between sites, sexes, and lineages (P <0.05 in all cases), with males having overall larger head dimensions than females in all cases. The native France population had significantly lower head width than seven other populations and significantly lower head length than eight other populations. Head height was significantly greater in the Worthing population compared to 9 of the other 13 populations. French and Italian lineages differed significantly across all head dimensions, with Italian lizards having greater means in all cases (Table 4.1).

Bite performance was generally consistent across all populations, though Bury (5.14 ± 0.36 N) had significantly weaker bite force than Worthing (7.19 ± 0.63 N), Eastbourne (7.11 ± 0.55 N) and Purbeck quarries (7.02 ± 0.44 N). Bite force differed significantly between the sexes (males, 9.63 ± 0.17 N, females, 4.83 ± 0.08 N). Between populations, the only significant difference in female bite force was between Shoreham (4.80 ± 0.29 N) and Bury (3.61 ± 0.18 N) (Tukey HSD, P = 0.32) (Fig 4.2 L). However, male bite force differed significantly, with Worthing and Purbeck Quarries having greater values than Portland Quarry, Wembdon, and Bury (Fig 4.2 K). Bite force differed significantly between lineages, with lizards of Italian origin having greater bite force on average (7.81 ± 0.17 N) than French (6.42 ± 0.21 N) (Tukey HSD, P<0.001).

Native vs non-native UK comparison- *P. muralis*, *Z. vivipara* and *L. agilis* differed in all morphometric variables and showed significant sexual size dimorphism in all traits, although the degree of dimorphism differed among species (Table 4.2, additional descriptive results are presented in Appendix 4.2).

Tukey's *post-hoc* analysis revealed that female *L. agilis* were significantly larger (SVL) than all other individuals, irrespective of sex and species. Body size was comparable between male *P. muralis* and male *L. agilis* (Tukey HSD, P = 0.59), as was body size of female *P. muralis* and female *Z. vivipara* (Tukey HSD, P = 0.21). Male *Z. vivipara* had significantly lower mean SVL than all other species/sex (Table 4.2).

Head size did not differ significantly between male *P. muralis* and male or female *L. agilis*. Female *P. muralis* possessed significantly different head size intermediate between all other pairs, whilst male and female *Z. vivipara* grouped together with similar mean head size (Tukey HSD, P = 1.0) (Fig 4.3 A). A similar pattern of divergence was apparent in response to head width, the only difference being female *P. muralis* having similar mean head width to male *Z. vivipara* (Tukey HSD, P = 0.19). Head height did not differ significantly between the sexes within *L. agilis* (Tukey HSD, P = 0.95) or *Z. vivipara* (Tukey HSD, P = 0.80). Male *P. muralis* did however have greater head height than female *P. muralis* (Tukey HSD, P<0.001) and grouped with female *L. agilis* (Tukey HSD, P = 0.50). Female *P. muralis* did not differ in head height to male *Z. vivipara* (Tukey HSD, P = 0.06). Head length did not differ between male *P. muralis*, or male and female *L. agilis*. Female *P. muralis* again differed significantly from other species/sexes by having intermediate head length, whereas head lengths of both sexes of *Z. vivipara* were significantly shorter than other pairings.

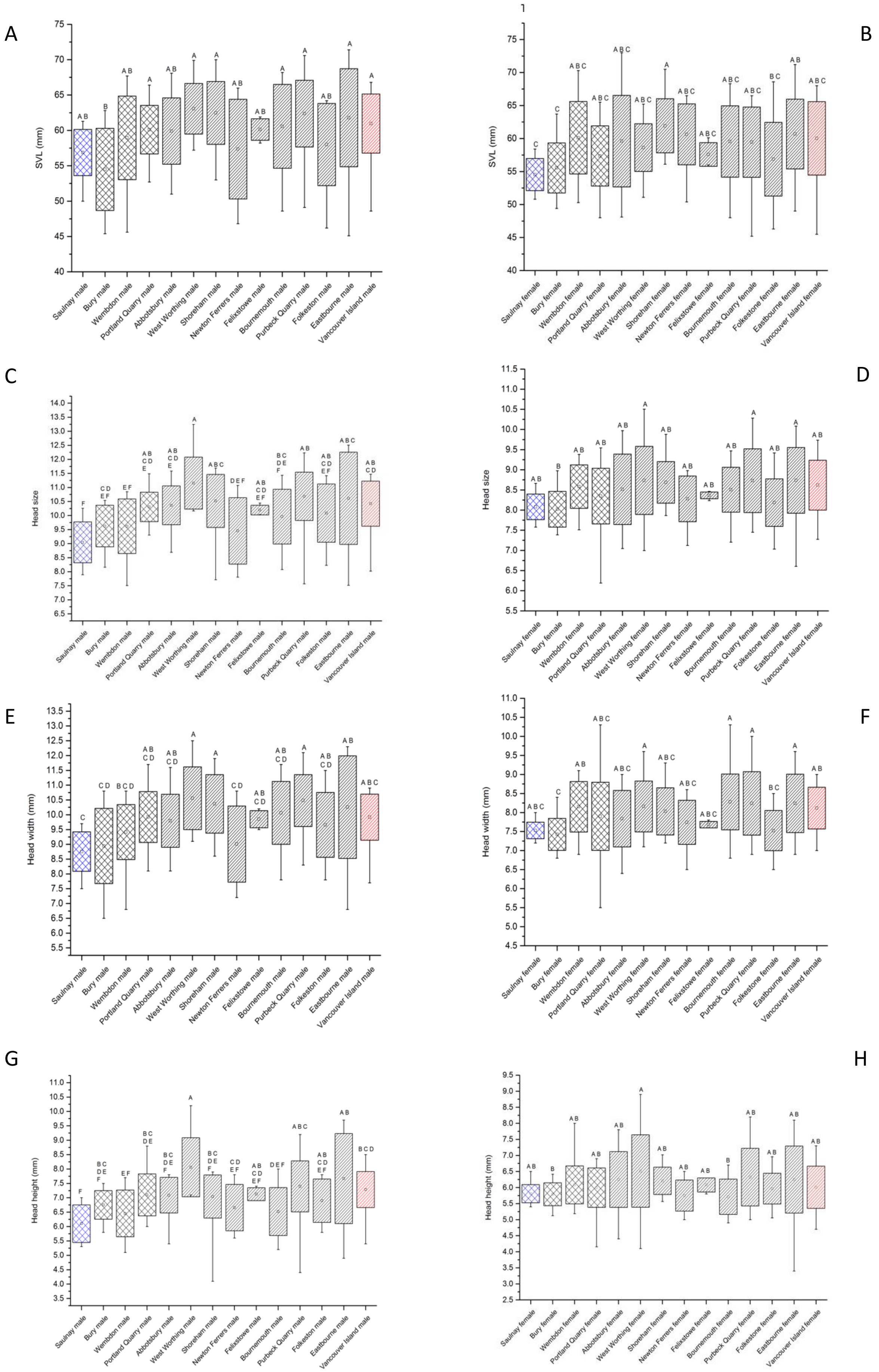
Divergence in bite force between sex and species matched that of head width, with *L. agilis* (both sexes) and male *P. muralis* having a similar mean bite force that was significantly greater than female *P. muralis* and *Z. vivipara* (both sexes) (Fig 4.3 C).

Native vs non-native Canada comparison- In comparing morphological traits of introduced *P. muralis* and native *E. coerulea* there was significant difference in all response variables between species, with *E. coerulea* being the largest species (Table 4.2, additional descriptive results are presented in Appendix 4.2). Sexual dimorphism (male bias) was present in all traits for *P. muralis*, but not in *E. coerulea*.

Despite the smaller size, *P. muralis* had the greater bite performance, a difference driven by high bite force of males compared to all other groups. Out of all response variables only bite force did not differ with the interaction between species*sex (P = 0.25) (Table 4.2).

Table 4-1 ANOVA results for body size (SVL), head size (HS), head width (HW), head height (HH), head length (HL), bite force (BF), and lineage for 13 introduced populations of *P. muralis* (12 in the UK and 1 on Vancouver Island) and a native population in Saulnay, France.

	SITE		**SEX**		**SITE * SEX**		**Lineage**	
	F	P	F	P	F	P	F	P
SVL	6.23	<0.001	4.70	0.030	1.39	0.15	28.33	<0.001
HS	7.56	<0.001	445.64	<0.001	2.15	0.01	19.54	<0.001
HW	7.49	<0.001	475.3	<0.001	1.88	0.02	17.30	<0.001
HH	7.66	<0.001	154.63	<0.001	1.91	0.02	18.28	<0.001
HL	6.32	<0.001	628.02	<0.001	3.75	<0.001	14.62	<0.001
BF	3.80	<0.001	507.73	<0.001	1.46	0.14	19.47	<0.001


A
SVL (mm)
B
SVL (mm)
C
Head size
D
Head size
E
Head width (mm)
F
Head width (mm)
G
Head height (mm)
H
Head height (mm)
Saulnay male
Bury male
Wembdon male
Portland Quarry male
Abbotsbury male
West Worthing male
Shoreham male
Newton Ferrers male
Felixstowe male
Bournemouth male
Purbeck Quarry male
Folkeston male
Eastbourne male
Vancouver Island male
Saulnay female
Bury female
Wembdon female
Portland Quarry female
Abbotsbury female
West Worthing female
Shoreham female
Newton Ferrers female
Felixstowe female
Bournemouth female
Purbeck Quarry female
Folkestone female
Eastbourne female
Vancouver Island female

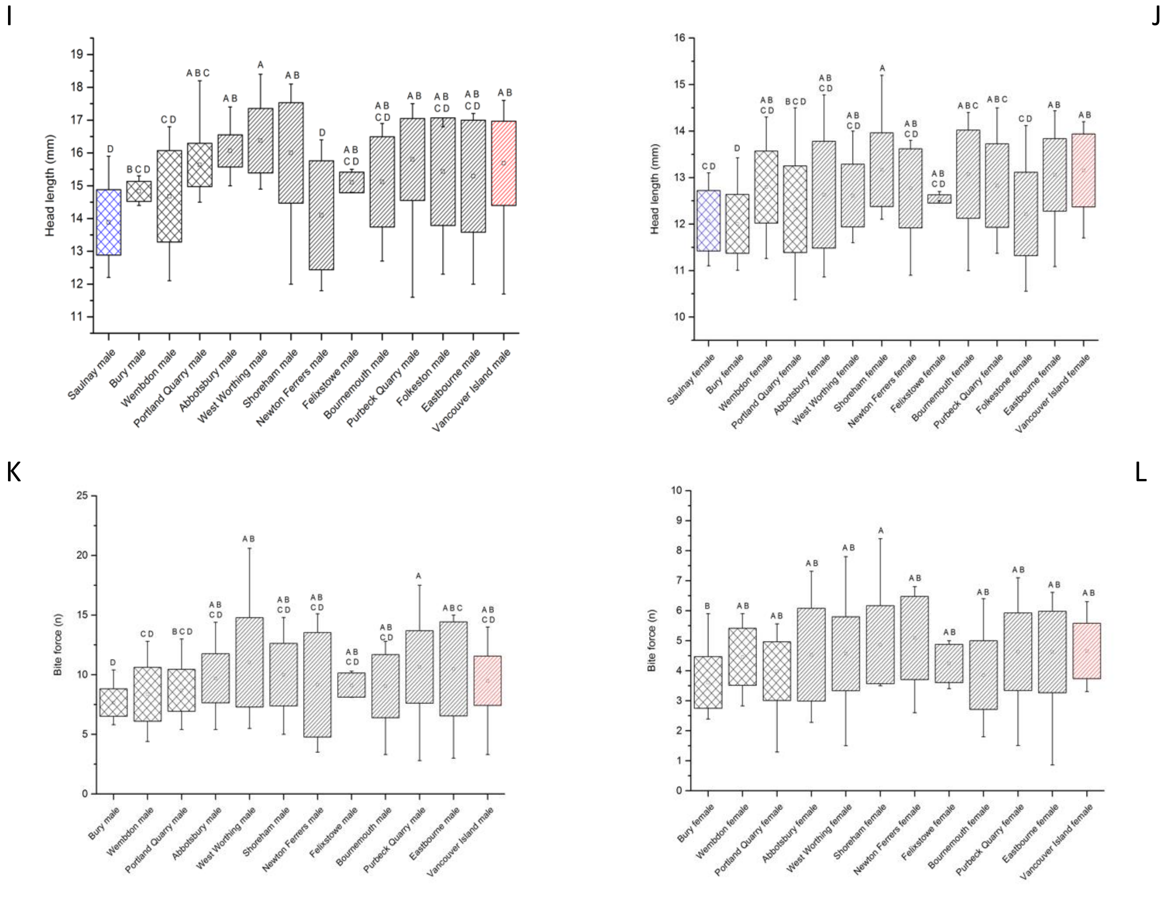


Figure 4-2 Box plots for comparison of means in morphological attributes and bite force across introduced *P. muralis* populations (male and female) in the UK and Vancouver Island, Canada, as well as a native population from Saulnay, France. Boxes represent range of standard deviation with max/min whiskers. Sparse hatch boxes represent populations of French lineage, dense hatch, Italian. Blue and red hatching highlight Saulnay and Vancouver Island populations respectively. Groups that share an initial (A,B,C etc) are not statistically different.

Table 4-2 ANOVA results for body size (SVL), head size (HS), head width (HW), head height (HH), head length (HL), and bite force (BF) for both sexes of UK populations of *P. muralis* and UK native *Z. vivipara*, and *L. agilis*, as well as for *P. muralis* on Vancouver Island and native *E. coerulea*.

	UK lizards						**Vancouver Island lizards**					
	SP		SEX		SP*SEX		SP		SEX		SP*SEX	
	F	P	F	P	F	P	F	P	F	P	F	P
SVL	40.9	**<0.001**	12.8	**<0.001**	13.2	**<0.001**	91.09	**<0.001**	3.67	0.05	6.01	**0.01**
HS	190.5	**<0.001**	19.5	**<0.001**	19.7	**<0.001**	10.63	**0.002**	4.86	**0.03**	27.77	**<0.001**
HW	69.3	**<0.001**	29.9	**<0.001**	16.7	**<0.001**	17.11	**<0.001**	6.30	**0.01**	24.07	**<0.001**
HH	57.8	**<0.001**	13.0	**<0.001**	3.5	**0.03**	5.49	**0.02**	3.03	0.08	25.28	**<0.001**
HL	154.2	**<0.001**	37.5	**<0.001**	22.9	**<0.001**	7.83	**0.006**	4.10	**0.04**	25.07	**<0.001**
BF	61.4	**<0.001**	42.6	**<0.001**	15.3	**<0.001**	4.30	**0.04**	20.05	**<0.001**	20.86	0.25

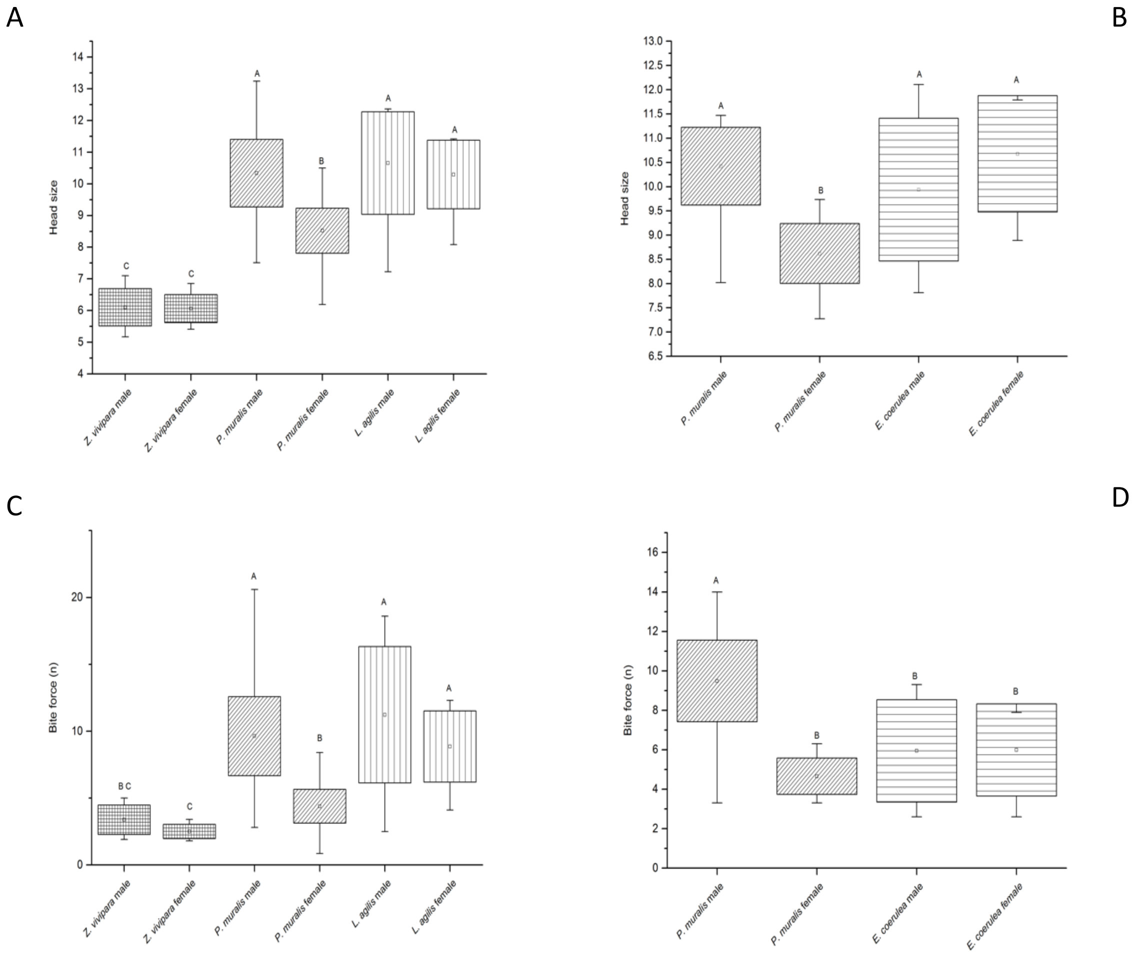


Figure 4-3 Box plots for comparison of means in head size and bite force across sexes in introduced *P. muralis* and native *Z. vivipara* and *L. agilis* in the UK (A,C), and with native *E. coerulea* on Vancouver Island, Canada (B,D). Boxes represent range of standard deviation with max/min whiskers. Box fill patterns differentiate species. Letters above boxes show the results of post-hoc tests where boxes that do not share a letter have significantly different means.

Table 4-3 Results obtained from linear models on bite force, with UK *P. muralis* populations (SITE) and SEX as categorical predictors and different morphological predictors (MORPHX) as covariates (specified in columns). R^2 is given for each morphometric predictor covariate model.

	SVL		**HS**		**HH**		**HL**		**HW**	
	F	P	F	P	F	P	F	P	F	P
MORPHX	87.69	**<0.001**	16.77	**<0.001**	42.16	**<0.001**	11.11	**0.001**	9.22	**0.003**
SITE	4.28	**<0.001**	1.43	0.164	1.47	0.147	2.71	**0.003**	2.13	**0.021**
SEX	1.13	0.289	0.05	0.819	0.37	0.544	0.03	0.867	0.15	0.695
MORPHX*SITE	4.48	**<0.001**	1.28	0.236	1.56	0.114	2.59	**0.005**	2.06	**0.026**
MORPHX*SEX	5.07	**0.025**	0.24	0.624	2.30	0.130	0.08	0.774	0.48	0.488
SITE*SEX	3.06	**0.001**	1.84	0.052	1.22	0.275	1.13	0.336	2.66	**0.004**
MORPHX*SITE*SEX	3.02	**0.001**	1.63	0.096	1.05	0.398	0.88	0.557	2.35	**0.010**
R^2	85.07%		88.01%		81.27%		84.86%		84.98%	

Table 4-4 Results obtained from linear models on bite force, with species (SP) and SEX as categorical predictors and different morphological predictors (MORPHX) as covariates (specified in columns). Tests carried out on UK lizards (introduced *P. muralis*, native *Z. vivipara*, and *L. agilis*) (SP), and Vancouver Island lizards (introduced *P. muralis* and native *E. coerulea*). R^2 is given for each morphometric predictor covariate model.

Relationship between bite force and morphology in UK Lizards

	SVL		HS		HH		HL		HW	
	F	P	F	P	F	P	F	P	F	P
MORPHX	69.36	**<0.001**	87.53	**<0.001**	30.72	**<0.001**	35.22	**<0.001**	34.77	**<0.001**
SP	0.77	0.463	7.29	**<0.001**	7.10	**<0.001**	2.21	0.110	5.90	**0.003**
SEX	6.72	**0.010**	2.92	0.088	0.92	0.338	2.41	0.121	4.17	**0.042**
MORPHX*SP	1.92	0.147	6.58	**<0.001**	9.11	**<0.001**	3.82	**0.022**	8.29	**<0.001**
MORPHX*SEX	10.45	**<0.001**	2.66	0.104	1.44	0.231	2.16	0.143	4.21	**0.041**
SP*SEX	0.15	0.860	0.45	0.641	0.56	0.571	0.18	0.838	0.69	0.502
MORPHX*SP*SEX	0.06	0.938	0.18	0.832	0.18	0.834	0.15	0.863	0.47	0.623
R^2	84.73%		87.23%		80.30%		82.24%		83.44%	

Relationship between bite force and morphology in Vancouver Island Lizards

	F	P	F	P	F	P	F	P	F	P
MORPHX	152.30	**<0.001**	115.43	**<0.001**	76.21	**<0.001**	85.42	**<0.001**	106.41	**<0.001**
SP	0.97	0.328	3.25	0.075	7.44	**0.008**	4.57	**0.035**	0.83	0.365
SEX	9.19	**0.003**	1.07	0.303	0.43	0.513	0.39	0.536	0.86	0.355
MORPHX*SP	0.91	0.343	1.31	0.255	5.20	**0.025**	2.43	0.122	0.01	0.906
MORPHX*SEX	23.73	**<0.001**	2.85	0.095	2.11	0.150	1.42	0.237	2.18	0.144
SP*SEX	13.50	**<0.001**	4.77	**0.032**	3.62	0.060	1.60	0.210	3.31	0.072
MORPHX*SP*SEX	23.92	**<0.001**	5.57	**0.020**	4.88	**0.030**	2.04	0.156	4.01	**0.048**
R^2	87.49%		86.78%		80.44%		84.92%		86.72%	

Considering form-function relationships, all morphometric variables had a significant effect on bite force in UK *P. muralis* populations (Table 4.3), and in analysis of *P. muralis*, *L. agilis*, and *Z. vivipara* (Table 4.4). There was a significant difference in the effects of SVL, head length, and head width on bite force between UK populations of *P. muralis* (Table 4.3), although this was driven by divergence between males among populations rather than females (Figs 4.4 A, B). The increase in bite force relative to body size was steepest in males from the West Worthing population (Fig 4.4 A). The effect of all variables on bite force differed significantly between UK lizard species, except for SVL and head length (Table 4.4). Head size and SVL had the strongest influence on bite force, and male *P. muralis* had the steeper regression slopes other groups in this regard (Fig 4.4 C).

All morphometric variables also had a significant effect on bite force in Vancouver Island lizards, although the effect of body size was the best model fit to the data (Table 4.4). The regression slope of body size vs bite force was uniform across groups, except for *P. muralis* males which had a greater bite force for a given body size than female *P. muralis* and both sexes of *E. coerulea.* Relative bite force was also greater in male *E. coerulea* than conspecific females (Fig 4.4 D).

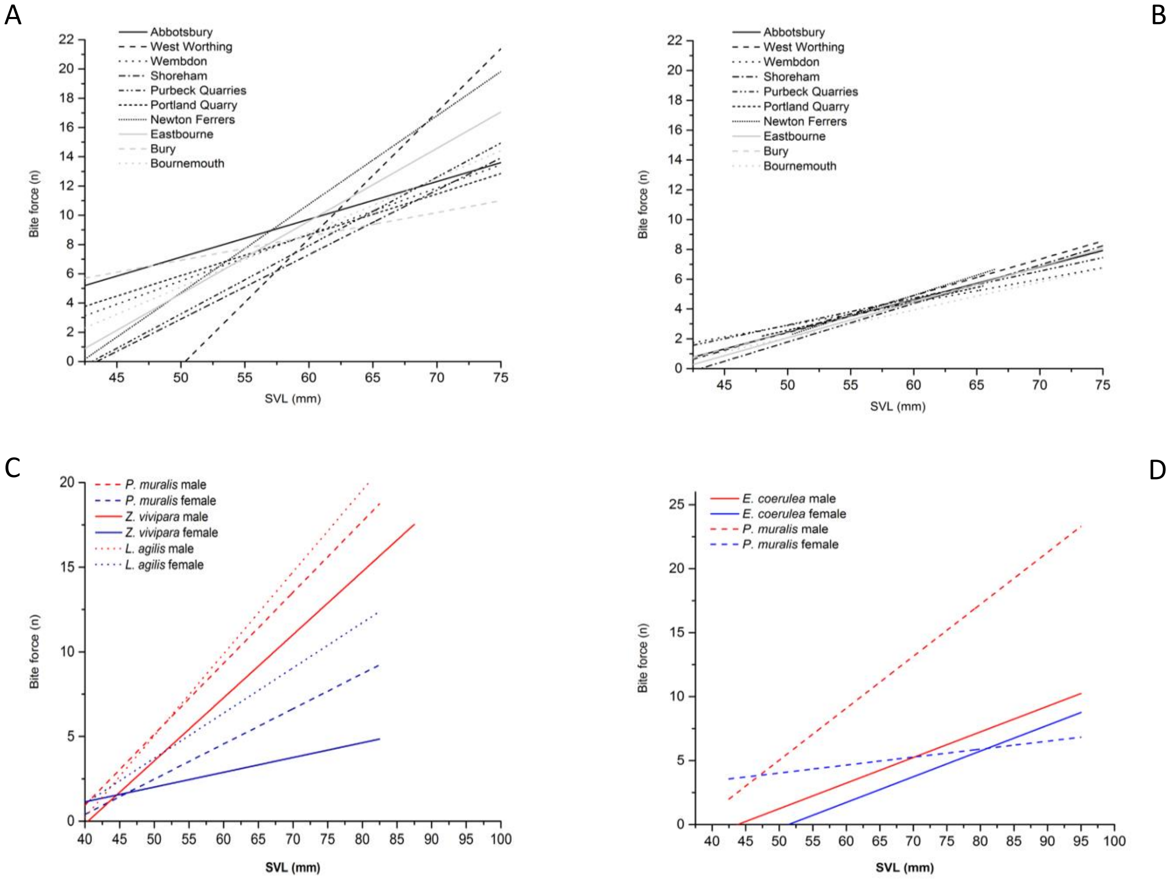


Figure 4-4 Allometric relationship between body size and bite force in male (A) and female (B) UK *P. muralis* populations. Relationship between body size and bite force across sexes of introduced *P. muralis* and native *Z. vivipara* and *L. agilis* in the UK (C), and (D): Relationship between body size and bite force in native *E. coerulea* and introduced *P. muralis* on Vancouver Island, Canada.

4.4.2 Diet composition

Coleoptera, Isopoda, Hemiptera, and Arachnida were the most commonly found prey of the 18 taxonomic units found in stomach analysis of *P. muralis* (Table 4.5). The West Worthing population had the narrowest niche breadth with only seven OTUs present; whereas the most diverse diet was found in the Vancouver Island population with 15 OTUs present (Table 4.5).

Table 4-5 Descriptive measures of diet in introduced populations of *P. muralis*. OTU: Operational taxonomical unit, %P: Percentage of presence, %N: Percentage of numerical abundance, IU: Resource use index, B_A: Levin's' measure of standardized niche breadth. Asterisk denotes OTU classed as hard prey.

OTU's	**Purbeck quarries**			**Portland quarry**			**West Worthing**			**Wembdon**			**Vancouver Island**		
	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU
Isoptera	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	19	6.30	5.04
Hymenoptera	0	0.00	0.00	28.5	8.79	5.48	20	4.35	2.78	8.3	6.82	4.43	38	18.11	14.49
Formicidae*	25	7.14	5.02	14.2	1.10	0.68	0	0.00	0.00	0	0.00	0.00	19	3.15	2.52
Coleoptera*	25	7.14	5.02	42.8	6.59	4.11	80	21.74	13.91	41.6	22.73	15.23	66.6	15.75	12.60
Diptera	25	10.00	7.03	85.7	7.69	4.79	40	8.70	5.57	16.6	4.55	3.05	4.7	0.79	0.63
Annelida	16.6	2.86	2.01	14.2	1.10	0.68	0	0.00	0.00	8.3	2.27	1.52	0	0.00	0.00
Hemiptera*	25	4.29	3.01	100	16.48	10.27	40	13.04	8.35	25	18.18	12.18	23.8	5.51	4.41
Aphidoidea	8.3	4.29	3.01	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	19	22.05	17.64
Microlepidoptera	16.6	2.86	2.01	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	9.5	1.57	1.26
Arachnida	58.3	14.29	10.04	71.4	38.46	23.97	0	0.00	0.00	33.3	9.09	1.52	19	3.15	2.52
Lepidoptera	8.3	1.43	1.00	14.2	1.10	0.68	0	0.00	0.00	0	0.00	0.00	4.7	0.79	0.63
Larvae	8.3	1.43	1.00	14.2	1.10	0.68	20	4.35	2.78	16.6	4.55	1.52	14.2	2.36	1.89
Gastropoda*	8.3	1.43	1.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	4.7	5.51	4.41
Psocoptera	8.3	2.86	2.01	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
Geophilidae	0	0.00	0.00	0	0.00	0.00	20	22.22	14.22	0	0.00	0.00	0	0.00	0.00
Dermaptera*	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	28.5	5.51	4.41
Isopoda*	58.3	40.00	28.11	85.7	17.58	10.96	60	39.13	25.04	41.6	31.82	21.32	28.5	7.87	6.30
Neuroptera	0	0.00	0.00	0	0	0	0	0	0	0	0	0	9.5	0	0
B_A	0.22			0.20			0.14			0.23			0.39		

Dietary niche overlap varied in pairwise comparisons (Table 4.6). The diverse diet of Vancouver Island lizards had no overlap with any of the UK populations. Between the UK populations there was surprisingly no overlap between lizards inhabiting the two quarry habitats (Purbeck and Portland). There was also no significant overlap between the West Worthing population and Portland quarry (Table 4.6).

Table 4-6 Pairwise comparison of Pianka's index of niche overlap in diet composition between five introduced populations of *P. muralis*. Shaded cells indicate significant overlap between populations.

	Purbeck quarries	Portland quarry	West Worthing	Wembdon	Vancouver Island
Purbeck quarries		0.67743	0.84463	0.8282	0.39051
Portland quarry	P= 0.062		0.50202	0.68355	0.36863
West Worthing	P= 0.011	P= 0.131		0.94177	0.46928
Wembdon	P= 0.004	P= 0.030	P= 0.001		0.54082
Vancouver Island	P= 0.273	P= 0.322	P= 0.195	P= 0.125	

The contribution of hard and soft prey varied significantly in the diet of five populations of *P. muralis* (X^2 = 21.16, df = 4, P < 0.001). Purbeck quarries, West Worthing, and Wembdon all had higher frequency of hard prey than expected, whereas Portland and Vancouver Island lizards consumed more soft prey and less hard prey than expected. The amount of hard prey consumed was not related to mean bite force in the sample populations (Fig 4.5).

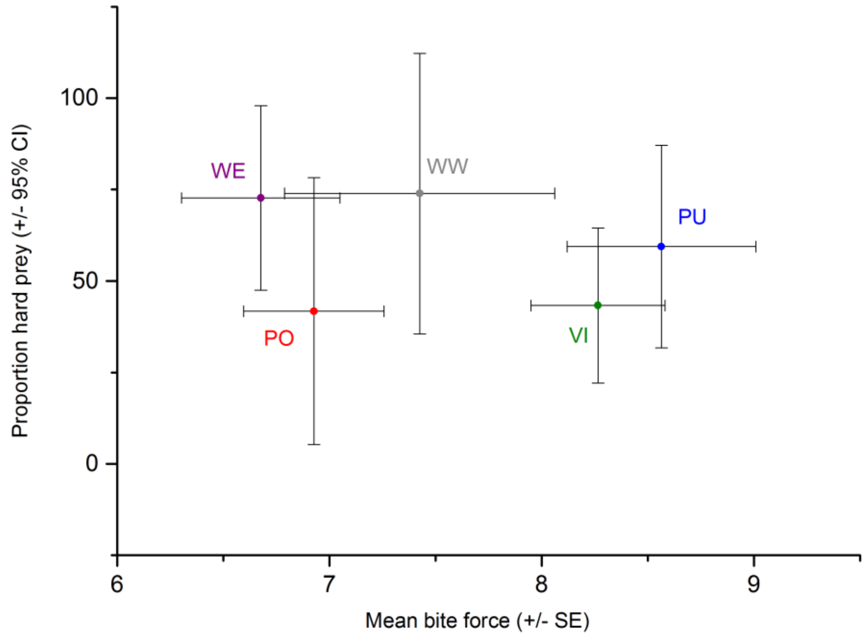


Figure 4-5 Percentage of hard prey items present in the diet of introduced populations of *Podarcis muralis* relative to bite force. WE = Wembdon, WW =West Worthing, PO = Portland quarry, PU = Purbeck quarries, VI =Vancouver Island

4.5 Discussion

Understanding how species adapt to novel environments following introduction is essential to predicting the invasion potential of introduced populations and gives insight into the processes underlying the generation of phenotypic diversity. My results suggest that whilst morphological variation may exist between introduced populations of *P. muralis*, this variance may be largely explained by ancestral divergence in morphology between animals of French and Italian lineage. The form-function relationship between head morphology and bite force is generally maintained within populations of shared lineage, although variation in relative influence of head components on allometric scaling of bite force with body size suggest this system is highly flexible and susceptible to natural and sexual selective forces. Comparison of morphological and form-function traits between introduced *P. muralis* and native lizards suggest considerable niche overlap and thus high potential for competitive interaction. In addition, the lack of dietary overlap between UK and Vancouver Island populations of *P. muralis* emphasises the flexibility and generality in diet that could ease establishment of the species in varied habitats and ecoregions.

4.5.1 Intraspecific variation

The analysis of morphometric variability among the native and introduced populations of *P. muralis* revealed significant morphological differentiation between populations. Such variation may have important effects on a particular populations' capacity to transition from local establishment to invasion with negative impacts.

Similar patterns of variance were generally observed between sexes, though different levels of variability existed at a local level. This interpopulation variation is not surprising considering the wall lizard in England can be traced to at least five geographically and genetically distinct lineages (at least 4 lineages represented in this study) spanning a large part of the species' native range, and is likely to include at least three subspecies representing French (*P. m. brogniardi*, *P. m. merremius*) and Italian (*P. m. nigriventris*) clades (Michaelides et al., 2013; 2015). Morphology varies considerably throughout the geographic range of *P. muralis* and much of the early subspecies classifications were based on biometric variance prior to review by molecular studies (Bellati et al., 2011). The variances observed in my study populations at a broad scale are therefore likely to reflect existing variability present in source populations regardless of any post-introduction adaptations. Unsurprisingly then, variation across all metrics was most pronounced in comparison of populations of French (native and introduced) and Italian lineage – a result likely due to the variation arising from the long period of evolutionary divergence between the two, with Italian clades having diverged in ice age refugia whereas the evolutionary split between Italian and two French clades (East and West) likely predates the Pleistocene (Giovannotti et al., 2010). As such, my results are in accordance with general patterns of greater sizes, bite force and pronounced sexual dimorphism in lizards of Italian origin compared to those of western European clades (While et al., 2015a).

Insights into how the assisted northward expansion of *P. muralis* may have resulted in morphological adaptation following macroecological patterns (i.e., latitudinal and thermal clines in body size) are complicated by the convoluted introduction history of my study populations and lack of comparable data from the native range in the literature. Broad scale analysis of body size patterns across squamates has shown European lizards generally adhere to Bergmann's rule (Olalla-Tárraga et al., 2006), whereas others have argued that the evolution of larger body size in colder environments appears to be a disadvantageous thermoregulatory strategy for ectotherms (Pincheira-Donoso et al., 2008). Body sizes across UK populations of *P. muralis* are similar (those of Italian origin) or slightly smaller (French) to those reported for a population at the northern extent of the species' natural range in Maastricht, Netherlands (Eastern France clade), which in turn have purportedly smaller mean size than those in more southern regions (Strijbosch et al., 1980). This lends some support to a negative correlation between body sizes and latitude in *P. muralis*, a pattern that may not be uncommon in lizards where selection for rapid heat gain in cooler areas may be responsible for the converse to Bergmann's rule (Ashton and Feldman, 2003). Counter to this reasoning however is the small mean size I recorded from the native population in Saulnay (Western France clade) which should have had the highest mean sizes to conform to this pattern.

Within lineages there was far less variation between populations. However, intrasexual differences in head measurements between males in some populations of shared origin provide some insight into possible sex specific phenotypic shifts between populations. This was most consistent in the greater head sizes of West Worthing males compared to those of Newton Ferrers - two primary UK introductions of Venetian origin (Michaelides et al., 2015). Disparity in levels of genetic diversity between introduced populations, caused by differential loss of diversity either through founder effects, bottlenecks, and genetic drift may explain these morphological differences (Dlugosch and Parker, 2008); see also Lescano (2010); and Schulte et al. (2013) for specific reference to *P. muralis*)); (Greenbaum et al., 2014). Indeed, the smaller head dimensions of the Newton Ferrers males is coincident with this being one of the oldest persisting population in the UK as well as having low levels of heterozygosity and allelic richness in relation to other introduced Italian populations (Michaelides et al., 2016). Male head traits are potentially under the influence of both natural and sexual selection due to the associations with biting performance and its functional role in various ecological and social tasks (Kaliontzopoulou et al. (2012) and references therein). Differing male-specific selection pressures between these two populations could therefore account for the variations in head dimensions observed. The most apparent difference between these two populations is habitat type. Newton Ferrers is a semi urban/rural habitat, whereas West Worthing is highly urbanised with high levels of human disturbance (Chapter 2). Differing habitat structure can also lead to intraspecific variation in head dimensions through mechanical restrictions related to microhabitat and refuge use, as seen in variation between males of saxicolous and ground-dwelling populations of *P. bocagei* (Kaliontzopoulou et al., 2010).

Increases in phenotypic variation within and among individuals can also arise under stressful conditions (i.e., sub optimal environmental conditions in which homeostasis may be disrupted, ultimately causing a decline in individual fitness), whereby the efficacy of the mechanisms which underlie developmental patterns that limit phenotypic variation (i.e., development stability and canalisation) is reduced (Lazic et al., 2015). Variation in habitat quality could therefore account for the observed divergence in head size of the Newton Ferrers population. The low body condition of the Newton Ferrers male lizards is further indication that this particular population may be under more environmental stress than those in urban areas (Chapter 2). Although contrary to my results, urban living is suggested to disturb development, and smaller head size has been associated with urban populations of *P. muralis* (Lazic et al., 2015). Furthermore, fitness costs are also attributed to disturbed habitats, with lizards from urban habitats having poorer physical condition compared to rural populations (Lazic et al., 2017). It is important to note, however, that urban settings do present unique selection pressures and multiple contexts for adaptation to occur, the direction of which is dependent on myriad of influences (Donihue and Lambert, 2015), for example: niche expansion due to novel habitat structure (Winchell et al., 2016; Battles et al., 2018), adaptation to thermal characteristics (Diamond et al., 2018), response to habitat fragmentation (Villalobos-Jimenez and Hassall, 2019), habituation to disturbance and predator prey interactions (Pellitteri-Rosa et al., 2017; Winchell et al., 2019).

Despite significant differences in head morphology between these populations, this variation did not translate into a constraint on bite performance for the Newton Ferrer males as might be expected owing to the intrinsic association between head traits and bite force (Verwaijen et al., 2002; Herrel et al., 2007; Huyghe et al., 2009). This suggests a shift in the form-function relationship that enables equal bite performance to be attained irrespective of morphological variation, thus allowing ecological (e.g., prey handling) and social demands (e.g., territory defence, mate attraction) to be fulfilled. Consideration of geometric morphometrics describing head shape have provided insight into how bite performance may be maintained despite morphological differences in head dimensions between males of *P. bocagei* and *P. hispanica*, through differential configuration of head components (Kaliontzopoulou et al., 2012). Without similar consideration of geometric head shape, it is not clear from my results what form-function relationship may be maintaining similar bite performance in males from Newton Ferrers and West Worthing populations. However, allometric trajectories of body size to bite force support the theory that selective forces (either natural, sexual, or an interplay between both) of an urban environment may be driving a more rapid increase in bite force relative to body size in the male population of West Worthing (Fig 4.4 A). Possible mechanisms driving this scaling of bite force with body size may include; defensive response to high predation pressure (Chapter 2), ontogenetic shifts or sex differences in prey availability or selection (i.e., bias towards hard bodied prey available to juvenile lizards, male bias in exploitation of a hard prey type), reduced home ranges and/or limited or disaggregated resources (refugia, basking spots) leading to increased intrasexual aggression. Such divergence in allometry in the Worthing population may be indicative of an adaptive response that could significantly influence range expansion and invasive potential through exploitation of urban/disturbed habitats (Gherghel et al., 2009; Donihue, 2016b).

Divergence in dietary niche may be expected in response to, or as a driver of, variation in head size, shape, and the functional association with bite performance (Verwaijen et al., 2002; Carretero, 2004; Herrel et al., 2008; Lailvaux and Gilbert, 2011; Dollion et al., 2017). I found considerable overlap in dietary niche between most of the UK populations tested (Table 4.6). Where variation did occur, patterns of dietary ecology were not reflected in observed differences in head traits and bite performance, implying that if trophic niche variation between populations exists, the reasons behind it cannot be directly attributed to head morphology and functional variation. I acknowledge that prey availability and differential prey consumption between sexes amongst other factors are likely to have influenced my results (Kaliontzopoulou et al., 2012; and references therein; and references therein). In a broader context, my results highlight the wide prey spectrum that can be utilised by *P. muralis*. This may have implications for local invertebrate communities and trophic ecology, particularly where introduced populations achieve high densities (Greenlees et al., 2006; Huang et al., 2008) and the dietary niche breadth surpasses that of native lizards (e.g., *Z. vivipara*).

4.5.2 Interspecific variation and implications for contest

Competition between native and invasive species may be a crucial determinant of invasion success, and outcomes of interactions between natives and novel antagonists can have severe implications for native species (Gao and Reitz, 2017). Introduced *P. muralis* have been observed to dominate in agonistic interactions with native *Podarcis* sp. elsewhere (Schulte et al., 2012b), however there are conflicting observations of the outcome of *P. muralis* introduced into sympatry with native populations of *L. agilis* (Mole, 2010; Heym et al., 2013). Males of both species are highly territorial, with individuals of greater body size being competitively superior in intraspecific encounters (Olsson, 1992; Sacchi et al., 2009). In interspecific interactions, variations in body size, head morphology and bite force can significantly influence species coexistence: by determining the outcome of agonistic encounters (Langkilde et al., 2005); by promoting spatial segregation in microhabitat use (Zagar et al., 2017) or by facilitating trophic niche segregation (Kaliontzopoulou et al., 2012). In this regard, my results suggest there is potential for considerable niche overlap (in terms of prey acquisition) and that competitive abilities may be equally matched owing to similar body size, head size, bite force (Fig 4.3 A, C) and their allometric relationships (Fig 4.4 C) in males of *P. muralis* and *L. agilis*. Both species are considered to be opportunistic feeders with a generalist diet (Strijbosch, 1986; Kuranova et al., 2005; Crovetto and Salvidio, 2013; Scali et al., 2016). Indeed, my observations of prey composition in introduced UK *P. muralis* (i.e., high proportions of Coleoptera, Isopoda, and Hemiptera (Homoptera) and Arachnida) is similar to that reported for *P. muralis* elsewhere (Strijbosch et al., 1980; Capula et al., 1993; Herrel et al., 2001; Scali et al., 2016) and for *L. agilis* (Gvozdik and Boukal, 1998; Kuranova et al., 2005). My observed values for dietary niche breadth (0.14-0.23) (Table 4.6) are also similar to those reported for *L. agilis* (Gvozdik and Boukal (1998), male 0.21, female 0.19). Altogether, the morphological, functional, and ecological similarities observed here make it difficult to predict the direction of competitive outcome between these two species through comparison of these traits alone. The relationship between these two species in sympatry may therefore be highly context dependent, with direct and indirect factors (abiotic or biotic) (e.g., population fitness and demography, movement to new resource patches, resource availability, common predators, parasites, habitat disturbance etc.) likely to determine the direction of competition (Mole, 2010; Zagar, 2016).

Observations of stark morphological and bite performance variation between *P. muralis* and *Z. vivipara* are concordant with previous studies – *P. muralis* being the larger species (body size and head morphology) and having greater bite force (Herrel et al., 2001). According to the form-function relationship of head morphology-bite force, the main food categories consumed by *Z. vivipara* are typically “soft” prey such as Araneae, Homoptera, and Diptera (Avery, 1966; Heulin, 1986; Strijbosch, 1986; Kuranova et al., 2005). Theoretically then, diet-niche differentiation through differences in morphology and bite force, could reduce trophic competition between these species, much in the same way that trophic segregation is likely to contribute to the coexistence of *Z. vivipara* and *L. agilis* (Strijbosch, 1986; Kuranova et al., 2005; Ekner et al., 2008). Alternatively, should environmental pressures lead to agonistic interactions between the highly territorial *P. muralis* and *Z. vivipara*, which is generally a nonterritorial species (Herrel et al., 2001), the latter is likely to be physically outcompeted. Field observations suggest that where introduced *P. muralis* has become established, *Z. vivipara* can become completely excluded or restricted to marginal habitat (Münch, 2001; Mole, 2010, RW. pers obbs, RW. pers obbs). Furthermore, in experimental trials *Z. vivipara* have shown signs of avoidance of *P. muralis* based on scent cues alone (Chapter 5).

The potential for competitive interaction between *E. coerulea* and *P. muralis* could arise through overlaps in head dimensions and bite performance and thus similarities in the prey size/hardness spectrum exploited. Supporting this theory is that Vancouver Island *P. muralis* have a relatively wide dietary niche breadth, one that is likely to have significant overlap to that of *E. coerulea*. Ecological differences between these two species may however reduce instances of direct aggression, with *E. coerulea* being semifossorial and, unlike *P. muralis,* rarely encountered basking in the open (Rutherford and Gregory, 2003; Bertram, 2004). Conversely, the reliance of both species on use of rocks for refuge (more so *E. coerulea*), and behavioural responses observed to interspecific scent cues (Chapter 5), may lead to direct interaction where this resource is limit (Bertram, 2004). In cases of direct interaction, the outcome may be directed by the superior relative bite force and aggressive nature of male *P. muralis*. Male aggression is rarely observed *in E. coerulea* (McBrayer and Anderson,

2007) and the lack of sexual dimorphism in head morphology observed suggests little intrasexual aggression in my study population.

In conclusion, I hypothesised that introduced populations of *P. muralis* may show divergence in adaptive morphological responses (body size and head morphology) and an associated performance trait (bite force) due to a varied introduction history and establishment in multiple habitat types. In addition, I considered how variation between introduced *P. muralis* populations might have significance for interaction with native lizard species and invasion potential. I found significant variation in body size and head morphology between introduced populations, although this variation may be largely explained by ancestral divergence in morphology between animals of French and Italian lineage rather than being reflective of adaptive response post-introduction. The results do, however, indicate that sex specific phenotypic shifts in head morphology are apparent between males of two populations of shared Italian lineage inhabiting contrasting habitats (urban and rural). Although I can only speculate on the possible mechanisms driving variance in head sizes between these populations, similar bite performances despite morphological variation across populations suggests a shift in the form-function relationship between head morphology and bite performance, indicating a highly flexible system susceptible to natural and sexual selective forces. Allometric trajectories of body size to bite force support the theory that site specific selective forces (either natural, sexual, or an interplay between both) may be driving a more rapid increase in bite force relative to body size in the male urban population. Such divergence could be indicative of an adaptive response to overcome specific challenges of urban life and may be integral to urban persistence and significantly influence range expansion and invasive potential through exploitation of urban/disturbed habitats. Comparison of morphology and allometric scaling of body size and bite force between introduced *P. muralis* and native lizards suggest considerable niche overlap, and thus high potential for competitive interaction. Furthermore, these comparative results infer superior (i.e., greater body size, head dimensions and/or greater bite force for a given size), or at least comparable, competitive ability of *P. muralis* with that of native lizards. Finally, a lack of dietary overlap between UK and Vancouver Island populations of *P. muralis* highlights a niche breadth in diet that is likely to overlap that of native lizards and may ease establishment of the species in a variety of habitats and ecoregions.

Chapter 5: Interspecific scent recognition between native lizards and invading wall lizard (*Podarcis muralis*): Implications for competitive interactions and invasion impacts

5.1 Abstract

The human assisted movement of species beyond their native range facilitates novel interactions between invaders and native species that can determine both whether an introduced species becomes invasive and any negative implications for native communities. However, avoiding costly interactions through recognition and avoidance can be compromised by the naivety of native species to novel invaders and vice versa. I test this hypothesis using the Common wall lizard (*Podarcis muralis*), and the native lizard species with which it may now interact with in the UK (*Zootoca vivipara*, *Lacerta agilis*) and on Vancouver Island (*Elgaria coerulea*) by exploring species response (tongue flicks, avoidance behaviour) to heterospecific scent cues in controlled experiments. Wall lizard tongue flick response varied in response to different species' scent, with significantly more tongue flicks directed to *E. coerulea* scent than the other species and control. This recognition did not however result in a behavioural response in *P. muralis*. *Lacerta agilis* showed a strong recognition response to *P. muralis* scent, with an average of 2.3 times more tongue flicks occurring in close proximity to treatment stimuli than control, and exhibited aggressive behaviour towards the scent source. Conversely, *Z. vivipara* spent less time on average (38%) in proximity to *P. muralis* scent cues than control, but demonstrated a higher rate of tongue flicks towards *P. muralis* scent in this reduced time, consistent with an avoidance response elicited by the scent cue. There was no evidence of *E. coerulea* recognition of *P. muralis* scent in terms of tongue flick or time spent in proximity to stimuli, although the native species did show a preference *for P. muralis* scented refugia. Overall, my results suggest a variable response of native species to the scent of *P. muralis*, from an avoidance response demonstrated by *Z. vivipara* that mirrors patterns of exclusion observed in the field, to direct aggression observed in *L. agilis*, and an ambiguous reaction from *E. coerulea* that may reflect a diminished response in line with threat sensitivity hypothesis. These results have significant implications for the invasive success and potential impacts of introduced *P. muralis* populations on native lizards.

5.2 Introduction

Competition within and among species arises through overlap in utilisation of food, space, or time niches, and plays an important role in determining species' distributions and abundance (Case and Gilpin, 1974; Schoener, 1983). The outcomes of conflict arising from such contest are often asymmetrical, commonly driven by factors such as contestant body size, residency, and prior experience (Schoener, 1974; Chen and Hsu, 2016; Chock et al., 2018). In time, contest can lead to niche segregation, character displacement, and exclusion of inferior competitors from optimal habitat (Losos, 2000; Peiman and Robinson, 2010; Heltai et al., 2015). Likewise, the introduction of a novel species can greatly disturb population and community dynamics through predation and competition, with the potential to cause trophic, temporal, spatial, and habitat niche shifts and drastic declines or local extinctions of native species (Cadi and Joly, 2003; Doody et al., 2009; Brzezinski et al., 2018; Hernandez-Brito et al., 2018; Dorrestein et al., 2019).

Conflict between species is a hierarchical process, beginning with contact and ending with physical interactions. However, mediating those physical interactions is a variety of behavioural decisions that can influence the severity out of the outcome for one or both organisms (Langkilde et al., 2005). Individuals might detect but choose not to interact with one another, such as if one individual perceives the other to be dominant (Brazill-Boast, 2013). Individuals might also engage in ritualised display behaviours that reduce the need for physical altercation by giving further information about the likely outcome (Edwards and Lailvaux, 2012; Reichert and Gerhardt, 2014; Baeckens et al., 2018). However, when native species encounter novel, non-native species, this system of recognition might be compromised by the lack of evolutionary history between two taxa. Without such recognition, naive/native species may exhibit suboptimal behavioural responses during encounters that leave them particularly vulnerable to pressures from introduced species (prey nativity hypothesis) (Sih et al., 2010; Ehlman et al., 2019). Avoidance of costly encounters therefore requires accurate recognition of potential threats through sensory discrimination, followed by an appropriately gauged responsive behaviour that weighs the relative costs of the threat. As stated by the threat sensitivity hypothesis, individuals should show stronger responses to chemical cues associated with higher risks/costs (e.g., trade-off between avoidance of threat and reduced foraging time), but should show weaker responses to cues with lower associated threat (Payne et al., 2004; Amo et al., 2005a; 2007b; Cisterne et al., 2014).

Chemosensory cues are an important source of information on which to base judgement of likely costs of encounters and a suitable response. They can reliably allow forewarning of the immediate or recent presence of predators, and in certain circumstances they may be the only cues available (Kats and Dill, 1998). Indeed, the majority of examples of behavioural response to chemical cues of novel species come from predator-prey systems (Cisterne et al., 2014; Stanbury and Briskie, 2015; Hoffmann et al., 2018). For example, responsiveness of woodfrog tadpoles to novel predators has been found to be dependent on the pre-exposure to a greater diversity of predator types (Ferrari et al., 2015). Foraging behaviour of two native Australian lizards was seen to be compromised when individuals were exposed to scents of both native predators and invasive mammalian predators (Webster et al., 2018), suggesting prey naivety is not the rule in native/non-native systems. The reverse situation, of invasive species response to cues from novel predators, has also received attention, as in the avoidance response of Asian house gecko (*Hemidactylus frenatus*) to some native predatory snake cues (Cornelis et al., 2019). There is, however, less known about behavioural responses to novel scent cues outside of predator-prey systems. It is reasonable to suspect that the presence of an introduced competitor species might have an effect similar to that of a novel predator, and therefore native species might learn to avoid cues from invasive species if these cues were previously associated with an encounter that incurred a cost. Examples come from Spanish terrapins' (*Mauremys leprosa*) avoidance of water pools with chemical stimuli of invasive Red eared slider (*Trichemys scripta*) (Polo-Cavia et al., 2009), and Honey bee (*Apis mellifera*) avoidance of flowers occupied by invasive Argentine ant (*Linepithema humile*) (Sidhu and Rankin, 2016). Responses may however be more ambiguous, such as the preference of both endemic Barbados leaf-toed gecko (*Phyllodactylus pulcher*) and an invasive House gecko (*H. mabouia*) for refugia conditioned with the scent of the other species (Williams et al., 2016).

Chemoreception is highly developed in squamate reptiles (Schwenk, 1993; Cooper, 1994) and has an important function in social interactions with conspecifics (i.e. mate selection, kin recognition, and territorial behaviour) (Lopez and Martin, 2002; Carazo et al., 2008; Pernetta et al., 2009; Mason and Parker, 2010; Font et al., 2012; Mangiacotti et al., 2019), and foraging (Cooper, 1994). Recognition of chemical cues is also fundamental to formulating antipredator responses in these taxa, as demonstrated by avoidance of refuges bearing only the scent of predators (Kats and Dill, 1998; Lopez and Martin, 2001; Amo et al., 2006a; Ortega et al., 2018). The ability of lizards to also discriminate between closely related sympatric species through pheromones has been demonstrated by the selective sexual behaviour and ethological isolation between *Eumeces* skinks (Cooper and Vitt, 1986), *Liolaemus* lizards (Labra, 2011), and the increased response of the lacertid lizard *Podarcis muralis* to chemical stimuli derived from conspecifics rather than from sympatric *P. bocagei carbonelli* (Cooper and Perez-Mellado, 2002).

Podarcis muralis is a small oviparous lizard native to Southern and central Europe and Northwestern Asia Minor, with successful introduced populations in Northern Europe, and North America (Kwiat and Gist, 1987; Hedeen and Hedeen, 1999; Bertram, 2004; Schulte et al., 2013; Michaelides et al., 2015). Being highly territorial, introduced *Podarcis* spp. populations pose a potential competitive (and predatory) threat to ecologically similar native species (Boag, 1973; Heym et al., 2013). On Vancouver Island, British Columbia (Canada), *P. muralis* now occurs in the habitat of the islands' only native lizard, the Northern alligator lizard (*Elgaria coerulea*) (Bertram, 2004). In the UK, *P. muralis* has been introduced to habitat of the native common lizard (*Zootoca vivipara*) and in some areas encroached upon habitat of the nationally rare sand lizard (*Lacerta agilis*) (Mole, 2010; Woodfine et al., 2017). There is however limited empirical evidence of adverse effects of *P. muralis* on native lizard communities (Münch, 2001; Kühnis and Schmocker, 2008; Schulte et al., 2008; Mole, 2010; Heym et al., 2013).

With a view to exploring the possible indirect competitive interaction between *P. muralis* and native lizards, the objective of this study was to examine experimentally the behavioural response of *P. muralis* individuals to scent cues of native lizard species within its introduced range of the UK and Vancouver Island, and vice versa. Based on the naivety hypothesis, I predicted that the taxonomic distance separating *P. muralis* and native *E. coerulea*, combined with the short period of sympatry (since 1970), would lead to no scent recognition. In the UK, I predicted that, despite being a relatively recent introduction to the UK (Foster, 2015), the closer phylogenetic relatedness and substantial sympatry in continental Europe between *P. muralis* and the lacertids *L. agilis* and *Z. vivipara* (Sillero et al., 2014) would produce differences in behaviour in response to scent cues.

5.3 Methods

The methodology for experimental trials of scent recognition was adapted from several chemosensory studies involving *Podarcis* spp. (Bertram, 2004; Barbosa et al., 2005; Font et al., 2012) and from pilot trials conducted in June 2017. Experimental procedure and husbandry methods were reviewed and approved by the ethics committees of the University of Leeds and BC Ministry of Forests, Lands and Natural Resource Operations and Rural Development. Experimental trials were conducted on Vancouver Island, BC, between 10-20th July 2018, and in the UK between 15-21st August 2018.

5.3.1 Animal collection and husbandry

All wild caught animals were health screened and checked for external parasites before being taken into captivity. Individuals were sexed by colouration, body shape, and inspection of the cloacal region.

Podarcis muralis: All *P. muralis* were caught by hand or noosing. Twenty-one adult males (SVL >45 mm) were collected from the introduced population around the Fairfield district of Victoria, BC (48.24 °N, -123.20 °E). Nineteen adult male *P. muralis* were collected from an introduced population at West Worthing, Sussex (50.48 °N, 0.22 °W). All *P. muralis* were euthanized (pithing and decapitation) following anaesthesia with 25% Benzocaine gel via oral administration (G.Hanke, pers comm.) and stored in 90% ethanol after the experimental trials and retained for further study.

Zootoca vivipara: *Z. vivipara* (11 females, 7 male) were caught as part of active mitigation translocations at two UK sites: High Wycombe, Buckinghamshire (51.61 °N, - 0.71 °E) and West Malling, Kent (51. 28 °N, 0.32 °E) between 1-5 August 2018. *Podarcis muralis* is absent at both of these sites. Individuals were caught by hand under artificial refugia. These lizards were retained in captivity for 10 days for inclusion in the scent recognition experiments and subsequently released to the respective translocation receptor sites.

***Lacerta agilis argus**:* Owing to the conservation status of *L. agilis* in the UK and necessary restriction on use of wild caught animals, I replaced the species with its most closely related subspecies *L. a. argus* (Andres et al., 2014). Five juvenile animals (3 female, 2 male) (born in August 2017) were acquired from captive stock in March 2018. These individuals were reared as a group in captivity and had reached adult size by August 2018. These animals were retained in private collection following this study.

Elgaria coerulea: *E. coerulea* (11 female, 7 male) were collected from Kingzett Lake quarry (48.67 °N, -123.63 °E) and Mt. Douglas (48.49 °N, -123.34 °E), on Vancouver Island in early July, and caught either by hand under natural refugia or by noose. All *E. coerulea* were returned to point of capture following this study. *Podarcis muralis* was absent at both of these sites.

All lizards were transported to the study facilities in plastic terraria (L20 × W12 × H16 cm) with natural substrate and refugia objects obtained at the capture site. Lizard species were housed separately in large plastic terraria (L70 x W30 x H50 cm), with water supplied *ad libitum* and provision for basking, thermal gradient (18 - 28°C), and shelter. Live food was offered every other day in the form of 3rd instar crickets, meal worms, and wax worms. Light and heat were provided by incandescent (40 W) bulbs placed above each terrarium to provide a 14-10 hour L:D cycle or terraria were moved outside during the day if weather conditions allowed. All lizards were marked dorsally with an identifying number in non-toxic marker and were given a 5-day acclimatisation period to allow habituation to the general disturbances and handling prior to the experimental trials beginning.

5.3.2 Scent recognition experimental procedure

Experimental trials were conducted between the hours of 9:00 and 17:00 to coincide with lizard period of daily activity. The experimental enclosure was a clear plastic storage container (L70 x W30 x H15cm) with the back and sides blacked out. Two textured washable liners were used as floor coverings which were alternated between trials to allow thorough cleaning in warm water and drying prior to next use. The centre line of the enclosure was marked on each liner to delineate treatment halves for observation and analysis. Two small refugia (L10 x W10 x H2 cm) with a single entrance (H1 x L3 cm) were created using slate and plastic building blocks and were placed against the side wall of each end of the enclosure (Fig 5.1). A 60W spot bulb was suspended directly overhead the experimental enclosure casting equal heat and light throughout.

Treatment was randomly assigned to each half of the enclosure prior to the start of each trial. Both treatments consisted of four cotton tipped swabs, one placed in the front and rear corners of the half, one at the entrance to the refugia, and one on top of the refugia (Fig 5.1). For control treatment, swabs were dipped in deionised water. I did not use a pungency control because in many previous studies, including those specifically dealing with *P. muralis* and *E. coerulea*, it has already been well established that these lizards have highly developed olfaction and can discriminate scent of congeners, predators and prey from biologically irrelevant scents (Cooper, 1990; Cooper and Perez-Mellado, 2002; Gabirot et al., 2010). Scent treatment was obtained by firstly dipping swabs in deionised water and then gently rubbing the swab over the body of the scent donor making sure to swab femoral pores and cloacal regions, since these are the body areas most frequently and intensely investigated by tongue-flicking during social encounters (Lopez et al., 2002; Amo et al., 2004; Lopez et al., 2006; Pellitteri-Rosa et al., 2014). Scent donors were always males randomly selected from the relevant test population.

Test subjects were introduced to the experimental enclosure underneath a clear container (15x10x10 cm) down the central line of the enclosure. Once the lizard settled to relaxed movement behaviour the container was slowly removed, and on the first tongue flick from subject a 10-min timer was started on the video camera recording the trial. Subsequent tongue flicks were tallied according to the treatment side in which they occurred. After the 10-min trial test subjects were returned to housing terraria and were only used in one trial a day. Fresh swabs were used for each trial, and the liner and refugia thoroughly washed and air dried before next use. Only UK *P. muralis* were subjected to multiple trials (I.e., each individual tested against *Z.vivipara* and *L.a.argus*). All other lizards were only involved in one trial, with no replicates, to avoid habituation to scent cues.

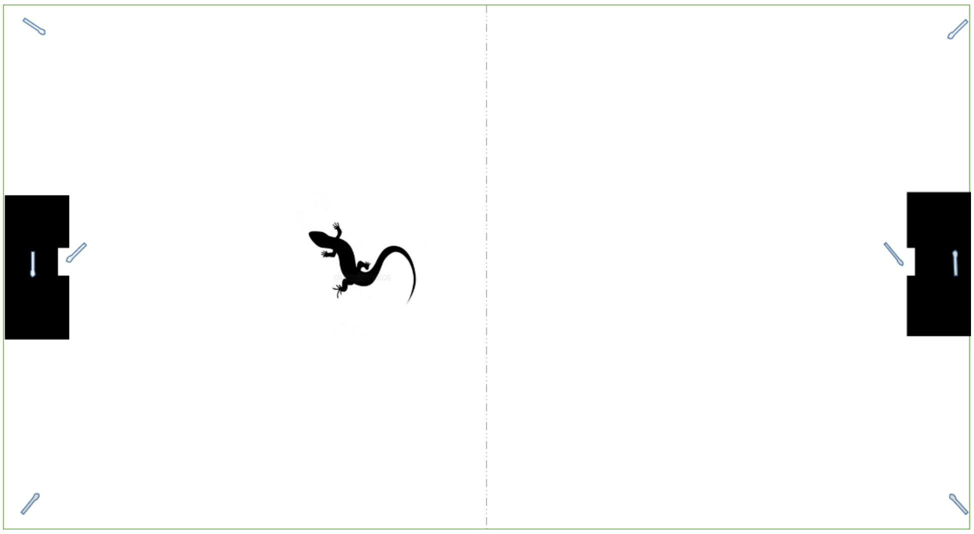


Figure 5-1 Diagram of enclosure in which controlled experiments of scent recognition between *P. muralis*, *Z. vivipara*, *L. a. argus*, *and E. coerullea* were carried out. Scent swabs are visible in the four corners of the enclosure and at the entrance to, and on top of, the refugia.

Cowlog 2.0 software was used to retrospectively analyse video recordings and quantify time spent between the enclosure halves (Hanninen and Pastell, 2009). I limited behaviour classifications to either the time spent in each half or the time spent exhibiting escape behaviour in each half of the terrarium. I defined escape behaviour as time spent standing in an upright position against the wall of the terrarium performing scratching movements with the forelegs. During escape behaviour the lizards were not engaged with tongue flicking or assessing their surroundings. The duration of escape behaviour in each half was thus subtracted from the total time spent in the half enabling quantification of only exploratory or stationary behaviour. Where variation in the time spent between treatment halves was observed I tested the rate of tongue flicks occurring in respective halves. I also recorded the number of times individuals entered either control/treatment refugia.

5.3.3 Data analysis

I applied generalised linear models (GLM) with binomial errors to test if *P. muralis* differed in its response to different species, where response was defined as number of tongue flicks in control vs treatment halves and time spent in control vs treatment halves. Individual paired t-tests were then used to test scent recognition and avoidance behaviour (time spent in each half) between species*.* Number of tongue flicks was normalised using square root transformation (O'Hara and Kotze, 2010).

5.4 Results

There was no difference between sexes in measured responses to the scent of *P. muralis* ($F_{1,88}$ = 0.41, *p* = 0.52) and so data were pooled for subsequent analysis. Species names are abbreviated to initials PM, EC, ZV*,* and LA throughout the Results section*.*

5.4.1 *P. muralis* response to native species

There was a significant difference in the response of PM towards the other three species in terms of ratio of tongue flicks in each treatment half: EC (*z* = 6.13, *p* <0.01), LA (*z* =-3.25, *p* <0.01), ZV (*z* = -4.81, p<0.01). *Post-hoc* Tukey's HSD tests showed that PM responded with more tongue flicks to the EC treatment compared to both ZV and LA treatments. There was no difference in the PM tongue flick response toward ZV and LA (*z* =-1.18, *p* = 0.46). Analysis of PM discriminatory response (tongue flicks) to control and treatment scents showed significantly greater response to EC scent vs control (Student’s t test; t = 2.63, df = 20, *p* = 0.01); no difference between ZV scent vs control (t = 0.14, df = 18, *p* = 0.88); and no difference between LA scent vs control (t = 1.20, df = 14, *p* = 0.24) (Fig 5.2 A).

There was also a significant difference in the response of PM towards the other three species in terms of the ratio of time spent in each treatment half: EC (*z* = 3.64, *p* <0.01), LA (*z* =-2.28, *p* = 0.02), ZV (*z* = -10.65, p <0.01). *Post-hoc* Tukey's HSD tests showed that PM spent more time in the ZV treatment half of the arena than it did in EC and LA treatments. There was no difference in the time spent by PM in proximity to EC and LA treatments (*z* = 2.28, *p* = 0.05). Analysis of PM aversion response (time spent) to control and treatment scents however showed no significant difference between time spent in scent vs control halves across groups (EC, t = 0.36, df = 20, *p* = 0.71); (ZV, t = -1.23, df = 18, *p* = 0.23); (LA, t = 0.01, df = 14, *p* = 0.99) (Fig 5.2 B).

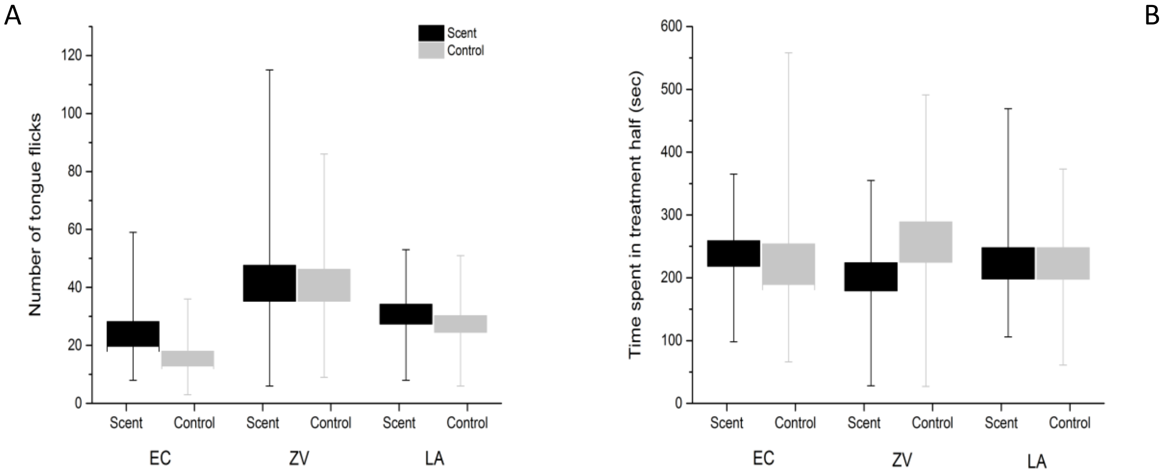


Figure 5-2 Responses of *Podarcis muralis* to scent cues of species that occur within its non-native range. (A) Number of tongue flicks (Mean ± SE) and (B) time spent (Mean ± SE) in proximity to source in response to scents from *Elgaria coerulea* (EC), *Lacerta agilis argus* (LA), and *Zootoca vivipara* (ZV). Errors bars = 95% CI.

5.4.2 Native species responses to *P. muralis*

Only LA showed a significant recognition response to PM scent, with a mean of 103 (SE ± 28.0) tongue flicks in the treatment end of the vivarium with PM scent and 42 (SE ± 8.0) tongue flicks in the control end of the vivarium (t = 2.99, df = 4, *p* = 0.04). There was no significant difference in the number of tongue flicks between PM scent and control ends of the vivaria for ZV (40.2 ± 6.1 scent vs 46.1 ± 8.6 control, t = -1.08, df = 17, *p* = 0.29) or EC (16.2 ± 2.4 scent vs 16.9 ± 3.9 control, t = -0.23, df = 16, *p* = 0.81) (Fig 5.3 A).

Neither group showed a significant aversion/attraction response to PM scent as indicated by time spent in each treatment half. Although LA spent a longer amount of time on average (66%) in the scented treated half than control (LA, t = 1.93, df = 4, *p* = 0.12), that time can be attributed to four instances of direct attack (biting) of a scented swab. Conversely, ZV spent less time on average (38%) in the scent treatment half (ZV, t = -1.88, df = 17, *p* = 0.07). Despite less time being spent in the scented treatment half the rate of tongue flicks by ZV was greater in this half (mean = 0.24 ± SD 0.13) than control (mean = 0.16 ± SD 0.12) (t = 2.10 *p* = 0.05). Average time spent in each treatment half was relatively even for EC (55% scented) (EC, t = 1.22, df = 16, *p* = 0.23) (Fig 5.3 B).

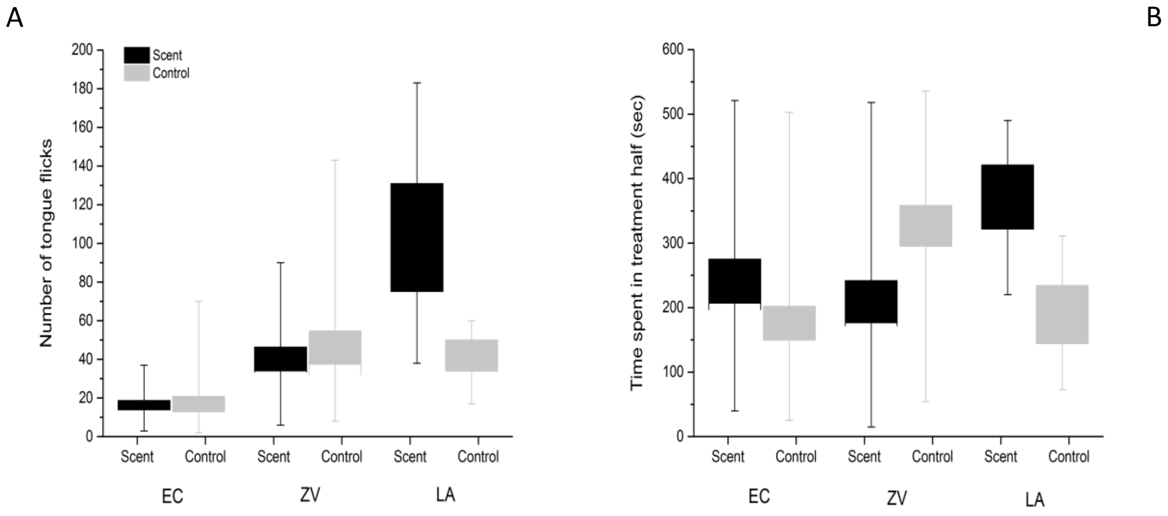


Figure 5-3 Responses of native lizards *Elgaria coerulea* (EC), *Lacerta agilis argus* (LA), and *Zootoca vivipara* (ZV) to scent cues of non-native Podarcis muralis. (A) Number of tongue flicks (Mean ± SE) and (B) time spent (Mean ± SE) in proximity to stimuli source. Errors bars = 95% CI.

Only EC used the scented refuge more often than the control refuge, whereas LA did not use either refuge. In all other experiments the control refuge received more visits than the scented refuge. The difference in visits between control and treatment refuge was greatest in ZV response to PM, with 4 and 9 visits respectively (Fig 5.4)

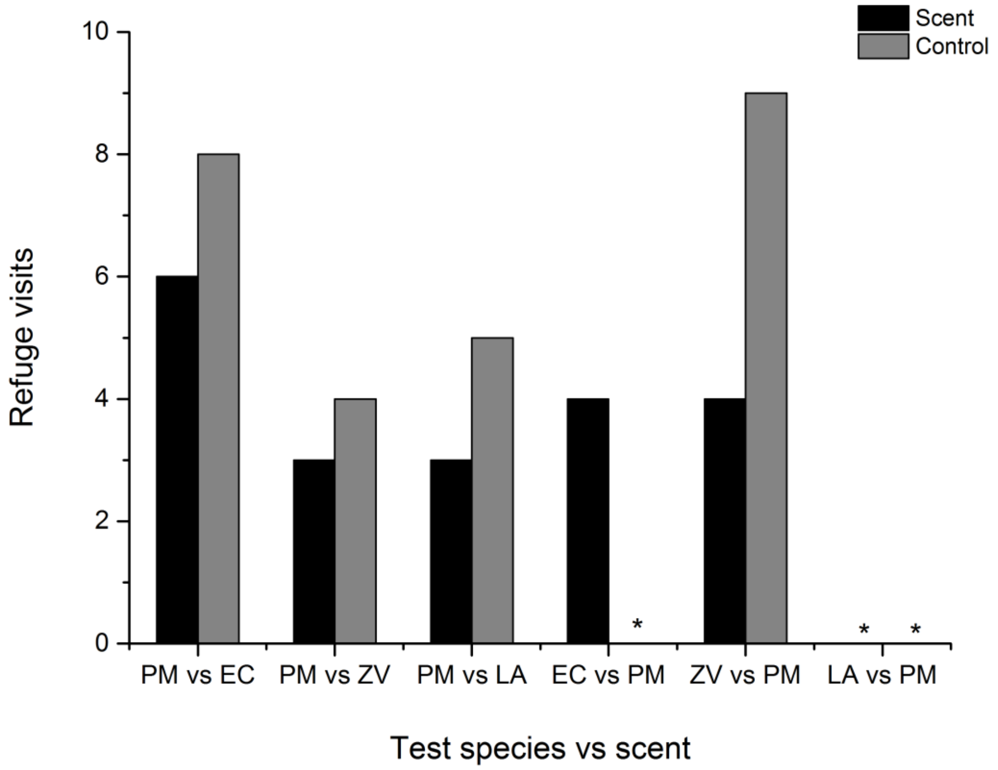


Figure 5-4 Rates of refuge use in response to scents from *Elgaria coerulea* (EC), *Lacerta agilis argus* (LA), *Zootoca vivipara* (ZV) and *Podarcis muralis* (PM) individuals in the laboratory. Letters beneath bars denote species pairings, such that the first of each pair is the focal species and the second is the scent treatment (e.g. "PM-EC" is *P. muralis* exposed to *E. coerulea* scent). * = zero.

5.5 Discussion

Understanding how species may interact when faced with novel competitors is an important part of assessing the invasion potential of non-native species introductions and their impacts on native communities. Avoiding costly interactions through recognition and avoidance can be compromised by the naivety of native species to novel invaders and vice versa. A mixed response to chemical cues was found in experimental trials of scent recognition between non-native *P. muralis* and native lizard species, ranging from a lack of response - suggesting a possible role for both the naivety and threat sensitivity hypotheses - to aversion, and direct aggression to scent stimuli.

The responses of *P. muralis* and *E. coerulea* to the scent of each other in my experiment complement the results of the only other study concerning behavioural interaction between the two species (Bertram, 2004). The previous study also found *P. muralis* scent to have no detectable effect on behaviour of *E. coerulea*. The lack of discriminatory response of *E. coerulea* in the two studies suggests that the species is either unable to detect the odour of *P. muralis*, despite the highly developed chemosensory abilities of the species (Cooper, 1990), or does not respond behaviourally to the stimulus. A possible explanation for the observed lack of *E. coerulia* response is that besides four snake species (three garter snake, *Thamnophis* spp. and the sharp tailed snake, *Contia tenuis*) there are no other native reptile species occurring in sympatry with *E. coerulea* on Vancouver Island (Gregory and Campbell, 1984), and therefore a complete naivety of *E. coerulea* to scent of a lacertid lizard species is not unexpected. My observations of *E. coerulea* readily using scented *P. muralis* refugia, seemingly in preference over unscented refugia, do however warrant further investigation into the species' ability to recognise the scent of *P. muralis* and supports the theory that the physical presence of *P. muralis*, not their scent alone, deters *E. coerulea* from cohabiting refugia with the non-native (Bertram, 2004). If chemosensory recognition was influencing selection for the *P. muralis* scented refugia, this could indicate that in the absence of visual cues and any previous negative experience there was perceived safety associated with the conditioned refuge in an otherwise novel and unfamiliar environment. A similar outcome has been observed in refuge selection trials involving a native and an invasive gecko where both species had preference for refuge previously occupied by the other (Williams et al., 2016). Identification with common compounds in species' scents may have driven refuge choice in such cases (Mason and Parker, 2010; Martin and Lopez, 2014; Garcia-Roa et al., 2016).

In contrast, the discrimination and heightened response of *P. muralis* towards *E. coerulea* scent, above that shown towards the scent of the other species in my experiments, is unexpected considering the taxonomic distance between the two. There are numerous examples across lizard species, including *Podarcis* spp. of an ability to discriminate among closely related species based on chemical cues alone (Cooper and Vitt, 1986; Cooper and Perez-Mellado, 2002; Barbosa et al., 2006; Gabirot et al., 2010; Labra, 2011). There is, however, little evidence for scent recognition of more taxonomically distant species outside of predator/prey systems (e.g., snake predator/lizard prey interactions) (Amo et al., 2004; Cabido et al., 2004; Labra and Hoare, 2015; Ortega et al., 2018), where appropriate behavioural response to the scent of a potential predator or prey is fundamental to individual fitness and survival (Kats and Dill, 1998; Sih et al., 2010). For example, *Blanus cinereus*, a fossorial amphisbaenian, reacted strongly to scent stimuli of sympatric snake and centipede predators, yet showed no difference in reaction towards water control and an innocuous, sympatric skink (Lopez and Martin, 2001). Male *Podarcis hispanica* are capable of discriminating conspecific scent from that of *Psammodromus algirus*, however no variation in tongue flick response between odourless control and *P. algirus* scent suggests a lack of behavioural response towards, or inability to detect, the latter (Gomez et al., 1993). Regardless of the context in which *P. muralis* explored the scent of *E. coerulea* (i.e. inquisitiveness towards a novel or biologically relevant scent) the fact that this discrimination of scent did not cause a behavioural response in *P. muralis* suggests that the stimuli (alone) may have been regarded as benign and posing no risk. A lack of behavioural response having distinguished the odour is to be expected if fitness costs associated with avoidance behaviour outweigh those of any naturally occurring interaction, such as limited agonistic behaviour between the two species (Langkilde et al., 2005). A generalised cautious response by non-native species to novel scent cues may be common, particularly in regard to antipredator behaviour, where it is argued that a general wariness may be a beneficial trait facilitating invasion success (Cisterne et al., 2014). Similarly, heightened boldness and willingness to explore unfamiliar stimuli, coupled with higher levels of behavioural plasticity to mediate response, may be common traits among species that become invasive (Damas-Moreira et al., 2019). These results and reasoning are in keeping with observations of a greater propensity for *P. muralis* to make the first approach in encounters with *E. coerulea*, but ultimately a lack of aggression arising through direct interactions between the two (Bertram, 2004).

In light of the recognition given towards *E. coerulia* scent by *P. muralis*, the lack of similar response towards the more closely related lacertids *L. a. argus* and *Z. vivipara*, strongly suggests a diminished response by *P. muralis* rather than inability to detect their chemical cues. This lack of response could indicate that *P. muralis* has no evolved or learned aversion to the scents (at least in the absence of other cues), in accordance with the threat sensitivity hypothesis, where in the absence of other cues, individuals should show stronger responses to chemical cues associated with higher risks/costs, but should show weaker responses to cues with lower associated threat (Sih et al., 2010; Cisterne et al., 2014). Threat sensitive response has been demonstrated by differential anti-predator responses of *P. muralis* dependent on influence of visual and scent cues (Amo et al., 2006a).

Podarcis spp. have an evolutionary history as part of a much richer reptile community (i.e., Scincidae, Anguidae, Gekkonidae, Lacertidae) in the native range in continental Europe compared to UK *L. agilis* and *Z. vivipara*, including syntopy with several other lacertids (Sillero et al., 2014). As such, the diminished response of *P. muralis* may be linked to inherent chemosensory abilities to discern non-threatening scent cues of sympatric species. Congenital chemosensory ability of lizards has been proven at least in regard to recognition of predatory snake cues (Van Damme et al., 1995; Van Damme and Castilla, 1996; Durand et al., 2012). Rather contradictory to this reasoning are my observations of heightened exploratory behaviour and even aggression directed towards *P. muralis* scent swabs by *L. a. argus*. If such a reaction represents an innate antagonistic response to *P. muralis* then an appropriate reciprocal behaviour might be expected in the reverse treatment. More likely however is that the sensory naivety of the captive born individuals used in my study led to misinterpretation of the scented swabs as a prey item. Similar attacks towards swabs have been observed in experiments specifically testing lizard discrimination of prey odours (Cooper, 1990; 1991; 1992).

Taken on its own there is a certain amount of ambiguity in the tongue flick response from *Z. vivipara* towards *P. muralis*. The greater amount of time spent in the control half (though not statistically significant) paired with more than twice the amount of visits to control refugia, and an increased rate of exploratory tongue flicking in the scented half, is however indicative of an aversion response to the non-native. This is in keeping with field observations of population declines and displacement of *Z. vivipara* in areas where introduced *P. muralis* are thriving (Mole, 2010; RW pers obbs; RW pers obbs). Avoidance behaviour elicited by indirect cues alone has obvious advantages to mediating potential fitness costs arising from direct encounters, particularly when the costs of avoidance are low (Langkilde et al., 2005).

My results support the conclusion of Bertram (2004) that the interaction between *P. muralis* and *E. coerulea* is likely to be complicated, context dependent, and possibly reliant on visual cues rather than scent alone. Further investigation is therefore needed to determine the nature and outcome of interactions in the context of limited resource (i.e. refuge) – likewise for interactions between *P. muralis* and the two UK lacertids. The extreme response from the captive bred *L. a. argus* to *P. muralis* in this study is unlikely to be representative of a response not unconfounded by the limited sensory experience of the captive bred animals and therefore is not particularly informative without further tests. Additional tests for discrimination of other cues (e.g., *L. a. argus* vs. *Z. vivipara*) and inclusion of visual stimuli would determine if the aggressive reaction was indeed an overzealous response to a potential prey item, as assumed, or a genuine agonistic response to an unfamiliar intruder.

The behavioural assays on tongue flick and aversion response strongly suggest that non-native *P. muralis* are unlikely to alter their behaviour in response to indirect chemical cues from native lizards with which they may potentially compete. Range expansion of non-native populations and greater overlap with native species' ranges in the UK and Vancouver Island is therefore likely to increase incidence of direct interaction and possible aggressive encounters that may have fitness costs for native lizards (and *P. muralis*). In the case of *Z. vivipara*, an aversion response to indirect cues from *P. muralis* may mitigate the chance of direct encounters but ultimately lead to displacement of the native from previously occupied areas. Conversely, interactions between *P. muralis* and *E. coerulea* and *L. agilis* have potential to be more direct, the outcomes of which are likely to depend on appropriate behavioural response to visual cues. Further research is needed to establish if recognition of visual cues between these species can mediate such encounters.

Results of this study highlight the potential for varied responses to chemical cues within a native/non-native species model. In accordance to the study hypothesis, the results provide evidence of differing responses with taxonomic distance that are demonstrative of naivety to scent cue of novel competitors, and threat sensitivity between more closely related species. As expected, a lack of response from Vancouver Island *E. coerulea* when exposed to scent of invading *P. muralis,* is indicative of naivety in a native species towards an invader with which there is no evolutionary history. However, naivety was not symmetrical in this pairing, and the heightened response of *P. muralis* towards the scent of taxonomically distant *E. coerulea* - over that shown towards closely related lacertid species - suggests a general wariness in the invader that may be a valuable behavioural trait facilitating expansion of the species' range on an intercontinental scale. Conversely, gauged responses to scent cues of *P. muralis* by more closely related*, Z. vivipara*, and *L.a.argus* appear to have been based on perception of potential for a costly encounter (threat sensitivity), eliciting definitive avoidance and aggressive behaviour in *Z. vivipara* and *L.a. argus* respectively. *Podarcis muralis*, however, appear to be unperturbed by the scent of the other lacertids, suggesting that in the absence of other cues, there was no perceived threat associated with the potential for a direct encounter. These results highlight how responses to indirect cues might act to shape the competitive interaction between an invading and native species, interactions that will ultimately determine the impact of invasions on native communities.

Chapter 6: Stakeholder discourse and opinion towards a charismatic non-native lizard species: potential invasive problem or a welcome addition?

6.1 Abstract

Analysis of discourse between stakeholders is becoming increasingly recognised for its importance in resolving conflicts of opinion regarding complex environmental issues such as the human mediated spread of invasive non-native species – one of the major drivers of biodiversity loss worldwide. Species' attributes, stakeholders' level of knowledge, perceptions of threat, attitudes towards intervention, and nature values all have subjective influence on opinion, often creating highly opposed interests and perspectives that can create barriers preventing effective management. Using a Q method approach towards analysis of subjective opinion among stakeholders, this study aimed to identify emerging viewpoints regarding the presence of Common Wall Lizards (*Podarcis muralis*) in the UK – an introduced, non-native species with which there are high levels of human interaction but low levels of knowledge regarding potential negative ecological impacts. It explores the ways in which different stakeholder groups (i.e., public, land managers, conservationists) might share views and the reasoning behind shared or opposing discourse between groups. Three clearly defined viewpoints on the species' introduction emerge from the analysis of Q-sorts: 'Innocent until proven guilty', 'Precautionary informed concern' and 'The more the merrier'. These perspectives reflect both stark differences and commonalities in stakeholder perceptions and opinion towards the species' introduction. Whereas the 'Innocent until proven guilty' and 'Precautionary, informed concern' views are defined by differences in levels of ecological knowledge and impact uncertainty between them, the divergence of the 'More the merrier' view from both other viewpoints appears to be more reflective of pronounced variation between the groups' deeper beliefs, perceptions and values about 'naturalness and balance', and overall relationship with nature.

These findings will be useful in identifying discordant attitudes and areas of potential contention between stakeholders that may arise in consideration of management decisions regarding non-native species more widely. The holistic method of interpreting the analysis gives insight into how and why stakeholders may have formulated certain viewpoints. This in turn could help conservation managers identify ways in which to appreciate and work with subjective influences on stakeholder perceptions in order to best communicate the complex challenges and opportunities presented by non-native species.

6.2 Introduction

The interaction between nature and society has never been more complex, politicised, or researched (Aitken, 2012; Biermann and Mansfield, 2014; Foss, 2018). This is particularly evident in relation to the causes and consequences of global loss in biodiversity, frequently regarded as one of the most pressing environmental challenges currently facing humanity (Skogen et al., 2018). Loss in biodiversity has negative impacts on both ecosystem function and ecosystem services, ultimately threatening human well-being (Cardinale et al., 2012; Naeem et al., 2016). Human activities are the predominant drivers behind biodiversity loss (e.g., over-exploitation, land use change, introduction of invasive species) (Maxwell et al., 2016) and, as such, there are a multitude of associated socio-environmental issues that are often defined by highly opposed interests and perspectives amongst stakeholders (i.e., economic, political, ecological, cultural, social) and that prevent unilateral solutions to the wider problem.

Box 1. Definition of terms

The term 'non-native species' (NNS) is the equivalent of 'alien species' as used by the Convention on Biological Diversity (CBD) to describe species that occur in the wild (following introduction) beyond their natural geographic range. INNS or 'Invasive non-native species' (the equivalent of 'invasive alien species' or 'IAS' are broadly defined as species whose introduction and/or spread threaten biological diversity or have other unforeseen impacts

The human-mediated introduction of invasive non-native species (INNS, see Box 1) beyond their natural range is one of the leading causes of biodiversity loss globally (Simberloff et al., 2013). With human dimensions being a feature of all aspects of the invasion process (Garcia-Llorente et al., 2008; Tassin and Kull, 2015), several studies have sought to explore variation and discord amongst stakeholder opinion with regard to INNS to assess implications for support of management practices (Bremner and Park, 2007; Gobster, 2011; Fischer et al., 2014). Species attributes, level of knowledge, perceptions of threat, attitudes towards intervention, and nature values have all been found to be subjective influences on stakeholder opinion (Garcia-Llorente et al., 2008; Gozlan et al., 2013; Verbrugge et al., 2013; Ford-Thompson et al., 2015; Shackleton and Shackleton, 2016). Indeed, the discourse surrounding issues of INNS appears to be beset not only by the inherent uncertainty that surrounds ecological knowledge of biological invasions, their management and environmental implications (Garcia-Llorente et al., 2008), but also by highly varied and subjective comprehension of emotive terms such as 'non-native', 'alien', ‘exotic’, ‘pest’, ’invasive species’, ‘ecological impact’, and the connotations that arise through social representation of these concepts as a whole (DEFRA., 2009; Tassin and Kull, 2015; Essl et al., 2018). The way in which people become familiar with complex ecological concepts also has an important influence on the development of opinions and formation of perceptions. Non-scientists and scientists have varied frames of reference, and make comparisons with existing personal understanding from other domains to formulate their comprehension of the complex (and relatively new in public conscience) ecological concept of INNS (Selge and Fischer, 2011; Fischer et al., 2014). Differences between viewpoints based on these utilitarian, moralistic, humanistic, or naturalistic values thus have potential to cause significant obstacles to management operations (e.g., public opposition to plans for eradication of the American grey squirrel in Italy where the species’ poses a threat to native red squirrel (Bertolino and Genovesi, 2003)). The myriad factors that might shape opinion and ultimately result in contesting viewpoints can be understood within a conceptual framework of hierarchal influence. Within that framework, attitudes and opinion are defined by an individual’s core values (i.e., stable mental constructs that transcend specific situations and represent personal needs according to enduring beliefs) and perceptions of risk (judgments of potential hazards influenced by heuristic rules and social context that simplify complex concepts and may misrepresent reality) (Estevez et al., 2015).

It has become increasingly recognised that discourses involving stakeholders should be a focus of analysis in environmental governance studies. These discourses are important for facilitating cooperation between diverse actors aimed at resolving complex environmental problems (Hajer and Versteeg, 2005; Hagan and Williams, 2016). Indeed, understanding of the role of discourse between actors of different status, and the inherent subjectivity that shapes personal perception and opinion driving the policy making process has become a burgeoning science all of its own (Frate and Brannstrom, 2017; Andersen et al., 2018).

Discourse analysis has received much attention in the environmental sciences, particularly in politically charged arenas of response to climate change (Lansing, 2013; Foss, 2018), renewable energy (Mukonza, 2017; Rennkamp et al., 2017), land use change, and sustainable development (Cook et al., 2004; Soini and Birkeland, 2014; Walder and Kantelhardt, 2018). Identification of social perspectives through such analysis may avoid conflict and barriers to planned strategies and suggest socially acceptable solutions for their implementation (Frate and Brannstrom, 2017; Mayett-Moreno et al., 2017). Arguably the most emotive and polarized discourse within environmental science can be found in regard to contention over issues of wildlife management. Such conflicts are often characterised by arguments over scientific truth claims and the addition of ethical/animal welfare dimensions as typified by such issues as the culling of badgers (*Meles meles*) to control the spread of bovine tuberculosis in the UK (Price et al., 2017), lethal control of wild deer populations, and other 'pest' species (White et al., 2003; Wallwork and Dixon, 2004; Dandy et al., 2012). However, uncertainty borne from knowledge gaps and deficiencies in data often pervades understanding of such environmental issues. Thus, in the absence of, and perhaps sometimes in despite of (Gozlan et al., 2013) empirical evidence, actors involved in associated discourses necessarily construct their viewpoints and understanding based on subjective influences (i.e., scientific reasoning/theory, personal experience, historical/cultural bias, economical, ethical values, heuristic judgement) (Davidson et al., 2013).

Studies investigating stakeholder discourse have done so largely through standard interview and questionnaire techniques and quantitative analysis of participant responses aimed at providing a representative overview of attitudes held (Bremner and Park, 2007; Garcia-Llorente et al., 2008; Poudyal et al., 2016; Hoyle et al., 2017). Other authors have employed qualitative techniques such as focus groups to delve deeper into the reasoning behind the formation of particular viewpoints, enabling an interpretation of the data that allows for a broader understanding and recognition of important patterns and themes within the discourse (Selge et al., 2011; Dandy et al., 2012). One method that combines both qualitative and semi quantitative analysis of subjective opinion among stakeholders is Q method (Brown, 1993; Yang, 2016). Although frequently used in analysis of discourse within the environmental sciences (Brannstrom, 2011; Lansing, 2013; Hagan and Williams, 2016; Walder and Kantelhardt, 2018) the method has seen very little application in regard to discourse on NNS (Falk-Petersen, 2014).

Here I use a Q method approach to investigate the discourse surrounding the presence of Common wall lizard *Podarcis muralis* in the UK – a species that has established numerous populations in the South of England following introduction from mainland Europe and is thriving in habitats ranging from coastal cliffs of Dorset to highly urbanised areas of West

Sussex (Michaelides et al., 2015). The presence of wall lizards poses a potential risk to native lizards through contest and transmission of pathogens, and possible wider impacts on invertebrate communities (Foster, 2015), although to date there is only anecdotal evidence to suggest negative impacts are apparent (Mole, 2010). Being locally abundant and gregarious in behaviour the lizards are frequently encountered by members of the public, particularly in areas of high public footfall such as the sea fronts of Bournemouth and Eastbourne. No control measures are currently in place to manage existing populations, and further ecological research into established populations is needed to assess viability and justification for management (Foster, 2015). This situation presents an interesting opportunity to investigate people's attitudes towards the lizards in the face of high levels of interaction but potentially low levels of knowledge regarding possible negative ecological impacts. Through use of a holistic Q method approach this study aims to identify emerging viewpoints regarding the presence of wall lizards, and explores the ways in which different stakeholder groups (i.e., public, land managers, conservationists) might share views and the reasoning behind shared or opposing discourse between groups. Such insight will be useful in identifying discordant attitudes and areas of potential contention between stakeholders that may arise in consideration of management decisions regarding NNS more widely. In addition, the analysis will also help illustrate how people reason their subjective views regarding complex ecological concepts in general. Specifically, I ask: How and why do stakeholders group in their opinions towards the lizard introduction? What does the discourse in this case study tell us about perceptions and attitudes towards management of introduced species more generally?

6.3 Methods

All Q studies are reconstructive and characterized by two key features. Firstly, the collection of data is done in the form of Q sorts (Watts and Stenner, 2012; Hagan and Williams, 2016). This is typically done by presenting people with a sample of statements (or items) about the given topic, which is referred to as the Q-set. The selected participants, or P-set, are then instructed to rank-order the statements from their personal point of view on a score sheet. Participants work with their subjective interpretation of the statements thus revealing their subjective viewpoint in the final rank order of statements. Secondly, these Q sorts are factor-analysed to establish different patterns ("discourses"). Unlike in standard survey analysis this factor analysis is not aimed at establishing patterns across individual characteristics such as age, gender and class, but rather patterns within and across individuals by focusing on their discursive understanding of a particular issue (Watts and Stenner, 2012; Hagan and Williams, 2016).

6.3.1 Q set design

The Q set was developed from statements generated from several sources in direct response to (or pertaining to) the open question of 'Do you have any thoughts or feelings about the presence of wall lizards in the UK?' Sources included; 1) responses from the general public, to whom this question was posed in conjunction with a 2017 citizen science campaign conducted through freepost survey returns and in the regional and national media aimed at garnering wall lizard sighting records (bit.ly/lizarduk); 2) informal conversations with the public and landowners/managers engaged with whilst conducting field work at wall lizard localities in southern England during 2016-2018 as part of wider ecological research into the species introduction; 3) Relevant statements that could be regarded as an opinion towards the presence of the lizards found through extensive internet searches of non-scientific press and on social media forums.

A total of 128 statements were collected, at which point no further original opinion/sentiment was found. A review process to fine tune the final Q set (in terms of reduction in number of statements and maintenance of plain language) was then undertaken through careful review of each statement, rewording, and removal or consolidation of statements conveying similar sentiment. This process was informed by piloting and input from peers with expert knowledge in ecology and public engagement regarding NNS. During this revision process several statements were found to confer a negative opinion of the wider issue of NNS and species introductions in general. Although the initial intention was to keep the discourse case specific, these very broad statements were retained and balanced with the inclusion of alternate broad views on NNS from the academic literature. This revision process resulted in the construction of a final Q set consisting of 76 statements that provided a comprehensive and balanced coverage of the study topic (Table 6.1).

Table 6-1 The final' Q Set' of statements (and their ID numbers) representing the overall discourse surrounding the presence of *P. muralis* in the UK

ID	Statements		
1	The more wall lizards the merrier	39	There is a bias against alien species
2	Wall lizards are much prettier to look at than our native lizards	40	We see less sand lizards due to loss of habitat so the wall lizards are a nice substitute
3	If wall lizards are in our garden then they become like our pets	41	Wall lizards live where other lizards don't, so that's ok
4	I would feel quite privileged to have wall lizards in my garden	42	It's nice to see wall lizards in the wild
5	I'm happy to have wall lizards here	43	wall Lizard spotting is great fun
6	I hope wall lizards thrive in the UK	44	As long as wall lizards don't upset local ecology then I enjoy their presence
7	I don't want to see the wall lizards killed	45	I'm unsure of their effect on populations of native lizards
8	Wall lizards are welcome wherever they are	46	It is good to see wall lizards appear to be thriving here
9	Wall lizards feel almost out of place here	47	It is a pleasure and a privilege to observe wall lizard behaviour
10	Wall lizards really shouldn't be here	48	I find wall lizards intriguing and interesting.
11	These wall lizards are invading the UK	49	Wall lizards are a great subject to photograph
12	Prefer if wall lizards were in their own environment best suited to their well being	50	It's great for the kids to have wall lizards in the garden
13	If wall lizards don't cost anything (financially) then their presence is not a problem	51	I don't mind that wall lizards are not native to the UK
14	Wall lizards co-exist quite happily with common lizards on the continent so there's no reason why they wouldn't here.	52	No problems with wall lizards being here as far as I am aware
15	Wall lizards seem harmless enough.	53	Nice to see wall lizards but I'd rather see a native lizard
16	I feel wall lizards are not competing with our native species.	54	The wall lizards always give a topic of conversation when they come out in the warmer weather
17	I cannot see that wall lizards are likely to become a problem	55	It's a shame people don't consider wall lizards when repairing/pointing walls
18	Wall lizards are not detrimental to our gardens	56	I would make special trips to see wall lizards
19	I think wall lizards should be protected here	57	Don't know how I feel about wall lizards being here
20	I am always unhappy about ANY introductions, which are usually bad news for native species.	58	I am concerned there are likely to be more currently unrecorded wall lizard populations.
21	The presence of species which did not arrive here under their own steam is a concern	59	I wish we had wall lizards in the garden. Can I have some
22	It would be a shame if native lizards got edged out of our landscape by wall lizards.	60	The wall lizards provide the only chance we get to see lizards
23	I don't want wall lizards to damage native species	61	I don't want wall lizards to be removed.
24	I'm concerned about Wall Lizards affecting native Sand Lizards and Common Lizards both in terms of competition and pathogens.	62	It's really nice to have this wildlife (wall lizards) in our garden
25	I do wonder if global warming is a factor to wall lizards being here	63	No strong feelings about wall lizards one way or another
26	I have nothing against wall lizards but would like to see some scientific studies investigating their impacts	64	Classifying wall lizards according to our standards of whether or not they should be here is not useful
27	It is worrying that wall lizards are surviving in a colder climate than they are used to.	65	Many non-native species have become established here, wall lizards are just another
28	We should stop wall lizards spreading if possible	66	The wall lizards add to the character of our garden and village
29	I feel that we don't know enough about what these wall lizards bring and take away from our native wildlife.	67	The wall lizards help to keep down garden pests

Table 6.1 (continued)

ID	Statements		
30	Just leave the wall lizards alone	68	What classes as native anymore!
31	I can't see how you can eliminate wall lizards without harming other species	69	Reptiles are so rare I'm excited to see any lizard, native or not
32	The authorities should do something about wall lizards spreading	70	Wall lizards cause a loss in conservation value of sites planned for reintroduction of sand lizard
33	We must embrace the fact ecosystems now incorporate many alien species and not try to achieve the often impossible goal of controlling their abundance	71	I know summer has arrived when wall lizards first start to appear on a sunny day
34	Conservationists should focus much more on the wall lizards ecological role, and much less on where they originated from	72	Wall lizards are killing off our native lizards
35	The public must be vigilant of such introductions and support management efforts	73	We have a somewhat impoverished fauna, but wall lizards add to it
36	It's like being on holiday with wall lizards here	74	If wall lizards are breeding they are obviously happy to be here
37	Having a local colony of wall lizards is great	75	We (humans)bought wall lizards here, so we shouldn't complain
38	We should be grateful wall lizards are here to enjoy	76	As average temperatures rise it is to be expected that wall lizards are thriving here

6.3.2 Participants

Twenty-six participants across seven stakeholder groups (Table 6.2) took part in the Q sorts in the summer of 2017. Participants from the land manager group were invited to take part through having had previous contact with the lead researcher in granting consent to conduct field work at wall lizard sites in Dorset and East/West Sussex as part of wider ecological research into the introduction. Although employed in environmental management/conservation officer roles, their specific knowledge of the wall lizard introductions was not assumed. The public group consisted of participants who again had previously been engaged with during ecological field work in Devon, Somerset and West Sussex during 2016/2017 and were known to at least be aware or have direct experience of wall lizards in their local area (e.g., has them present in garden, encounters them frequently). Members of the public with no experience of the lizards were not considered to take part in this Q sort as many of the statements in the Q set would have no personal relevance to such a group, thus making interpretation and sorting of statements problematic (see Q sort Methods). Participants forming the environmental advisory group were invited to take part based on their expertise in the field of INNS and national biosecurity - their specific knowledge of the wall lizard introductions was also not assumed. Reptile enthusiasts were represented by three individuals who share a passion for herpetology, two of which keep exotic lizards in private collections (including *P. muralis*), and one individual who volunteers in monitoring reptile species locally (Dorset). The participant ecological consultants (n=2) were both experienced ecologists working nationally, with no presumed knowledge of wall lizard populations in the UK. Perhaps most familiar with the topic at hand were representatives from a reptile conservation NGO. Both participants are concerned with active conservation and management of native species and familiar with the UK wall lizard populations. The two academics selected to participate had specific interest in biosecurity and reptile ecology respectively, with no specific knowledge of wall lizard introductions. A greater number of participants were included for the land manager and public groups as it was considered there might be greater scope for variation in experience and opinion within these sectors compared to other groups. Participants were given the same background information before the Q sort regarding the non-native status of wall lizards in the UK, but no other information was given about the consequences of their presence. Instructions were also careful to point out that none of the statements were to be considered as ‘scientific fact’, and merely represent a point of view.

6.3.3 The Q sort

The Q sort was administered either in person or online using software developed by Pruneddo (2013). Thirteen participants conducted their Q sorts in the presence of the lead researcher. The Q set was given to the respondent in form of a deck of randomly numbered cards. Each card contained one of the 76 statements from the final Q set. The participant was first instructed to sort the deck into three piles; “identify/agree,” “neutral/undecided,” and “do not identify/disagree,” depending on his/her personal point of view. This initial ‘sort’ served to familiarize the participant with the nature of the statements and start formulating their own viewpoint. Thereafter, the respondent was instructed to sort out the statements on a score sheet with a pyramidal, or “quasi-normal,” sorting distribution, ranging from “strongly disagree” (−6) to “strongly agree” (6). The sorting distribution was pre-arranged; the whole Q set had to be allocated a ranking relative to one another within this distribution (Watts and Stenner, 2012) (see Appendix 6.1). Participants were encouraged to rearrange the position of statements until they were satisfied their placement represented as closely as possible their personal point of view. Each Q sorting was combined with discussion with the researcher during the process where participants were asked to elaborate on his/her point of view, explain the most salient statements, and discuss whether there were any themes not represented by the items in the Q set. Participants (n=13) completing their Q sort online (Q–sortware (Pruneddo, 2013)) followed exactly the same procedure by dragging and dropping items into their desired arrangement in the fixed distribution. Follow up discussion were conducted via email.

Table 6-2 Participant groupings and number of representative participants

Group	Number of participants
Land managers (local council conservation officers, National Trust)	6
Public	8
Environmental Advisory	3
Reptile enthusiast	3
Ecological consultant	2
Reptile Conservation NGO	2
Academic	2

6.3.4 Ethics Statement

This research received ethics approval from the Biological Sciences Faculty Research Ethics Committee, University of Leeds. Written consent was secured in advance of every Q sort undertaken in person. Those participating online consented by proceeding to the start screen following the introductory brief. The following statement was included in the introductory brief: I agree to complete this online/in person questionnaire for research purposes and that the aggregate anonymous data derived from this questionnaire may be made available to the general public in the form of public presentation, report, and journal article.

6.3.5 Statistical analysis

A total of 26 Q sorts were intercorrelated and factor-analysed using the dedicated computer package PQMethod (Schmolck, 2002). Factors were extracted (centroid analysis) and rotated using an initial varimax rotation followed by additional by-hand adjustments to ensure the maximum number of participants could be included within the Q sort groupings across factors and to bring said groupings ‘into focus’ (Brown, 1993; Watts and Stenner, 2012). In this case an anti-clockwise rotation of -2 degrees was applied to Factors 1 and 2. The common criterion in deciding how many factors to retain for rotation is for the eigenvalue of each factor to be greater than 1 (Addams, 2000; Brannstrom, 2011). Others have suggested a suite of criteria should be considered that ultimately lead to a reasoned extraction of factors of both statistical and theoretical significance (Eden et al., 2005; Watts and Stenner, 2012). I selected significant factors for rotation from an initial extraction of seven factors based on consideration and reasoned assessment of the factor eigenvalues (from both centroid and PCA methods of extraction), % variance explained by each factor, the scree slope, the ‘composite reliability’ of factors (a statistical criterion which depends on how many respondents define a particular factor; the more respondents that define a factor, the higher the reliability (Hagan and Williams, 2016)), and factors presenting a meaningful social perspective (see Watts and Stenner (2012) for in depth process behind criteria used in factor extraction).

Conceptually, Q sorts that load significantly on a particular factor (i.e., factor defining Q sorts) do so because they exhibit a very similar sorting pattern and therefore share a distinct viewpoint in respect to the presence of wall lizards in the UK. These defining Q sorts were then merged to form a single idealised-typical Q sort for each factor called a factor array. The factor array looks like a single complete Q sort and is calculated by a procedure of weighted averaging (i.e., defining Q sorts are given more weight in the averaging process since they better exemplify the factor (Watts and Stenner, 2012) (Appendix 5.1). Factor arrays then provided the basis for interpretation of each individual factor by means of a careful and holistic inspection of the patterning of items in each factor array using a crib sheet system (Stenner et al., 2003; Watts and Stenner, 2012). Crib sheets enable factor arrays to be systematically organised allowing identification of the important issues about which a given viewpoint is polarized, and how the viewpoint is polarized relative to the views defining the other factors. The interpretation aimed to uncover, understand, and fully explain the viewpoints captured by each factor and thus shared by significantly loading participants. Credence was given to correct interpretation by insights gained from the open-ended discussion held with participants during or after (online) their sort was completed. Comments made by participants are quoted where they clarify the interpretation and are indicated in italics.

6.4 Results

Each of the factors extracted from the analysis has been given a summary title and a textual interpretation of the subject viewpoint which the factors express. To ease interpretation, numbers in brackets have been included to refer to the statement number (in bold) (see Table 6.1) and the array score. For example, (**8**, -3) refers to a score of minus three (relatively strong disagreement) given to statement eight for the particular viewpoint/factor.

The factor analysis revealed three lines of discourse relating to the presence of wall lizards in the UK. These three factors together explained 53% of the study variance. Twenty-three of the 26 Q sorts loaded on one or other of these three factors. Factor loadings of ±0.31 or above were significant at the p <0.01 level (Brown, 1980). However, due to several confounding Q sorts (Q sorts with significant loading on more than one factor) in the solution using this loading parameter, the level of significant factor loading was raised to > 0.5 (Table 6.2 rotated factor matrix). This higher threshold is justified as long as it is applied consistently across all factors (Watts and Stenner, 2012). Of the three Q sorts that did not load on any factor (15, 23, 26) two were from the ‘public’ group, the other ‘academic’. Factor characteristics are also summarised in Table 6.3.In this three-factor solution, factor 3 had a negative correlation with factor 1 (-0.16) and factor 2 (–0.37). Factor 1 was positively correlated with factor 2 (0.79), indicating commonalities between the constituent defining Q sorts (Table 6.2).

Table 6.4 reports the items for which there was most consensus across the three factors. Respondents were in general agreement that wall lizard spotting is great fun; that the lizards are intriguing and interesting, and that their presence adds character to the local area. Impacts to gardens were scored neutrally across factors. The desire to have wall lizards in the garden received consistently negative rankings. It is important to note that Q sorts giving negative scores for this item (59) could reflect either disagreement with the statement or indicate they have lizards in the garden already.

Table 6-3 Rotated factor matrix and factor characteristics following Q sort analysis pertaining to attitudes towards introduced wall lizards in the UK. Values in bold indicate significant loading for given factor. Asterisk denotes Q sorts that did not load on any factor.

Q SORT	**Factor 1 'Innocent until proven guilty'**	**Factor 2 'Precautionary, informed concern'**	**Factor 3 'The more the merrier!'**
Land manager	0.59	0.46	0.05
Land manager	0.33	0.54	-0.08
Land manager	0.55	0.47	-0.07
Land manager	0.73	0.34	0.12
Land manager	0.57	0.42	-0.19
Land manager	0.49	0.69	-0.15
Ecology consultant	0.56	0.03	0.12
Ecology consultant	0.64	0.49	-0.19
Reptile enthusiast	0.12	0.71	0.01
Reptile enthusiast	0.48	0.52	0.04
Academic	0.45	0.71	-0.29
Academic *	0.23	0.11	-0.14
Environmental Advisory	0.18	0.67	-0.27
Environmental Advisory	0.65	0.49	-0.33
Environmental Advisory	0.44	0.65	-0.12
Public	0.53	0.42	-0.01
Public	0.01	-0.16	0.52
Public	-0.08	-0.25	0.61
Public *	0.29	0.42	0.41
Public	0.04	-0.44	0.65
Public	0.53	0.1	0.11
Public *	0.40	0.45	0.02
% Explained Variance (rotated)	19	25	9
Number of defining variables (Q sorts)	9	10	4
Composite Reliability %	97.3	97.6	94.1
Correlation between factor scores			
Factor 1		0.79	-0.16
Factor 2			-0.37

Table 6-4 Top 10 statements and factor scores sorted by consensus following Q sort analysis of attitudes towards presence of wall lizards in the UK.

Item number/statement	**Factor 1 'Innocent until proven guilty'**	**Factor 2 'Precautionary, informed concern'**	**Factor 3 'The more the merrier!'**	**Z-Score Variance**
43. Wall lizard spotting is great fun	3	2	2	0.003
66. The wall lizards add to the character of our garden and village	2	1	1	0.004
67. The wall lizards help to keep down garden pests	1	1	0	0.007
18. Wall lizards are not detrimental to our gardens	0	0	0	0.015
54. The wall lizards always give a topic of conversation when they come out in the warmer weather	2	2	1	0.017
48. I find wall lizards intriguing and interesting.	3	2	4	0.032
69. Reptiles are so rare I'm excited to see any lizard, native or not	-1	1	0	0.037
59. I wish we had wall lizards in the garden. Can I have some	-3	-2	-3	0.041
74. If wall lizards are breeding they are obviously happy to be here	3	2	1	0.058
56. I would make special trips to see wall lizards	-2	0	-2	0.059

6.4.1 Factor interpretation

6.4.1.1 Factor 1: 'Innocent until proven guilty'

This viewpoint identifies a lack of personal knowledge and stresses need for evidence of specific impacts of wall lizards on native fauna (**29**,6; **26**,5; **45**,5; **34**,4; **57**,1) in order to be able to express strong positive or negative feeling towards the lizards (**63**,0). Despite this lack of knowledge it is considered that, in principal, the introduction and presence of wall lizards in the UK is not a good thing (**10**,3; **9**,2; **38**,-3; **46**,-3; **51**,-3; **75**,-4; **41**,-5; **1**,-5; **13**,-6). This is likely based on existing broad theoretical understanding held about the potential ecological impacts of NNS in general (**21**,4; **68**,-2; **33**,-4). However, there is a feeling that in the case of wall lizards their ecological role is far more pertinent in making a judgment on their presence than the species origins alone (**34**,4), and that there is an automatic negative bias against NNS in the absence of ecological knowledge (**39**,1).

“We just don’t know if they are causing any harm. It’s difficult! I don’t want them to push out native species but I would want to see evidence that this is happening. If it’s not, then is there really a problem with them being here?”

Although native fauna is held in greater regard than non-native wall lizards (**23**,6; **53**,4; **73**,-5), and encounters with native lizards are not uncommon (**69**,-1; **60**,-6), the viewpoint acknowledges a value in the presence of wall lizards in terms of the opportunity they provide to engage with wildlife (**42**,3; **43**,3; **54**,2; **66**,2; **62**,1; **49**,1). There is however little sentimental attachment towards the wall lizards (**55**,-1; **59**,-3; **3**,-4) and thus control of the species (on condition of proven impact) may be acceptable to this group.

6.4.1.2 Factor 2: ‘Precautionary, informed concern’

Whilst similar to factor 1 in many ways, the factor 2 perception varies in that the presence of wall lizards is viewed as a very definite ecological threat (**11**,0; **15**,-3; **17**,-5) without the expressed need for scientific evidence of impact. This opinion is based on existing subject knowledge about specific potential risks, and perhaps first-hand experience/observations driving perceptions of negative impacts on native lizards (**24**, 6; **70**,5; **72**,1; **52**,-4; 14,-4; **16**,-4). Existing theoretical knowledge about the invasion process and concern about the ecological impacts of species introductions in general may also be an *a priori* influence on this perceived risk associated with wall lizards (**20**,4; **21**,4; **65**,-1; **64**,-2). The viewpoint considers climate change and evolutionary adaptability as having a key role in the long-term survival and range expansion of wall lizard populations in the UK (**76**,2; **27**,1; **25**,1).

“I know they’re entertaining to watch and it’s nice that people get protective about them, but any impact that wall lizards are having may be so subtle we might not notice till it’s too late. Native lizards have enough to contend with, a potential competitor or novel disease is the last thing they need.”

Proponents of this viewpoint see no place for wall lizards within our wildlife, particularly at the expense of native lizards (**22**,6; **9**,2; **40**-5), and in the absence of sentimental attachment to wall lizards (**42**,0; **4**,-2; **37**,-2; **38**,-3; **46**,-3, **5**,-3; **19**,-5) their presence is not at all welcomed (**10**,3; **1**,-5; **6**,-6; **8**,-6). As such, there is concern about the likelihood of there being more wall lizard populations in the UK than currently documented (**58**, 5) and a belief that the public have a role to play in being vigilant about introductions and supportive of a proactive approach to managing the species. (**28**,5; **35**,4; **32**,3; **7**,-1; **61**,-2; **31**,-3; **30**,-4). Despite the unfavourable opinion towards the wall lizard introduction, their presence does hold a novelty value (**54**,2; **36**,0) and their conspicuousness compared to native lizards provides opportunity for education and engagement (**50**,3; **49**,1; **69**,1;**60**,0) which is more likely to be actively sought than in other viewpoints (**56**,0).

6.4.1.3 Factor 3: The more the merrier!

Framing this viewpoint are scores for statement indicating very strong feelings about the lizards and their presence in the UK (**63**,-5; **57**,-5). These feelings are expressed in extremely positive ways towards wall lizards from a very personal point of reference (**4**,6; **5**,6; **44**,5). The wall lizards are enthusiastically welcomed (**8**,3; **38**,3, **12**,-4) with an accompanying desire for them to thrive here (**6**,5; **1**,4; **46**,3, **27**,-5), providing there are no financial implications (**13**,4). Furthermore, wall lizards are more likely to be seen as a welcome addition to UK fauna than in other viewpoints (**73**,0). This positive sentiment would appear to result solely from glad acceptance of having a local colony of wall lizards (**37**,2; **9**,-6) and the opportunities it has provided to become familiar with the lizards and to enjoy observing their behaviour (**47**,5; **48**,4). Familiarity borne from frequent, incidental, observation rather than actively sought engagement (**56**,-2), may have shaped a unique view of perceived ownership and sentimental attachment (**71**,2) to the wall lizards, to the point where they are considered almost as 'pets' (**3**,0). With this frequent 'up close and personal' interaction being limited to wall lizards however, no such attachment is applied to native lizards (**53**,-1). Even so, beyond this very personal interaction there is a general feeling of apathy towards engaging with wall lizards (**50**,-1; **62**,-1; **56**,-2; **49**,2; **59**,-3), perhaps because there is no particular novelty value attributed to them (**36**,-2; **2**,-3).

"I see the lizards all the time. I'm glad they are doing so well…we don't have much wildlife in the garden so I'm glad they are here. They're not causing any harm, so I'd rather they were just left alone".

The strong feelings extend to certainty about the wall lizards being harmless and posing no threat to native fauna. As far as this viewpoint is concerned there is no knowledge gap regarding the potential ecological impacts of wall lizards (**45**,-1; **29**,-3) and there are no perceived potential threats (**15**,3; **17**,1; **52**,0). Additionally, the statement scores indicate a belief that wall lizards are having no negative effects on native lizards and the introduction does not represent an 'invasion' (**70**,-1; **72**,-3; **11**,-6). Any concern for disturbance to local ecology by wall lizards (**44**,5; **24**,0) is muted by this conviction that there are no negative impacts, and the prospect of there being further populations therefore raises no concern (**58**,-3). Agreement with the statement 'what classes as native anymore!' (**68**,1), suggests the concept of NNS and biological invasions is perhaps not fully understood, although certainly not seen as cause for concern (**21**,-3; **20**,-4). Neither are the origins of the wall lizards (**64**,2; **51**,3; **10**,-4). In fact, the prevalence of NNS is seen as just one of several conditions justifying the presence of wall lizards (**33**,4; **14**,3; **65**,2; **68**,1; **75**,0) and their 'right' to be here (**10**,-4). There is no agreement with any statements relating climate to the wall lizard introduction (**76**,-1; **25**,-2; **27**,-5). The sentiment highlighted so far underlies a definite protectionist attitude towards interference and outside interest in the lizards (**30**,4; **55**,2), regardless of any ecological knowledge that might be gained (**26**,0; **34**,-1). This 'hands off' opinion is expressed particularly strongly in opposition to statements about potential management and control of wall lizard populations (**7**,5; **31**,3; **61**,1; **28**,-3, **35**,-4, **32**,-5).

6.5 Discussion

In this study, I used Q methodology to identify and describe stakeholders' perspectives towards the established presence of a non-native lizard species introduced to the UK. I was able to extract three clearly defined viewpoints on the species' introduction, which term: 'Innocent until proven guilty', 'Precautionary informed concern' and 'The more the merrier'. These perspectives reflect both differences and commonalities in stakeholder perceptions and opinion regarding the species' presence, which are discussed here with reference to the conceptual framework for understanding social perceptions towards NNS described by Estevez et al. (2015).

In comparing and contrasting the three viewpoints, I identified four key areas of disagreement, specifically ‘acceptance of wall lizards’, ‘concern about the ecological threat posed by wall lizards’, ‘attitudes toward NNS in general’ and ‘opinion toward management/control of the species’. These four areas of disagreement are inextricably linked and may arise due to variation in the level of knowledge (actual or perceived) and uncertainty of actors within each group regarding the ecological impact posed by wall lizards. Accordingly, theory holds that when faced with insufficient information individuals will process this limited information and develop their judgement heuristically (Trumbo, 2002). Levels of knowledge (or lack thereof) and uncertainty are thus likely to be the main drivers shaping all subsequent opinion within each viewpoint (i.e., whether or not the lizards are welcomed, support for management/control) as individuals rely on heuristic value methods to reach their conclusions and assessment of risk (Kahan et al., 2012; Davidson et al., 2013). Defining themes and values between groups are discussed below.

6.5.1 How and why do stakeholders group differ in their opinions?

Both the ‘Innocent until proven guilty’ and the ‘Precautionary, informed concern’ views appear to build their opinions by drawing on a source of theoretical knowledge of species introductions and the associated potentially negative ecological implications. This is not surprising considering the majority of actors (84% across both views) expressing these views come from an environmental science background and are likely to be familiar, to varying extent, with concepts and terminology regarding NNS (Selge and Fischer, 2011). As a result, both views express elements of a precautionary approach to NNS introductions conforming to some degree with guiding principles of best practice that permeate through such professions (DEFRA, 2003). There are however significant differences in perceived knowledge and levels of uncertainty between the two groups.

The reluctance for the ‘Innocent until proven guilty’ view to make a judgment in the case of wall lizards is due to self-confessed personal knowledge gap regarding the species’ impacts, suggesting participants were more likely to evaluate the species via heuristic methods (Trumbo, 2002; Davidson et al., 2013). This makes sense considering the majority of the participants holding the ‘Innocent until proven guilty’ view come from backgrounds conferring a broad ecological knowledge rather than being specialist in a particular field (i.e.

ecological consultants, land managers). Interestingly, the ‘Innocent until proven guilty’ view also hints at a deviation (at least where wall lizards are concerned) from the normative assumption that all NNS should be treated as a potential threat (Simberloff et al., 2011; Rejmanek and Simberloff, 2017). Instead, this discourse is inclined to agree that there is a pervasive bias against NNS and that detailed case specific knowledge is a prerequisite for judgements about whether a particular species’ should be labelled a threat or not (Davis et al., 2011; Van Der Wal et al., 2015; Warren et al., 2017; Guerin et al., 2018). This finding is very much the basis for the viewpoints’ ‘Innocent until proven guilty’ label and is the traditional and assumed approach in empirical scientific research and, within this, impact studies (Mapstone, 1995; Davidson et al., 2013). Knowledge gaps and uncertainty are recognised as important factors in predicting concern about NNS impacts (Gozlan et al., 2013; Verbrugge et al., 2013). Biosecurity experts assessing the risk posed by aquatic non-native species tended to assign lesser concern about potential impacts when faced with little information and other uncertainties about species traits (Davidson et al., 2013). In this study, when faced with great uncertainty over impacts, the ‘Innocent until proven guilty’ view also appears to use another heuristic influence to form its perceptions of the lizard introduction. This appears to be formed on the relationship between the positive value (benefits) exponents place on engagement opportunities with the lizards and the perceived ecological risks of the species. Judgement based on this emotive ‘affect heuristic’ follows theory of a negative correlation between risk and benefit in the decision making process (Finucane et al., 2000) (i.e., positive feelings garnered from opportunities for engagement with wall lizards translates to lower perceived risk).

In contrast, the theoretical knowledge drawn upon to form the ‘Precautionary, informed concern’ viewpoint appears to be supported by heuristics based on direct experience and/or specialist knowledge leading to less uncertainty and more concern about the potential impacts of wall lizards on native fauna, thus informing a more hard-line precautionary approach to the introduction than that of the ‘Innocent until proven guilty’. In this case, negative feelings towards the wall lizards arising from observed or anecdotal evidence of ecological impact has resulted in an opposite pattern to ‘Innocent until proven guilty’, whereby negative feeling and experience translates as higher perceived risk (Finucane et al., 2000). Those holding the ‘Precautionary, informed concern’ view are also those most likely to have specialist knowledge of invasion biology and/or reptile ecology (i.e., environmental advisory, conservation NGO, academia) and be in professions where standards (in this case the precautionary approach) are often ingrained, creating a filter through which the individual perceives risk, often unconsciously and through conformance with policy (Sjoberg, 2002).

Despite indicating assured knowledge that there are no adverse consequences to the wall lizard introductions, the ‘More the merrier’ view is not anchored in the same theoretical knowledge domain as the other two viewpoints. This is not entirely surprising given the ‘More the merrier’ group constituents (three members of the public and one reptile enthusiast) are less likely to have either empirical or specialist scientific knowledge of the discourse topic. Instead, ‘More the merrier’ protagonists have constructed a viewpoint purely from a positive affect heuristic, creating a parochial knowledge that appears to have limited engagement with scientific evidence and is derived from positive personal experience (i.e., perceptions based on encounters with wall lizards in the garden). Positive personal experience or perceptions amongst the public have also been associated with supportive attitudes and increased doubts in evidence of ecological impacts regarding the presence of non-native deer (Ford-Thompson et al., 2015).

Whereas the ‘Innocent until proven guilty’ and ‘Precautionary, informed concern’ views are defined by differences in levels of ecological knowledge and impact uncertainty between them, the significant divergence of the positive ‘More the merrier’ view from these two viewpoints in the absence of such influence (a lay person perspective) appears to be more likely a reflection of pronounced variation between the groups deeper beliefs, perceptions and values about ‘naturalness and balance’, and overall relationship with nature. This is in accordance with the *visions of nature* concept (Van Den Born et al., 2001; Dandy et al., 2012), wherein those who place value in the functionality of nature for humans may have a different perspective on NNS than people who highly value the (albeit subjective) ‘authenticity’ of nature (Verbrugge et al., 2013). A study of social perceptions of the impacts and benefits of NNS within the Doñana region of Spain also found remarkably different perceptions between professional and non-professional stakeholder groups (Garcia-Llorente et al., 2008). The same study also identified two different conservation professional groups defined by slightly divergent viewpoints very much akin to those of the

‘Innocent until proven guilty’ and ‘Precautionary, informed concern’ groups emergent in this study. Similarly, both studies found a small subset of the public (nature aware/nature tourists) having a shared perception of NNS with conservation professionals. Other studies have also found little divergence between public and professional views on NNS and go further to argue that although the content of their thoughts might diverge slightly, ecological professionals and the lay public essentially share the same structure of thought about the natural environment in general (Selge et al., 2011; Fischer et al., 2014; Van Der Wal et al., 2015). My findings do not entirely support this, as the ‘More the merrier’ viewpoint was held by a majority of lay public participants who clearly constructed their opinions from different values and influences to those in other groups.

6.5.2 What does this case study tell us about perceptions and attitudes towards management of introduced species more generally?

The discourse emerging in this study provides an insight into attitudes regarding the potential management of an introduced species’ when faced with little knowledge or evidence of negative impact. My findings are in concordance with higher levels of knowledge (of biological invasions, ecological principles) being associated with increased support for NNS management options (Bremner and Park, 2007; Garcia-Llorente et al., 2008) - in this case adoption of either the precautionary (‘Innocent until proven guilty’, ‘Precautionary, informed concern’) as opposed to the ‘hands off’ (‘More the merrier’) approach. Perceptions of risk, abundance, and detrimental impacts have also been seen to strongly inform participants’ attitudes towards management of NNS (Selge et al., 2011), with some authors suggesting that these factors, rather than non-nativeness, have greatest influence on judgment (Gobster, 2011; Estevez et al., 2015; Van Der Wal et al., 2015). In my analysis, the origins of the wall lizards per se certainly appear to be of less concern in this overall discourse compared to perceived risks and impacts. This is most apparent in the ‘More the merrier’ viewpoint where the foreign origins of the lizards have no bearing on the perception of there being no negative ecological impacts, leading ultimately to the ‘hands off’ approach. Meanwhile the ‘innocent until proven guilty’ group are more concerned with the potential impacts of non-native species, but appear to evaluate on a case by case basis rather than assuming that all non-native species are inevitably detrimental (Davis et al., 2011). Although beyond the scope of this discussion, my findings are indicative of the wider discussions on the dichotomy of native species-good, non-native species-bad, and the deeper arguments regarding ideologies of ‘nativeness’ and ‘naturalness’ (Low; Goodenough, 2010; Schlaepfer et al., 2012; Rejmanek and Simberloff, 2017).

The wall lizards evidently have a charismatic appeal, as shown by the items of consensus amongst the three viewpoints (Table 6.3). Attractiveness and charisma are well recognised as key influences on peoples attitude towards to NNS (Bremner and Park, 2007; Verbrugge et al., 2013; Fischer et al., 2014), and can thus have significant bearing on support for species management operations (Estevez et al., 2015). Although, as is the case in this study, others have found that whilst those from ecology backgrounds appreciate these values they often regard them as ambiguous attributes that are not necessarily a legitimate criterion to which to base their judgments about species management (Selge et al., 2011). In this study it is the ‘More the merrier’ viewpoint again that appears most influenced by these attributes, perhaps because the wall lizards are amongst the most conspicuous of wildlife regularly encountered by this group.

6.5.3 Limitations

It is important to recognise that the Q methodology and subsequent analysis can provide only a limited description of the prevailing discourses surrounding a topic at a given time and place, and that the resultant interpretation is not directly transferable. For example, notably different discourses may be evident surrounding introductions of *P. muralis* elsewhere (i.e. Vancouver Island, BC, Cincinnati, USA).

Whilst every care was taken to remove ambiguous statements from the Q set and make the Q sort as intuitive as possible to all participants, I recognise that this is difficult to achieve when studying responses of such a heterogeneous group of participants. As a consequence there is the possibility that some statements may have been perceived as having little relevance to an individuals’ personal experience and would thus have been difficult to rank objectively. My Q set of 76 statements could also be considered fairly large. Although this lends confidence to having obtained a comprehensive representation of the available discourse, engagement with the Q sort process may have been adversely affected as a result. This may be particularly true for those Q sorts conducted electronically in the absence of the lead researcher. In addition, the simple ‘drag and drop’ method of sorting statements used by the software may have reduced the diligence applied to rearranging such a large number of statements into the final sort arrangement.

6.6 Conclusions and wider implications

The holistic method of interpreting the analysis gives insight into how and why stakeholders may have formulated certain viewpoints regarding their perceptions towards introduced NNS. This in turn could help conservation managers identify ways in which to work with these subjective influences in order to best communicate the dichotomies and complexities surrounding the introduction of NNS, with an aim towards a more informed and balanced discourse. My analysis of the discourse highlights three interesting issues that relate not only to the wall lizard introduction, but approaches to NNS and their management more generally. Firstly, there is significant variation between stakeholder groups regarding the presence and management of NNS. The analysis flags early signs that opposing views between a subset of the public and decision makers has potential to present obstacles should management of the species ever be considered justifiable and practical. Indeed, with the majority of the UK wall lizard populations being found in residential or busy public areas, any operation involving the lizards is likely to be met with some opposition from those with a protectionist view that may not be equipped, or care, to reconcile with views of conservation managers (Temple, 1990). Furthermore, finding such strong positive sentiment towards the lizards amongst a subset of the public holding a possessive view about the wildlife they frequently encounter is illustrative of a mind-set that could facilitate the spread of a charismatic NNS where ecological impacts are not known, or are perhaps considered but disregarded. Secondary human movement of wall lizards from established populations is the most likely pathway for rapid range expansion of wall lizards into new areas of the UK (Foster, 2015; Michaelides et al., 2015). Secondly, the discourse analysis illustrates that awareness of the wider concepts of NNS (invasion ecology) is lacking, particularly amongst the general public, and suggests that in the public domain scientific evidence alone may not be sufficient to inform perceptions of risk. In this regard, engagement with a characterful, conspicuous NNS may provide useful opportunities not only to educate the public on the ecological concepts and dichotomies associated with NNS and INNS, but also to promote wider interaction with nature and general interest in conservation. On another level, my analysis shows that communication of scientific evidence between scientists and conservation managers implementing policy is wholly necessary in order for personal judgment of NNS risks and management decisions to be made. Finally, the discourse highlights that a softer view of NNS, one that does not assume negative impacts in the face of limited evidence, is held personally by some professional’s in contention to the policy of a precautionary approach that governs their profession.

Chapter 7: General Discussion

The research presented in this thesis provides a comprehensive investigation into the ecology of introduced populations of *Podarcis muralis* in the UK and on Vancouver Island, British Columbia. Through the use of a combination of approaches including population ecology, functional ecology, predictive modelling, social science, and behavioural experiments, I present significant, new information on the hitherto unstudied aspects of *P. muralis* ecology post-introduction, with a focus on invasive potential, adaptive responses, and implications for ecological impacts on native lizards. A broader aim of this work is to serve as a detailed case study in which the findings regarding the ecological ramifications and societal perceptions of an introduction contribute to our wider understanding of the invasion process, and attitudes towards non-native species in a changing world.

In Chapter 2, I present the first population estimates using capture-mark-recapture methods for introduced *P muralis* populations in the UK. Densities in these populations are lower than those reported in the literature for native populations. Despite these low densities, analysis of indicators of individual fitness (body size, body condition, parasite load, predation pressure) and habitat use suggest there is little constraining population growth, and that capacity for greater rates of increase (i.e., increased fecundity at larger body size) may be facilitated by predicted climate change. Models of spatial and demographic dynamics of introduced populations presented in Chapter 3 indicate that range expansion through natural diffusion is likely to be slow, owing to the generalist nature of the species and abundance of suitable habitat allowing populations to maximise locally. Predictive models showing exponential growth do, however, suggest that populations may be approaching the end of an inherent lag phase which could see an increase in rates of expansion facilitated by fragmented patches of habitat in disturbed habitats. Extensive spread at the national level is, however, likely to be constrained to the south of the UK due to unfavourable climatic conditions further north. The possibility for populations to show rapid morphological and functional adaptive responses to these northerly extremes, and divergence between populations inhabiting different habitats, was explored in Chapter 4. Divergence in morphological traits (body size, head morphology) and performance (bite force) were however largely explained by ancestral differences between French and Italian lineages. When compared to native lizards, these physical and performance traits, in addition to a broad dietary niche of *P. muralis*, constitute considerable overlap between *P.*

muralis and native lizards, suggesting high potential for competitive interaction. In Chapter 5, the likely outcome of competitive interactions was investigated in experimental trials testing behavioural responses of *P. muralis* to scent cues of native lizards and vice-versa. There was no evidence in the results from these experiments that scent cues from native lizards illicit a behavioural response in *P. muralis*. The response from native lizards, however, was varied, ranging from attraction (use of conditioned refuge by *E. coerulea*), aggression (*L. a. argus* attacking swab), and avoidance (less time spent close to scent cue by *Z. vivipara*). Lastly, stakeholder perceptions and opinion towards the presence of *P. muralis* in the UK were explored in Chapter 6. Discourse analysis revealed the extremes in opinion that surround this particular model system, and invasive species more generally, and allowed insights into how subjectivity and uncertainty form such opinion.

The following chapter synthesises the research, highlighting how these key findings contribute to my project aims, and identifies areas for further work.

7.1 Invasive potential

With an expanding intercontinental non-native range, and a long, multifaceted introduction history (e.g., variable origins, founder sizes, propagule pressure, recipient habitat types), *P. muralis* populations currently occupy something of a grey space in terms of placement within the framework of linear progression along the introduction–naturalisation–invasion continuum (Chapter 1) (Blackburn et al., 2011). The introduced range is undoubtedly expanding, with new populations periodically being reported in both Europe and North America; established populations are spreading, and pathways to further primary and secondary introductions are very much active. As such, this places the majority of populations firmly towards the latter stages of Blackburn's (2011) unified framework (C3 onwards) (Fig 1.1). And yet, since there is little empirical evidence for negative environmental impacts, researchers necessarily stop short of describing these introduced populations as 'invasive' and the introduction has not been classified as anything more than a status of moderate concern.

Location on the invasion continuum is, however, temporally and spatially context dependent and offers limited insight about likely progression beyond a given point. This is particularly true at these latter stages of invasion where, having cleared all other barriers, population dynamics of the invader are the main driver of invasion outcome (i.e., forward progression to full invasion or ‘boom and bust’) (Fig 1.1). Similarly, unified classification based on magnitude of impact (Blackburn et al., 2014) can only consider a static state and does not account for the shifting dynamics of species interactions as an invasion progresses. For instance, a species’ progression through the invasion process may be protracted due to population and community dynamics, evolutionary constraints, and environmental factors causing temporal lags in which impacts may take considerable time to become apparent (Crooks, 2005). Are the current and future impacts of *P. muralis* therefore in danger of being overlooked by virtue of a long residency (40+ years in some well-known populations) without obvious consequences?

The uncertainty surrounding the invasive status of *P. muralis* therefore exemplifies, as a case in point, the state of paradox in which invasion science finds itself, having low predictive value despite strong, identifiable covariates of invasion performance (Hui and Richardson, 2019). Whilst recognising the important contribution made by the numerous hypotheses attempting to describe the invasion process (Catford et al., 2009), invasion scientists have long advocated for a move towards more inclusive and mechanistic conceptual frameworks for describing invasions that facilitate quantitative and testable evaluation of causal factors influencing invasion processes (Gurevitch et al., 2011). The conceptual approaches of both Gurevitch et al. (2011) and Hui and Richardson (2019) (Chapter 1) propose that the invasion process can be mapped on dynamic, adaptive ecological networks that go beyond simply identifying the functional traits that enable a species to penetrate specific filters along a linear invasion continuum. Fundamental to both concepts however is an emphasis on the centrality of demographic dynamics of abundance and population growth as the primary driver of invasion; systematically breaking away from invasion assessment based solely on trait matching (Hui and Richardson, 2019).

Here, I discuss the invasive potential of *P. muralis* populations within the context of the conceptual meta-framework of ecological and evolutionary processes that influence population growth and invasion outcome proposed by Gurevitch et al. (2011). As a result, the inherent complexity of interactions between multiple causal factors and feedback loops influencing the invasion process becomes evident, and as such I have strived to synthesise my findings in terms of how they suggest populations may succeed or fail in demonstrating any of the three defining characteristics of invasions (i.e., rapid populations growth, dominance, range expansion) (Gurevitch et al., 2011) (Fig 7.1).

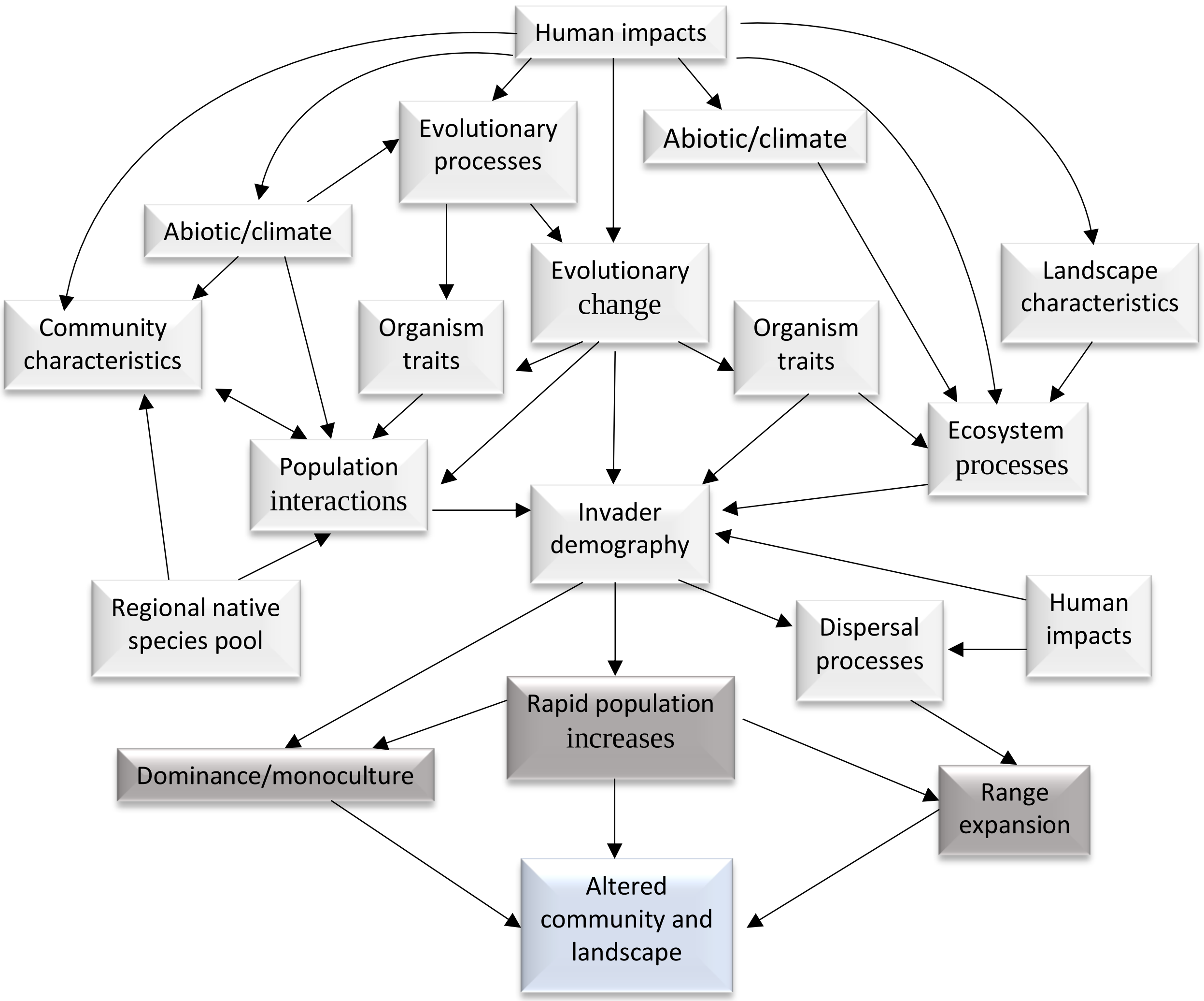


Figure 7-1 A conceptual synthetic invasion meta-framework incorporating fundamental ecological and evolutionary processes and states. The three defining characteristics of invasions are shown in dark grey, with their linkage to effect on altering communities and landscapes (light blue). Arrows indicate transition paths between the processes and states. Components found in more than one position affect or are affected by more than one set of other processes (redrawn after Gurevitch et al., 2011).

There is empirical and theoretical evidence for at least three broad mechanisms driving changes in demography, vital rates, and population growth of introduced populations as invasions progress: founder effects, novel environmental interactions, and adaptive evolution (Yokomizo et al., 2017) (Chapter 1). Small numbers of colonizing individuals (founders) at point of introduction or along invasion fronts can cause Allee effects and alter genotypic and phenotypic diversity, typically reducing fitness and population growth (Kanarek et al., 2013; Dlugosch et al., 2015a; Kramer et al., 2018). Novel abiotic and biotic environmental interactions following introduction including fluctuating abiotic conditions (Guisan et al., 2014), interactions with native communities (Pearson et al., 2018), and control by enemies (or lack thereof, as in ‘enemy release’ theory) such as pathogens, parasites and predators (Colautti et al., 2004; Poole and Bajer, 2019), can potentially have positive or negative effects on demographic rates. In turn, an organism’s capacity for adaptive evolution of traits that increase survival and reproduction in these novel conditions can be fundamental to establishment, proliferation, and invasive success (Colautti and Lau, 2015).

I found current densities of *P. muralis* - at the five UK sites where I determined population estimates by capture-mark-recapture - to be relatively low compared to data from native and introduced populations in the literature (Chapter 2). These results, coupled with the predicted growth curves for UK populations projected from the various times since introduction to 2040 (Chapter 3), suggest all the populations modelled may be in the early stages of exponential growth, and have demonstrated (or are demonstrating) a lag before the onset of appreciable population growth that is often associated with such a growth trajectory (Sakai et al., 2001).

Beyond the ecological phenomenon of an inherent lag with exponential growth, other explanations for the current low densities observed could be: lags in population growth due to stochastic loss of propagules (e.g., yearly fluctuations in overwintering survival/growing season, severe disturbance/loss of habitat) (Sakai et al., 2001); time required for adaptive responses to overcome climatic constraints or those imposed by the new habitat (Guisan et al., 2014); and time required for the evolution of invasive life-history characteristics, or the purging of genetic load responsible for inbreeding depression (Crooks, 2005). A previous study has found high embryonic mortality amongst non-native UK populations of Italian origin consistent with high loss of genetic diversity (Michaelides et al., 2016), and whilst this may be limiting population growth, the same study did not find individual and population-level genetic diversity to be statistically correlated with inbreeding depression. Climatic conditions are also undoubtedly currently constraining population growth, as proven by shifts in reproductive effort to the first clutch of the season in an adaptive response to the cooler climate experienced in the UK (While et al., 2015b; MacGregor et al., 2017). However, disparity in body size between lizards of French and Italian origin does suggest greater capacity for the latter to respond to suitable climatic conditions with increased fecundity in second/third clutches (Chapter 2).

The results presented in Chapter 2 of this thesis indicate there is apparently little constraint to population growth of introduced *P. muralis* populations in terms of individual fitness. I provide evidence of this with analysis of individual fitness in relation to species traits (lineage, body size); habitat characteristics (habitat use), and species interactions (parasites, predation attempts).

Firstly, body size and body condition were largely similar across populations regardless of microhabitat characteristics at introduction sites; highlighting the ability of *P. muralis* populations to function in a variety of habitats, including urban and disturbed environments - a trait commonly linked with invasive success (Marvier et al., 2004). This has already facilitated a route to achieving community dominance in many instances as introductions have been to areas (both in the UK and on Vancouver Island) where native lizards are already likely to be in decline, scarce, or absent due to habitat disruption/alteration (Wilkinson and Arnell, 2013). This fits with the core–satellite hypothesis detailed by Hanski (1982), which posits species with a large range and high local density (core species) are expected to have strong interactions with other species and are therefore more likely to persist under constant perturbation (including from invasions), whereas those with a small range and low local density (satellite species) are expected to interact weakly and be more dynamically unstable (Hanski, 1982; Hui and Richardson, 2019). This leads to the argument that rare species (rarity in three dimensions: geographical range, local density, and habitat specificity) hold the key to network instability and invasibility (Hui and Richardson, 2019). In this respect, the mere establishment of introduced *P. muralis* populations in many areas where native lizards are scarce/absent is likely to have impact on the ecological network as the vacant niche is filled and trophic interactions are altered (i.e., impacts on invertebrate prey, supplementation of predators (Huang et al., 2008; Sih et al., 2010; Pintor and Byers, 2015). This idea is in line with thinking that introduced species frequently fill novel or recently vacated functional roles in communities, perhaps even reinstating benefits to the ecosystem where native biodiversity has declined (Dlugosch et al., 2015b). In this regard it is feasible that in some locations wall lizard populations may be potentially benefiting native predators such as adder (*Vipera berus*); a species for which there is growing conservation concern in the UK (Gardner et al., 2019). A similar situation has been seen in the abundance of invasive apple snail having direct trophic benefits to survival of endangered snail kite juveniles (*Rostrhamus sociabilis*) (Cattau et al., 2016). Future research should therefore consider in more detail the trophic interactions of *P. muralis* populations.

Second, although rates of tail damage indicative of predation attempts varied between populations and habitat type, there is no evidence that this pressure has adverse effects on body condition. This result has several interpretations in terms of relevance to *P. muralis* population growth, dominance and range expansion. Taken in isolation, the generally high incidence of tail damage may simply reflect that local dominance has already been achieved and that predators are responding to an abundant prey resource. Prey switching of resident predators in response to an abundance of a novel introduced prey is common in invaded communities (Heinonen and Auster, 2012; McLoone et al., 2019). Whether or not resident predators can provide biotic resistance to invasion by excluding or limiting the non-native prey population through high consumption, is determinant on the preferences and efficiency of predators, and the defences of the novel prey (Yorisue et al., 2019). When there is no or minimal consumption of non-native prey this can lead to enemy release that may facilitate the invasion (Sih et al., 2010; Pintor and Byers, 2015). As I do not have data on mortality rates, and my data is necessarily biased to only survivors, I can only surmise from rates of tail damage (and population persistence) that resident predators are largely inefficient at catching *P. muralis* and therefore may have little effect in regulating size, dominance, and spread of introduced populations. In addition, the comparable mean body condition of individuals in urban habitats to those occupying more rural habitat - despite higher levels of tail damage in the latter, suggests that populations can not only maintain dominance in the face of high predation pressure, but can also mediate any negative effects of predator avoidance to individual fitness and population growth (Chapter 2).

Finally, I found very low occurrence of hemoparasites amongst the introduced populations. This was somewhat unexpected considering the wide prevalence of these parasites in *Podarcis* spp. and many lacertids (Hassl, 2012). There are several ways in which parasites can have an influence on invasion success: hosts may lose their parasites as a result of introduction; novel parasites may be acquired from the new environment or introduced by the invading host, and differential effects of parasites on native and invading host fitness may mediate invasion success (Dunn, 2009). If the negative results in all but one of my study populations suggest a loss of hemoparasites with introduction, this could – again in accordance to enemy release hypothesis (Colautti et al., 2004), have important ramifications for population growth and achieving community dominance, particularly if there is disparity in parasite prevalence between native and non-native lizards conferring a fitness advantage to *P. muralis.* My findings highlight a need for further research into the parasite-vector-host dynamics accompanying these introductions and suggest *P. muralis* populations present a rare model of study in which such interactions can be practically studied with a terrestrial vertebrate in the early stages of invasion.

Population growth and community dominance are also dependent on the outcome of direct and indirect competitive interactions between species who overlap in their ecology and niche requirements (Gao and Reitz, 2017). The introduction of a novel species can greatly disturb population and community dynamics through competition, with the potential to cause trophic, temporal, spatial, and habitat niche shifts and drastic declines or local extinctions of native species (Cadi and Joly, 2003; Hernandez-Brito et al., 2018). My results indicate there is potential for considerable niche overlap (in terms of prey acquisition) between *P. muralis* and native *L. agilis* in the UK, and *E. coerulea* on Vancouver Island, and that competitive abilities in direct agonistic interactions may also be equally matched owing to similarities in body size, head dimensions, bite force, and their allometric relationships (Chapter 4). Furthermore, experimental trials testing behavioural response to indirect, interspecific scent cues suggests that there is no behavioural mediation to avoiding potential direct interactions between these species (Chapter 5). Although I have contributed evidence to indicate that a competitive interaction (direct and/or indirect) between *P.*

muralis and these species is highly likely, I cannot conclude that the outcome of such interactions alone would lead to dominance of *P. muralis*. My results do, however, back-up field observations of *P. muralis* achieving dominance and apparently displacing resident *Z. vivipara* in the process (Münch, 2001; Mole, 2010, RW. pers obbs, RW. pers obbs). The allometric differences in body size and bite performance between the two; whilst having potential to facilitate trophic niche segregation and coexistence, may also confer a considerable size/performance advantage to *P. muralis* should agonistic encounters arise (Chapter 4). In addition, the pattern of *Z. vivipara* avoidance of *P. muralis* scent cues in experimental trials gives an indication of how displacement of resident populations may arise (Chapter 5). I acknowledge however that displacements typically result from interactions of multiple mechanisms, not all of which involve direct competition, and that various biotic and abiotic factors (e.g., habitat loss/quality, predation, resource availability) mediate these mechanisms so that variable outcomes may occur between the same interacting species in different environments (Gao and Reitz, 2017).

The emergent views resulting from my analysis of stakeholder opinion towards the presence of *P. muralis* in the UK (Williams et al., 2019. See Chapter 6.) provide a valuable insight into how social attitudes and perceptions may influence the demographic rates and local dominance, and thus invasive success, of an introduced species. Firstly, a theme of positive sentiment towards the lizards born from personal beliefs and subjectively informed perceptions about origins and ecological implications – largely from members of the public – can clearly translate to individuals/authorities taking practical measures to encourage local populations to thrive. A prime example of this is the implementation of mitigation measures to safeguard the non-native *P. muralis* population during civil engineering works on the Isle of Wight (On The Wight, 2017). Secondly, a lack of case-specific, empirical evidence of impacts; personal knowledge gaps, and uncertainty about ecological impacts of non-native introductions in general, have undoubtedly prevented some local authorities from acting towards management of *P. muralis* populations at the early onset of establishment. At the other extreme, however, the overwhelming dominance and abundance of *P. muralis* at some locations on Vancouver Island has led some residents to implement their own measures of lethal control of the species (G. Hanke pers comms), which raises the interesting question 'is there a threshold of acceptable abundance beyond which perceptions of impacts and public attitudes towards a non-native species change?' These findings substantiate claims from previous qualitative research that a species' perceived abundance and impact are more influential to people's attitudes than species origins and 'non-nativeness' (Van Der Wal et al., 2015).

My models of natural range expansion (Chapter 3) confirm existing notions that spread at the local level is likely to remain slow (Foster, 2015). This is largely due to the habitat generalist nature of the species (Chapter 2) allowing for exploitation of an abundance of suitable habitat able to support locally high densities (Chapter 3). Greater range expansion, on the other hand, appears to be facilitated by increasing fragmentation of suitable habitat acting as steppingstones during dispersal, particularly apparent in urban-suburban areas. This pattern of spread in my model system illustrates how local landscape characteristics play an important role in determining the spread of invasions and how management/change of particular features can either promote or suppress range expansion dependent on species traits. For example, in this model system *P. muralis* is likely to benefit from operations carried out that aesthetically improve or develop urban areas (i.e., clearance of dense scrub, maintenance/creation of ornamental gardens, and coastal developments). Conversely, increasing fragmentation of tree canopy cover has shown to have supressed the spread of grey squirrels in urban areas (Bonnington et al., 2014), likewise the limited spread of *Anolis. cristatellus* in urban areas of Miami, USA, is explained by the patchy, low-density distribution of wooded habitat, limiting dispersal (Kolbe et al., 2016).

Models of habitat suitability also highlighted the largely isolated nature of some rural populations that are surrounded by arable land, with rail lines providing the only likely corridors for natural dispersal from some sites (Chapter 3). Several studies have brought attention to the importance of rail lines in facilitating spread of *P. muralis* (Covaciu - Markov et al., 2006; Kühnis and Schmocker, 2008; Strugariu et al., 2008; Gherghel et al., 2009), and my models support that use of such corridors may be more important where adjacent habitat is less suitable (Hedeen and Hedeen, 1999). The isolated nature of some of these populations, whilst not posing much threat of further advancement, does still add to the pool of propagules available for assisted secondary introduction. Coupled with the findings derived from models in Chapter 3 of currently low density, highly concentrated populations, at the early stages of exponential growth, these results indicate that (in the spirit of the precautionary approach) now might be a good time to test efficacy of control/eradication methods. These existing models provide a foundation on which simulations of hypothetical control efforts could now be tested. Such an approach has been employed to inform management of invasive eastern brook trout (*Salvelinus fontinalis*) (Day et al., 2018). In addition, removal experiments in the field that incorporate community responses could yield much insight into as yet unforeseen impacts of *P. muralis* and contribute important knowledge regarding thresholds for effective control of invasive species in general. For example, eradication of isolated gypsy moth populations has been shown to be possible by following a treatment of >80% mortality (i.e., extinction induced by subsequent Allee effects, and stochastic processes) as long as populations were relatively low (Liebhold and Bascompte, 2003).

Although I factored in losses incurred during juvenile dispersal into my model based on survivorship data in the literature (Barbault and Mou, 1988; While et al., 2015b), I do not have site specific data on juvenile survivorship and therefore cannot discount the variable impact predation may have on constraining population spread through effects on juvenile dispersal. I have shown high rates of predation attempts (albeit unsuccessful) on the adult population and assume some degree of adult mortality from predation (Chapter 2), but it is likely that these rates are higher still on dispersing, inexperienced juveniles (Hoy et al., 2015). Furthermore, predation attempts on juveniles are also more likely to be successful due to ontogenetic variation in the efficiency of tail autotomy and other behaviours as a defence (Bateman and Fleming, 2009). As a result, the current pattern of low dispersal (whether constrained by predation or facilitated by plentiful local resources), and thus aggregated nature of individuals in UK populations, may actually be contributing to successful invasion from the small founder sizes through a weakening of Allee effects - the trade-off being slower overall population growth and spread (Kanarek et al., 2013).

Significant range expansion through deliberate and accidental human mediated jump dispersal is increasingly likely as local abundance increases in areas of human activity such as allotments, garden centres, builder’s merchants that may provide a pathway to transportation (Chapter 3). On Vancouver Island, this secondary movement of lizards is believed to have brought about an abrupt end to an apparent ~40 yr. lag phase of slow spread and population growth (G. Hanke pers comms). In Chapter 6, I demonstrated how attitudes and opinion amongst sections of the public may facilitate this spread and highlight the challenges that subjective influences and reasoning brings to managing the spread of non-native species, particularly those that have charismatic appeal.

I concur, however, with assessment that the likelihood of extensive range expansion in the UK is low (Foster, 2015). My climate suitability model at the national scale (Chapter 3) supports the reasoning that establishment success of further secondary introductions in the UK is likely to be limited to the far south due to climate restrictions – mainly harsher overwintering conditions – decreasing suitability at more northerly latitudes.

7.2 Final conclusions

In order to improve how uncertainties in invasion science are captured and characterized, Latombe et al. (2019) suggest a framework divided into four components: the need (1) to clearly circumscribe the phenomenon (with precise definitions), (2) to measure and provide evidence for the invasion phenomenon (i.e., confirmation of processes occurring against uncertainties linked to available data and perceptions), (3) to understand the mechanisms that cause the spread of species, and (4) to understand the mechanisms through which the phenomenon results in consequences (uncertainty of impacts). These four components tend to be characterized by different types of uncertainty: linguistic (e.g., ambiguity in terminology and vagueness in describing specific situations), psychological (subjective judgement), and epistemic uncertainties (context dependence, model uncertainty, etc.) (Latombe et al., 2019). In this thesis I have presented a case study of an ongoing invasion that, in many ways, epitomises these uncertainties that are inherent in invasion science. And in doing so, have demonstrated how some of these uncertainties may be addressed with multi-faceted, interdisciplinary, empirical research.

An important conclusion of this work is that it highlights the context-specific nature of invasions. I have demonstrated, for example, that divergence in aspects of ecomorphology between populations of different ancestral origin may have profound implications for invasion outcomes, and that invasion success and options for management of invasive species are likely to be relative to the specific traits of the invading population, time since establishment, local characteristics of the invaded landscape, and social opinion/perceptions towards the particular species. These subtle and perhaps often overlooked, context dependent aspects of invasion are thus important considerations that preclude making generalisation in assessment of risk and impact of invasive species, particularly if introductions involve multiple introduction events over protracted time scales, multiple pathways of introduction, and introduction to multiple locations (e.g., island chains, intercontinental).

It is often the case that social aspects of invasions are considered only in terms of gauging public attitudes towards eradication of invasive species. In this study, I found clear indication that charismatic non-native species such as *P. muralis,* may have use as model species with which to raise awareness and minimise the subjectivity shaping perceptions of invasive species in general. In addition, such introductions provide opportunities for the public to engage and interact with nature that are perhaps not readily afforded by native species, which, if tactfully encouraged, can be exploited to foster concern for native biodiversity conservation issues.

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Appendix 2.1 Detailed analysis of site-specific habitat use by introduced *P. muralis* in the UK.

Portland: Factor analysis of 16 habitat variables recorded at locations of lizard sightings (*n* =21) and random points (*n* = 20) within the Portland quarry produced three significant factors, cumulatively accounting for 68% of variance within the data. Prominent variables in Factor 1 describe a gradient from negative loadings of natural stone features (i.e., stone substrate, rock ground cover), humidity, perch temperature and short distance to refuge, towards positive loadings describing more vegetated microhabitats of soil substrate, increased vegetative ground cover, height and shade, and vegetation refugia. There was no significant variation ($F_{1,39}$ = 1.31, *p* = .26) between mean factor loadings for lizard locations (Mean = -0.17, ± SD 0.52) and random points (Mean = 0.18, ± SD 1.32) for Factor 1- with both sets of observations scaled towards the negative on the Factor 1 axis (Fig A 2.1). Factor 2 highlights positive scores for five variables describing microhabitat that features more

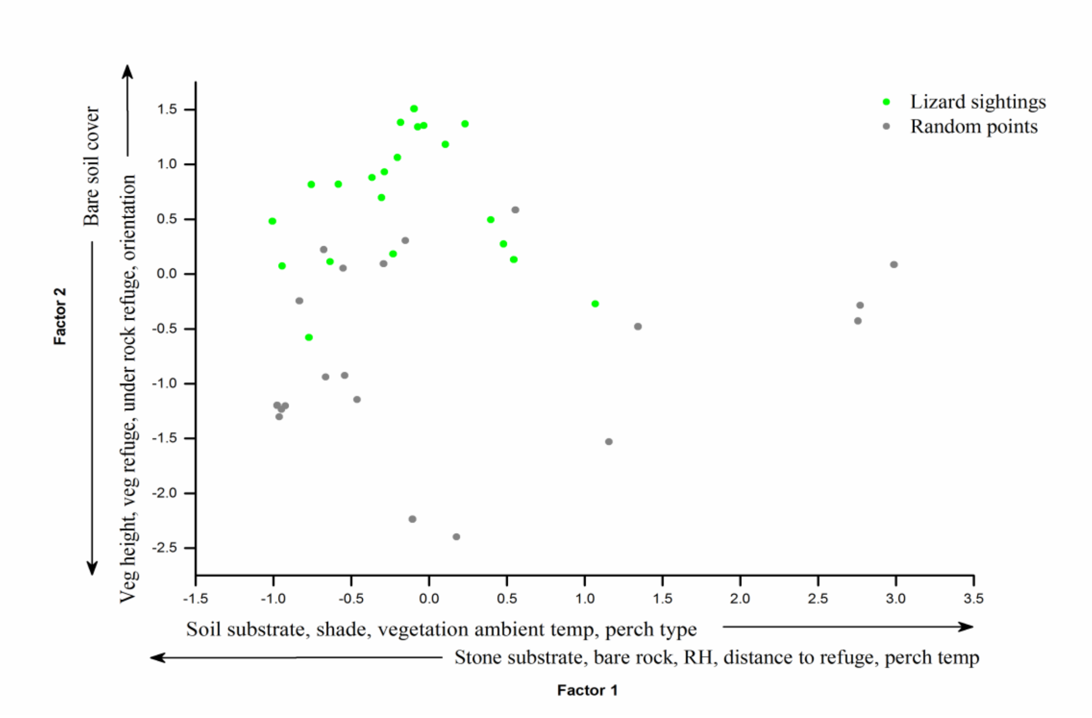

Figure A 2-0-1 Relationship between mean scores for Factors 1 and 2 of wall lizard locations and random points in a Portland quarry.

under rock and vegetative refugia, greater vegetation height, and more vertically orientated perches. At the opposite end of the Factor 2 axis is amount of ground cover being bare soil. Mean scores for lizard locations and random points differed significantly in regard to Factor 2 (Mean = 0.67 ± SD 0.59; Mean = -0.71 ± SD 0.83 respectively) ($F_{1,39}$ = 38.02, p <.0001), with random points featuring more bare soil (Fig A 2.1).

Purbeck: Factor analysis of 19 habitat variables recorded at locations of lizard sightings (n =25) and random points (n = 19) within the Purbeck quarry produced three significant factors, cumulatively accounting for 59% of variance within the data. The Factor 1 axis describes a gradient between areas of open ground within the quarry (positively scored variables) of soil substrate, bare soil ground cover, and increasing distance to refuge, and areas of exposed rock fall (negative scores) (Fig A 2.2). Mean scores for lizard locations (Mean = -0.340 ± SD = 0.686) varied significantly from random point mean scores (Mean = 0.447 ± SD = 1.179) ($F_{1, 42}$ = 7.73, p = .008) with regard Factor 1.

Positively loaded variables in Factor 2 describe a thermal microhabitat of higher ambient and substrate temperature, with shaded areas. Negatively loaded variables highlight the presence of some man-made (stone) structures within the quarry. Lizard locations and random points differed significantly in their mean scores for Factor 2 (Lizard: Mean = 0.429 ± SD = 0.873; Random: Mean = -0.565 ± SD = 0.883) ($F_{1, 42}$ = 13.87, p = .001) (Fig A 2.2)

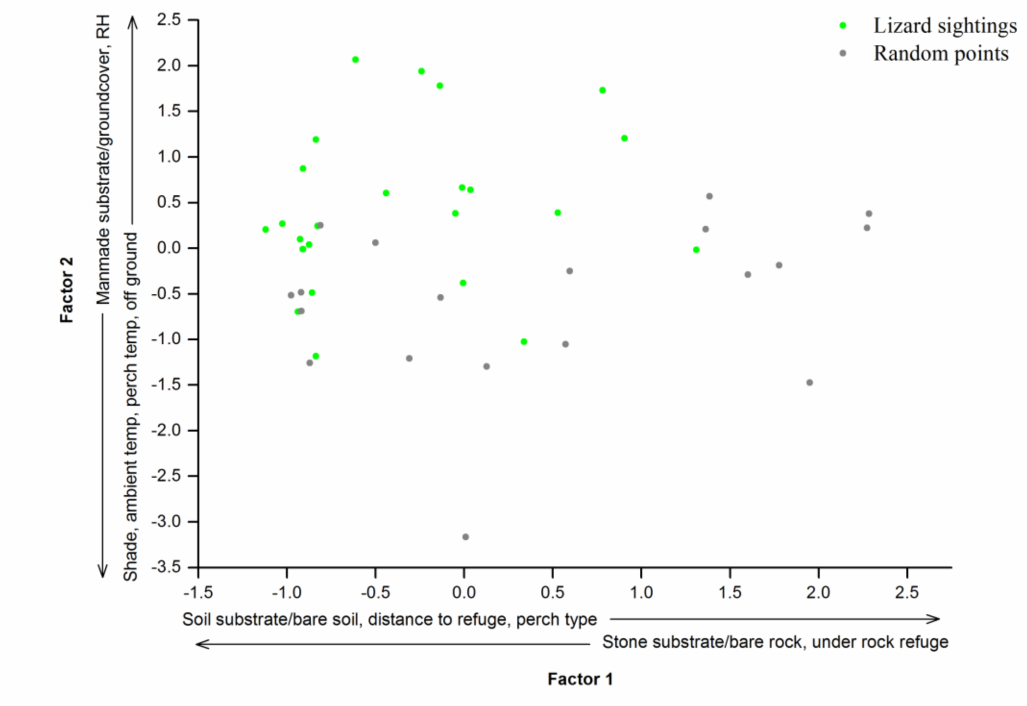

Figure A 2-0-2 Relationship between mean scores of Factors 1 and 2 for wall lizard locations and random points within a Purbeck quarry

Shoreham: Factor analysis of 20 habitat variables recorded at locations of lizard sightings (n =24) and random points (n = 20) at Shoreham Beach produced three significant factors, cumulatively accounting for 62% of variance within the data. The Factor 1 axis describes a gradient from manmade features associated with beach front properties (positive scores) to areas of exposed shingle beach (negative scores) (Fig A 2.3). Mean scores for lizard locations (Mean = 0.409 ± SD = 0.742) varied significantly from random point mean scores (Mean = -0.491± SD = 1.063) ($F_{1, 42}$ = 10.89, p = .002) with regard Factor 1.

The Factor 2 axis again included man-made features, this time in negative correlation with heavily vegetated areas of the beach. Mean scores for lizard locations (Mean = -0.317 ± SD = 0.975) varied significantly from random point mean scores (Mean = 0.381± SD = 0.912) ($F_{1, 42}$ = 5.93, p = .019) with regard Factor 2.

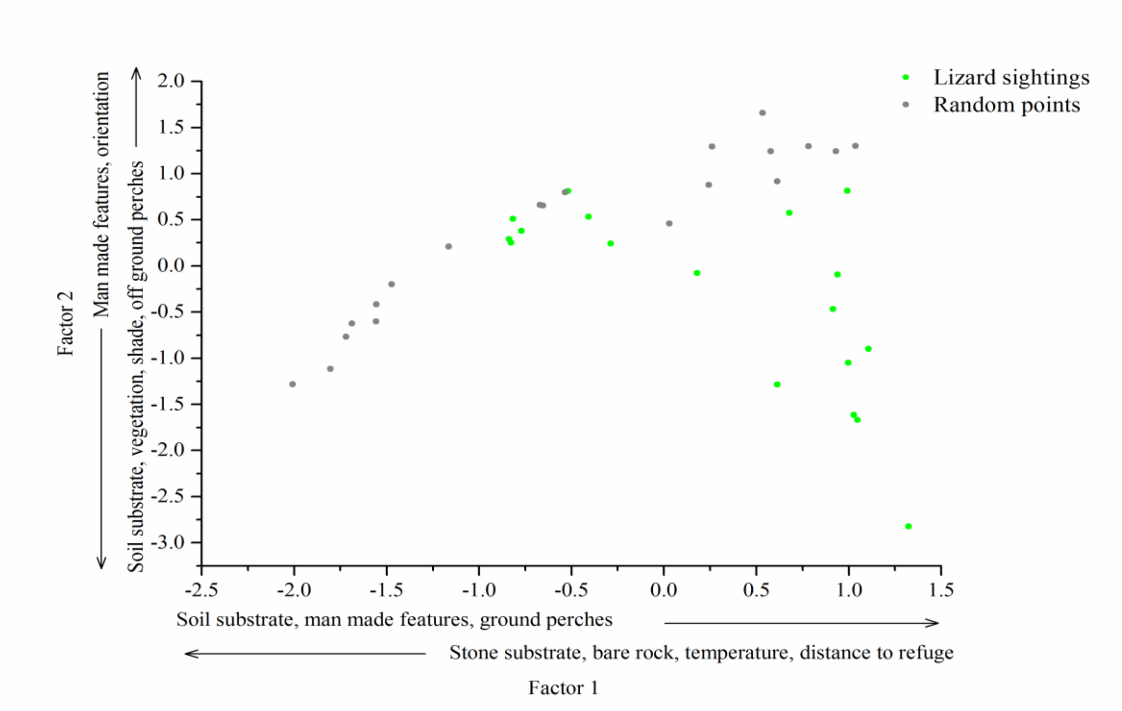

Figure A 2-0-3 Relationship between mean scores of Factors 1 and 2 for wall lizard locations and random points at Shoreham

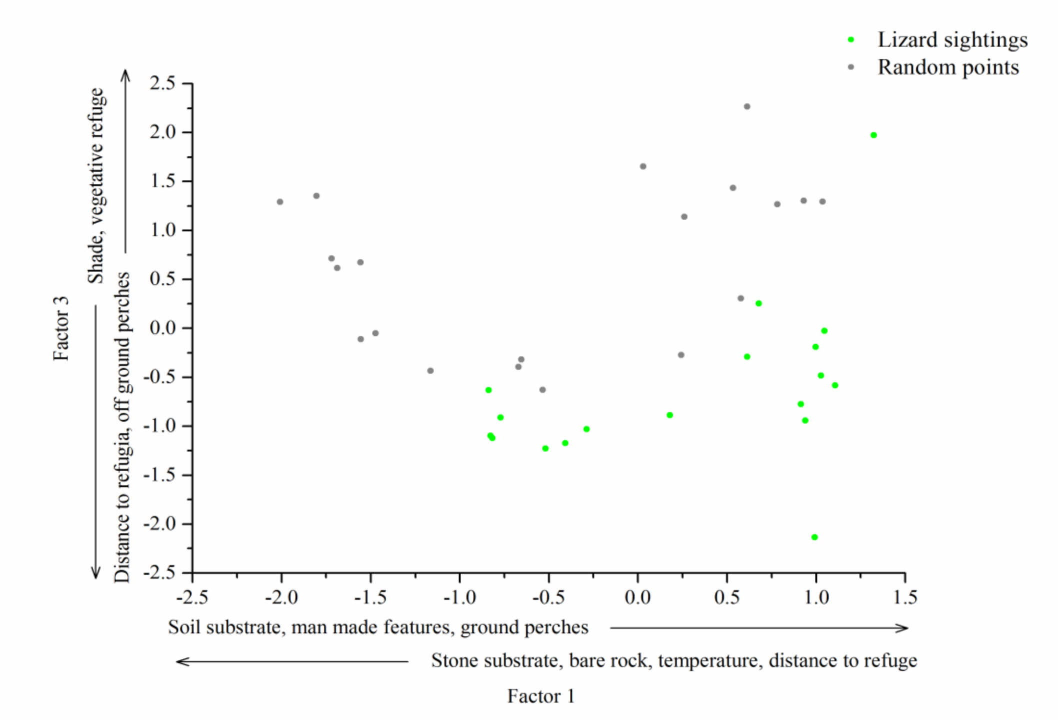

Figure A 2-0-4 Relationship between mean scores of Factors 1 and 3 for wall lizard locations and random points at Shoreham Beach

Mean scores for lizard locations (-0.546 ± 0.773) and random points (0.656 ± 0.843) also varied significantly for Factor 3 ($F_{1, 42} = 24.30$, $p = .000$). This factors axis described a gradient from off ground perches with increased distance from refuge to shaded areas offering vegetative refuge (Fig A 2.4)

Folkestone: Factor analysis of 20 habitat variables recorded at locations of lizard sightings ($n = 47$) and random points ($n = 34$) at Little Switzerland touring park, Folkestone produced two significant factors, cumulatively accounting for 47% of variance within the data. The Factor 1 axis described a gradient from the predominant grassland and associated vegetative refugia (positive scores) to attributes of the manmade features of the caravan park and elevated temperatures (negative scores). Although lizard locations tended to be associated more with manmade features, mean scores for these locations (Mean = -0.168 ± SD = 0.916) did not differ significantly from random point mean scores (Mean = 0.233 ± SD = 1.076) ($F_{1, 79} = 3.26$, $p = 0.075$) with regard Factor 1. The only significant scores for Factor 2 were negative scores for stone substrate, bare soil and bare rock ground cover, and frequency of under rock refuge. These features were not common in the immediate habitat. Mean scores for Factor 2 did not differ significantly between lizard points (Mean = 0.145 ± SD = 1.249) and random points (Mean = -0.199 ± SD = 0.423) ($F_{1, 79} = 2.38$, $p = 0.127$). Factor 3 represented a gradient from percentage of leaf litter ground cover and availability of manmade refugia (positive scores) to increasing distance to refuge and use of off ground perches (negative scores). Lizards locations had a positive mean score for Factor 3 (Mean = 0.41 ± SD = 0.76), significantly greater than the mean for random points (Mean = -0.56 ± SD = 1.02) ($F_{1, 79} = 24.43$, $p < 0.001$).

Eastbourne: Factor analysis of 18 habitat variables recorded at locations of lizard sightings ($n = 28$) and random points ($n = 21$) at Eastbourne produced three significant factors, cumulatively accounting for 60% of variance within the data. The Factor 1 axis graded from positively scored variables associated with dense vegetation (soil substrate, vegetative ground cover, shade, vegetation height, vegetated refugia) and off ground perches, to negative scores for manmade substrate, ground cover and perch types, and increasing distance to refugia. There was significant variation in mean scores for Factor 1 between lizard locations (Mean = 0.54 ± SD = 0.49) and random points (Mean = -0.73 ± SD = 1.03) ($F_{1, 47} =$ 32.79, p <0.001). There was no significant variation in mean scores between groups for Factor 2 ($F_{1, 79}$ = 3.44, p = 0.07) or Factor 3 ($F_{1, 79}$ = 0.42, p = 0.52). Neither Factor 2 nor 3 lent useful further description to lizard habitat use than was shown in Factor 1.

Abbotsbury: Factor analysis of 17 habitat variables recorded at locations of lizard sightings (n = 54) and random points (n = 28) at Abbotsbury Sub-tropical Gardens, produced three significant factors, cumulatively accounting for 63% of variance within the data. Variables with significant negative scores for Factor 1 described the highly vegetated ornamental boarders of the gardens. Significant positive scores were associated with variables describing the man-made structures at the site and perches on the ground. Lizard locations had a negative mean score (Mean = -0.157 ± SD = 0.840) for Factor 1 which differed significantly from random points (Mean = 0.303 ± SD = 1.213) ($F_{1, 80}$ = 4.04, p = 0.048). Factor 2 highlighted the use of trees by *P muralis* at the site, with significant positive scores for vegetation variables, and vertical orientation on off ground perches. Conversely, significant negative values corresponded with variables describing surrounding lawns and boarders with few opportunities for refuge. Mean scores differed significantly between lizard locations (Mean = 0.220 ± SD = 1.045) and random points (Mean = -0.425 ± SD = 0.757) ($F_{1, 80}$ = 8.38, p = 0.005) for Factor 2. Mean scores for Factor 3 did not differ significantly between lizard locations (Mean = -0.098 ± SD = 1.009) and random points (Mean = -0.189 ± SD = 0.972) ($F_{1, 80}$ = 1.53, p = 0.220). Significant variables of Factor 3 reiterated the use of trees by *P. muralis* and the tendency for random points to fall in open areas of lawn or dense vegetation.

Bury: Factor analysis of 15 habitat variables recorded at locations of lizard sightings (n = 31) and random points (n = 20) at Bury produced two significant factors, cumulatively accounting for 57% of variance within the data. The Factor 1 axis clearly describes the gradient from significantly negative scoring variables associated with vegetated garden microhabitat, to variables of manmade features, perch types and higher temperatures associated with buildings and wall structures (positive scores). Lizard sightings showed a significant trend towards use of the manmade microhabitat (Mean = 0.237 ± SD = 0.680) when compared with the mean score for random points (Mean = -0.36 ± SD = 1.29) ($F_{1,\ 49}$ = 4.79, $p = 0.03$). Factor 2 further described the use of manmade features by *P. muralis*, this time emphasizing vertical orientation on off ground perches and availability of both manmade and vegetative refugia (positive scores) versus a significant negative score for increasing distance from refuge. There was significant difference in mean scores between the lizard locations (Mean = 0.59 ± SD = 0.64) and random points (Mean = -0.92 ± SD = 0.71) for Factor 2 ($F_{1,\ 49}$ = 62.72, $p < 0.001$).

Appendix 3.1 Extent of 2018 linear survey transect for *P. muralis* along rail track at Worthing, West Sussex, UK

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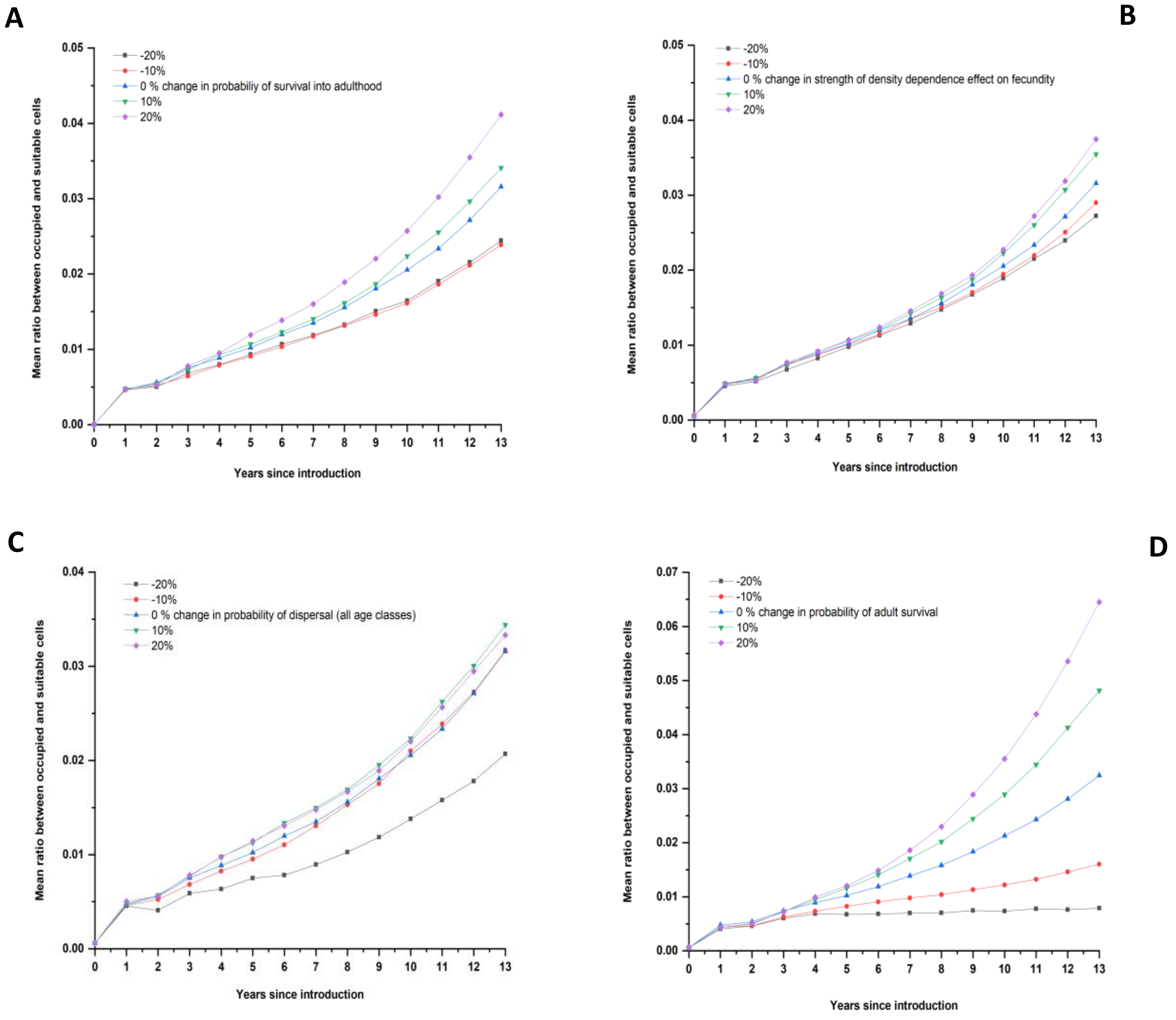
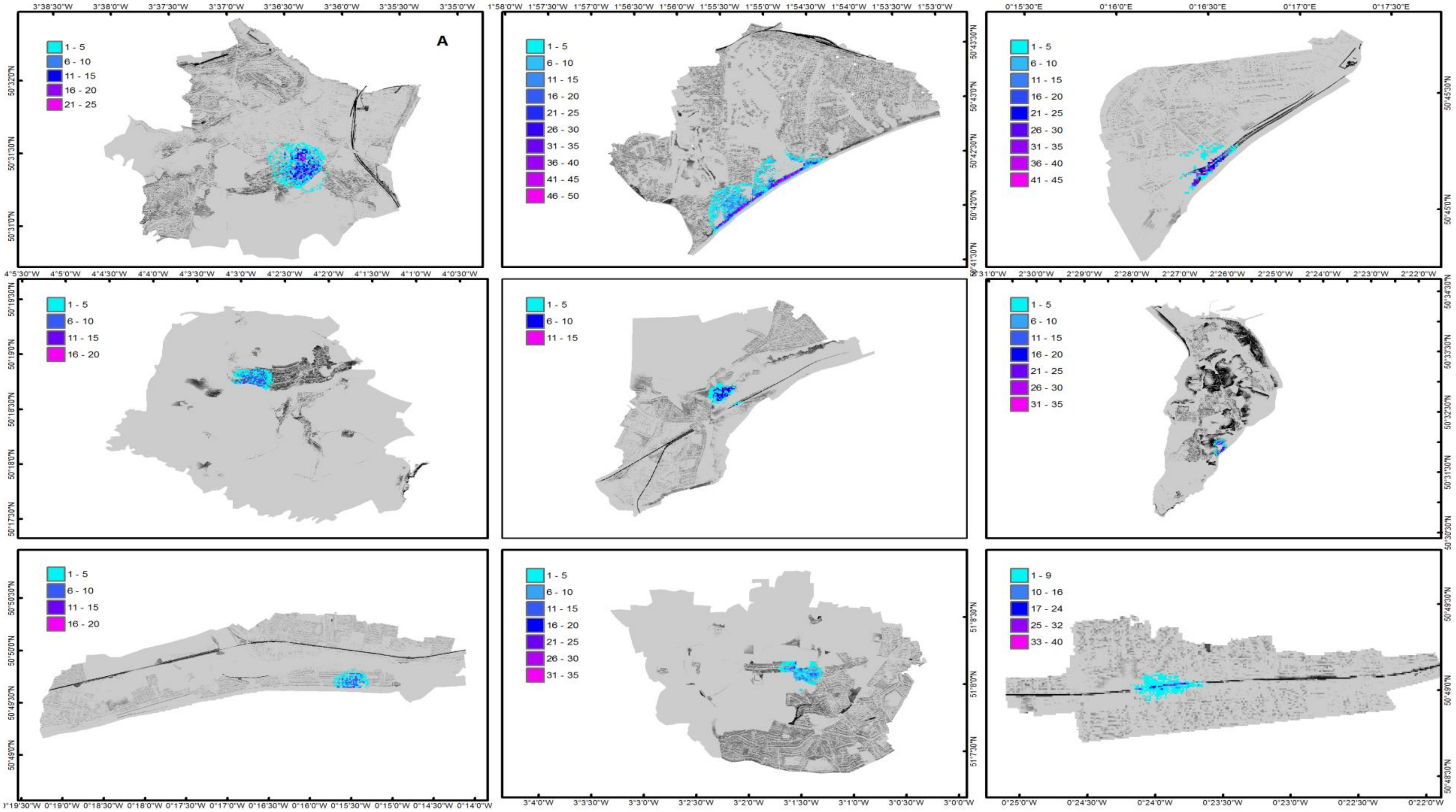
Appendix 3.2 Model description and input parameters relating to *P. muralis* biology as used in individual based models (Rangeshifter simulations) and sources informing input values

Sexual model	Explicit mating system, overlapping generations	
Proportion of males	0.5	(Vogrin, 1998), this study
Max age	15	(Eroglu et al., 2018)
Harem size	3	(Oppliger et al., 2007)
Stage structure	3	
Max fecundity	12	(Ji and Brana, 2000; Michaelides et al., 2016)
Breeding chance	1	(Pellitteri-Rosa et al., 2012)
Density dependent fecundity	yes	(Massot et al., 1992)
Probability survival to adulthood (yr 2)	Male .22 female .28	(Barbault and Mou, 1988; While et al., 2015b)
Adult survival probability	Both sexes 0.8	
Strength of density dependence 1/b (i.e., slope of the negative exponential function which governs density dependence in fecundity) inds/ha	1500 inds / ha (assuming 100% habitat suitability)	
Transfer mechanism	Stochastic movement simulator	Cost layer derived from local maxent models
Emmigration probability	Density dependent (sex and stage dependent) Juvenile male *D0* 0.9; female 0.9 Stage 1 male *D0* 0.8; female 0.7 Stage 2 male *D0* 0.2; female 0.1	(Vignoli et al., 2012)
Dispersal range	600m yr	(Schulte et al., 2013)
Step mortality	0.01 -- 0.05	
Perceptual range	4	
Directional persistance	5	
Settlement (both sexes) density dependent	Find a suitable cell + density dependent. Density dependence slope -10 infl. point 0.7	
Min steps	0	
Max steps	420	
Max steps per year	40 (600m yr)	(Schulte et al., 2013)

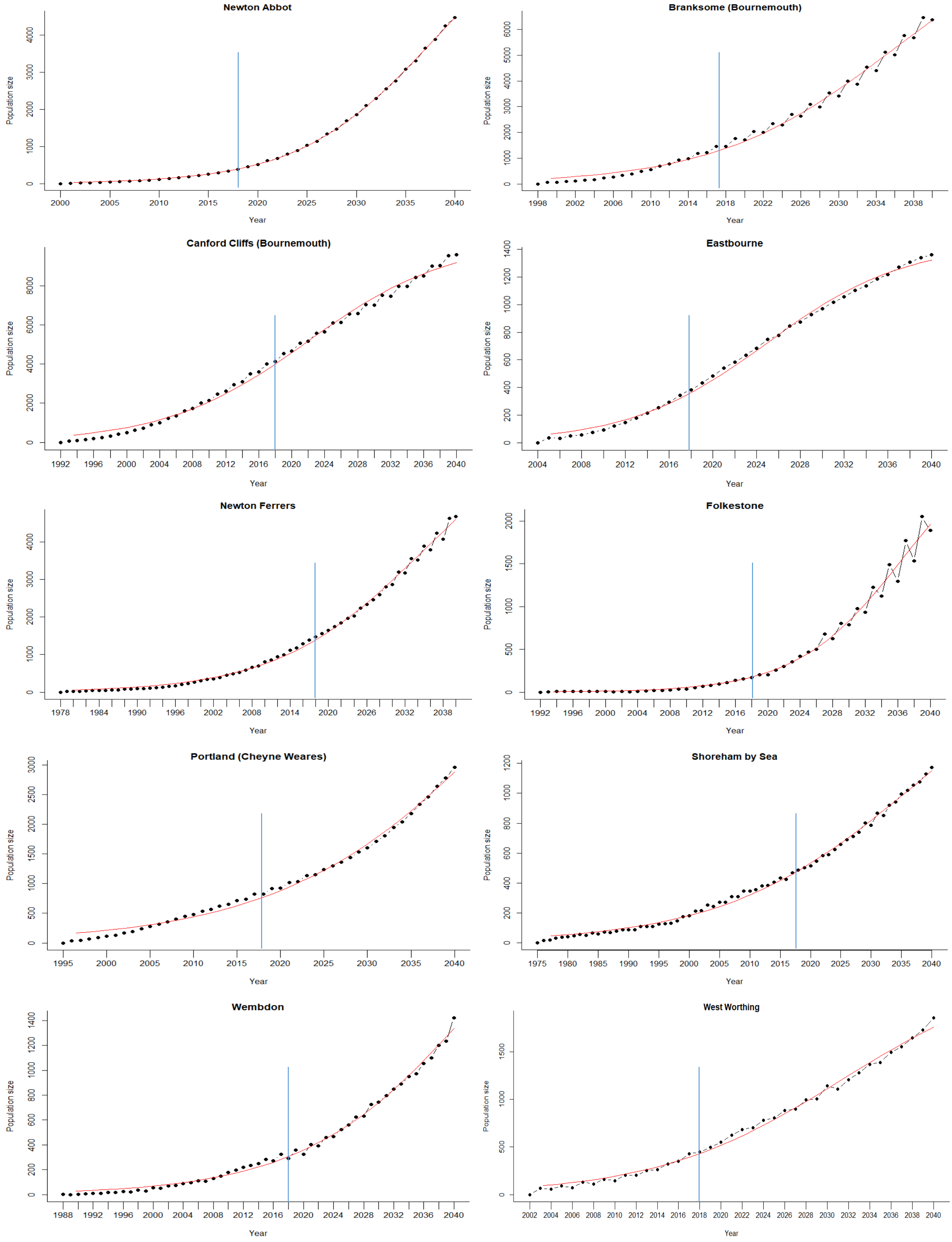
Appendix 3.3 Effects of incremental change in four key parameters on model output (annual mean ratio of occupied cells to available suitable cells) from Rangeshifter simulations of *P. muralis* invasions at UK sites (example shown, Eastbourne); A) probability of survival into adulthood (2nd Yr), B) strength of density dependent effect on fecundity, C) probability of dispersal at each life stage, and D) adult survival probability



Appendix 3.4 MaxEnt outputs showing local extent and configuration of suitable habitat (dark areas) for *P. muralis* populations in the UK: A) Newton Abbot, B) Bournemouth (including Boscombe and Canford populations), C) Eastbourne, D) Newton Ferrers , E) Folkestone, F) Portland, G) Shoreham, H) Wembdon, I) West Worthing. Outputs from RangeShifter models are overlain, indicating patterns of population dispersal projected from year of introduction to 2040 and number of lizards per occupied 225m^{2}ce**ll.**



Appendix 3.5 Predicted growth curves for ten introduced population of *P. muralis* in the UK



Appendix 4.1 Descriptive results of morphological data for introduced populations of *P. muralis* (sample size in parenthesis, male:female) and results of ANOVA tests between site, sex, and their interaction site*sex. Shaded rows are results for females. Mean ± SD with range below. All morphometrics in mm, bite force measured in newtons. SVL (body size), HS (head size), HW (head width), HH (head height), HL (head length), BF (bite force). Populations: AB (Abbotsbury), VI (Vancouver Island), BM (Bournemouth), BU (Bury), EA (Eastbourne), FX (Felixstowe), FO (Folkestone), PQ (Portland quarry), WW (West Worthing), WE (Wembdon), PU (Purbeck quarry), SH (Shoreham), SA (Saulnay), NF (Newton Ferrers)

	AB (21:29)	**VI (59:20)**	**BM (19:18)**	**BU(14:23)**	**EA (36:23)**	**FX (4:5)**	**FO (7:28)**	**PQ (43:26)**	**WW (19:24)**	**WE (29:22)**	**PU (49:26)**	**SH (41:20)**	**SA (11:14)**	**NF (12:10)**		**SITE**	**SEX**	**SITE * SEX**
SVL	59.9±1.0	60.9±0.5	60.5±1.3	54.4±1.5	61.7±1.1	60.1±0.7	58.0±2.2	60.0±0.5	63.0±0.8	58.9±1.1	62.3±0.6	62.4±0.6	56.8±0.9	57.3±2.0	*F*	6.23	4.70	1.39
	51.0-68.1	48.6-66.8	48.6-68.2	45.4-62.8	45.1-71.4	58.2-61.9	46.2-64.2	52.7-66.4	57.2-69.9	45.6-67.7	49.1-70.6	53.0-70.0	50.0-61.3	46.8-66.0				
	59.6±1.2	60.0±1.2	59.5±1.2	55.5±0.7	60.6±1.1	57.5±0.8	56.8±1.0	57.3±0.8	58.6±0.7	60.1±1.1	59.4±1.0	61.9±0.9	54.5±0.6	60.6±1.4	*P*	**<0.001**	**0.030**	0.15
	48.1-73.0	45.5-68.0	48.0-68.3	49.4-63.7	49.0-71.2	56.0-60.1	46.3-68.6	48.0-65.5	51.1-65.2	50.3-70.3	45.2-66.5	56.1-70.5	50.8-58.4	50.4-66.5				
HS	10.3±0.1	10.4±0.1	9.9±0.2	9.6±0.1	10.6±0.2	10.1±0.1	10.0±0.3	10.2±0.0	11.1±0.2	9.6±0.1	10.6±0.1	10.5±0.1	9.0±0.2	9.4±0.3	*F*	7.56	445.64	2.15
	8.6-11.5	8.0-11.4	8.0-11.4	8.1-10.5	7.5-12.5	10.0-10.4	8.2-11.4	9.3-11.4	10.1-13.2	7.5-10.8	7.5-12.2	7.7-11.6	7.8-10.2	7.8-11.0				
	8.5±0.1	8.619±0.1	8.5±0.1	8.0±0.1	8.7±0.1	8.3±0.0	8.1±0.1	8.3±0.1	8.7±0.1	8.5±0.1	8.7±0.1	8.6±0.1	8.0±0.1	8.2±0.1	*P*	**<0.001**	**<0.001**	**0.01**
	7.0-9.9	7.2-9.7	7.2-9.4	7.3-8.9	6.6-10.0	8.2-8.4	7.0-9.4	6.1-9.5	6.9-10.5	7.5-9.3	7.4-10.2	7.8-9.8	7.5-8.6	7.1-8.9				
HW	9.7±0.1	9.9±0.1	10.0±0.2	8.9±0.3	10.2±0.2	9.8±0.1	9.6±0.4	9.9±0.1	10.5±0.2	9.4±0.1	10.4±0.1	10.3±0.1	8.7±0.2	9.0±0.3	*F*	7.49	475.3	1.88
	8.1-11.6	7.7-10.9	7.8-11.7	6.5-10.8	6.8-12.3	9.5-10.2	7.8-11.5	8.1-11.7	9.1-12.5	6.8-10.8	8.3-12.1	8.6-11.9	7.5-9.7	7.2-10.8				
	7.8±0.1	8.1±0.1	8.2±0.1	7.4±0.08	8.2±0.1	7.6±0.0	7.5±0.1	7.9±0.1	8.1±0.1	8.1±0.14	8.2±0.1	8.0±0.1	7.5±0.0	7.7±0.1	*P*	**<0.001**	**<0.001**	**0.02**
	6.4-9.0	7.0-9.0	6.8-10.3	6.8-8.4	6.9-9.6	7.6-7.8	6.5-8.5	5.5-10.3	7.1-9.6	6.9-9.1	6.9-10.0	7.2-9.3	7.2-8.0	6.5-8.6				
HH	7.0±0.1	7.2±0.1	6.5±0.1	6.7±0.1	7.6±0.2	7.1±0.1	6.9±0.2	7.0±0.1	8.0±0.2	6.4±0.1	7.3±0.1	7.0±0.1	6.1±0.2	6.6±0.2	*F*	7.66	154.63	1.91
	5.4-7.8	5.4-8.5	5.2-8.0	5.8-7.5	4.9-9.7	6.9- 7.4	5.8-7.8	6.0-8.8	7.1-10.2	5.1-7.7	4.4-9.2	4.1-7.9	5.3-7.0	5.6-7.8				
	6.2±0.1	6.0± 0.1	5.7±0.1	5.7±0.0	6.2±0.2	6.0± 0.1	5.9±0.1	5.9±0.1	6.5±0.2	6.0±0.1	6.3±0.1	6.2±0.1	5.8±0.0	5.7±0.1	*P*	**<0.001**	**<0.001**	**0.02**
	4.4-7.8	4.7-7.3	4.9-6.7	5.1-6.4	3.4- 8.1	5.8-6.3	5.0-6.9	4.1-6.9	4.1-8.9	5.1-8.0	5.0-8.2	5.5-7.0	5.4-6.5	5.0-6.5				
HL	16.0±0.1	15.6±0.1	15.1±0.3	14.8±0.08	15.2±0.2	15.1±0.1	15.4±0.6	15.6±0.1	16.3± 0.2	14.6±0.2	15.8± 0.1	16.0±0.2	13.8±0.3	14.1±0.4	*F*	6.32	628.02	3.75
	15.0-17.4	11.7-17.6	12.7-16.9	14.4-15.3	12.0-17.2	14.8-15.5	12.3-16.8	14.5-18.2	14.9-18.4	12.1-16.8	11.6-17.5	12.0-18.1	12.2- 15.9	11.8-16.4				
	12.6±0.2	13.1±0.1	13.0± 0.2	12.0±0.1	13.0± 0.1	12.5±0.0	12.2±0.1	12.3±0.1	12.6±0.1	12.7± 0.1	12.8±0.1	13.1±0.1	12.0±0.1	12.7±0.2	*P*	**<0.001**	**<0.001**	**<0.001**
	10.8-14.7	11.7-14.2	11.0-14.4	11.0-13.4	11.0-14.4	12.5-12.7	10.5-14.1	10.3-14.5	11.6-14.0	11.2-14.3	11.3-14.5	12.1-15.2	11.1-13.1	10.9-13.8				
BF	9.6±0.4	9.4±0.2	9.0±0.6	7.6±0.3	10.4±0.6	9.1±0.5	-	8.7±0.2	11.0±0.8	8.3±0.4	10.6±0.4	10.0±0.4	-	9.1±1.2	*F*	3.80	507.73	1.46
	5.4-14.4	3.3-14.0	3.3-12.8	5.8-10.4	3.0-15.0	8.1-10.3	-	5.4-13.0	5.5-20.6	4.4-12.8	2.8-17.5	5.0-14.8	-	3.5-15.1				
	4.5±0.2	4.6±0.2	3.8±0.2	3.6±0.1	4.6± 0.2	4.2±0.2	-	3.9±0.1	4.5±0.2	4.4±0.2	4.6±0.2	4.8±0.2	-	5.0±0.4	*P*	**<0.001**	**<0.001**	0.14
	2.2-7.3	3.3-6.3	1.8-6.4	2.3-5.8	0.8-6.6	3.4-5.0	-	1.2-5.5	1.5-7.8	2.8-5.9	1.5-7.1	3.5- 8.4	-	2.6-6.8				

Appendix 4.2 Descriptive results of morphological data for introduced populations of *P. muralis* and native lizards in the UK and on Vancouver Island, with results of ANOVA tests between species, sex, and their interaction species*sex. Mean ± SD with range below. All morphometrics in mm, bite force measured in newtons. SVL (body size), HS (head size), HW (head width), HH (head height), HL (head length), BF (bite force). PM (*P. muralis*), ZV (*Z. vivipara*), LA (*L. agilis*), EC (*E. coerulea*).

	UK lizards										**Vancouver Island lizards**							
	PM male	PM Female	ZV male	ZV Female	LA male	LA Female		SP	SEX	SP*SEX	PM male	PM female	EC male	EC Female		SP	SEX	SP*SEX
SVL	60.6±0.3	58.9±0.3	49.5±0.6	55.6±1.1	62.7±2.2	69.2±2.4	*F*	40.9	12.8	13.2	60.9±0.5	60.0±1.2	73.4±4.0	81.2±4.0	*F*	91.09	3.67	6.01
	45.1-71.4	45.2-73.0	45.6-52.5	48.9-62.5	42.8-75.8	49.4-78.2	*P*	**<0.001**	**<0.001**	**<0.001**	48.6-66.8	45.5-68.0	56.3-91.8	65.0-91.9	*P*	**<0.001**	0.06	**0.01**
HS	10.3±0.0	8.4±0.0	6.1± 0.1	6.0±0.1	10.6±0.3	10.2±0.3	*F*	190.5	19.5	19.7	10.4±0.1	8.6± 0.1	9.9±0.4	10.6±0.4	*F*	10.63	4.86	27.77
	7.5-13.2	6.1-10.5	5.1-7.1	5.4-6.8	7.2-12.3	8.0-11.4	*P*	**<0.001**	**<0.001**	**<0.001**	8.0-11.4	7.2-9.7	7.8-12.1	8.8-11.7	*P*	**0.002**	**0.03**	**<0.001**
HW	10.0±0.0	7.9±0.0	7.2±0.0	6.7±0.0	10.1±0.3	9.8± 0.3	*F*	69.3	29.9	16.7	9.9± 0.1	8.1±0.1	9.7±0.5	10.3±0.4	*F*	17.11	6.30	24.07
	6.5-12.5	5.5-10.3	6.8-7.7	6.2-7.2	6.9-12.2	7.7-11.2	*P*	**<0.001**	**<0.001**	**<0.001**	7.7-10.9	7.0-9.0	7.5-12.5	8.7-11.8	*P*	**<0.001**	**0.01**	**<0.001**
HH	7.1±0.0	6.1±0.0	5.4±0.1	4.9±0.0	7.9±0.2	7.6±0.2	*F*	57.8	13.0	3.5	7.2±0.0	6.0±0.1	6.7±0.3	7.4±0.2	*F*	5.49	3.03	25.28
	4.1-10.2	3.4-8.9	4.5- 6.2	4.5-5.7	5.1-9.7	6.3-8.5	*P*	**<0.001**	**<0.001**	**0.03**	5.4-8.5	4.7-7.3	5.3-8.3	5.9-8.3	*P*	**0.02**	0.08	**<0.001**
HL	15.5±0.07	12.6±0.0	10.3±0.1	9.7±0.1	15.0±0.5	14.5± 0.4	*F*	154.2	37.5	22.9	15.6±0.1	13.1±0.1	14.8.1±0.6	15.9±0.6	*F*	7.83	4.10	25.07
	11.6-18.4	10.3-15.2	9.5-11.2	9.1-10.5	10.7-17.4	10.9-16.2	*P*	**<0.001**	**<0.001**	**<0.001**	11.7-17.6	11.7-14.2	12.0-17.6	13.7-17.8	*P*	**0.006**	**0.046**	**<0.001**
BF	9.6±0.1	4.3±0.0	3.3±0.3	2.5±0.1	11.2±1.1	8.8± 0.8	*F*	61.4	42.6	15.3	9.4±0.2	4.6±0.2	5.9±0.8	5.9±0.8	*F*	4.30	20.05	20.86
	2.8-20.6	0.8-8.4	1.9-5.0	1.8-3.4	2.5-18.6	4.1-12.3	*P*	**<0.001**	**<0.001**	**<0.001**	3.3-14.0	3.3-6.3	2.6-9.3	2.6-7.9	*P*	**0.04**	**<0.001**	**<0.001**

Appendix 6.1 Q sort factor array demonstrating the fixed quasi-normal distribution of statements. Ranking values range from -6 to 6

-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6
13. If wall lizards don't cost anything (financially) then their presence is not a problem	1. The more wall lizards the merrier	19. I think wall lizards should be protected here	59. I wish we had wall lizards in the garden. Can I have some	68. What classes as native anymore!	16. I feel wall lizards are not competing with our native species.	64. Classifying wall lizards according to our standards of whether or not they should be here is not useful	20. I am always unhappy about ANY introductions, which are usually bad news for native species.	66. The wall lizards add to the character of our garden and village	47. It is a pleasure and a privilege to observe wall lizard behaviour	34. Conservationists should focus much more on the wall lizards ecological role, and much less on where they originated from	45. I'm unsure of their effect on populations of native lizards	23. I don't want wall lizards to damage native species
60. The wall lizards provide the only chance we get to see lizards	73. We have a somewhat impoverished fauna, but wall lizards add to it	75. We (humans) bought wall lizards here, so we shouldn't complain	31. I can't see how you can eliminate wall lizards without harming other species	2. Wall lizards are much prettier to look at than our native lizards	52. No problems with wall lizards being here as far as I am aware	4. I would feel quite privileged to have wall lizards in my garden	67. The wall lizards help to keep down garden pests	58. I am concerned there are likely to be more currently unrecorded wall lizard populations.	43. wall Lizard spotting is great fun	53. Nice to see wall lizards but I'd rather see a native lizard	22. It would be a shame if native lizards got edged out of our landscape by wall lizards.	29. I feel that we don't know enough about what these wall lizards bring and take away from our native wildlife.
	41. Wall lizards live where other lizards don't, so that's ok	40. We see less sand lizards due to loss of habitat so the wall lizards are a nice substitute	51. I don't mind that wall lizards are not native to the UK	61. I don't want wall lizards to be removed.	27. It is worrying that wall lizards are surviving in a colder climate than they are used to.	15. Wall lizards are not detrimental to our gardens	49. Wall lizards are a great subject to photograph	28. We should stop wall lizards spreading if possible	42. It's nice to see wall lizards in the wild	12. Prefer if wall lizards were in their own environment best suited to their well being	26. I have nothing against wall lizards but would like to see some scientific studies investigating their impacts	
	8. Wall lizards are welcome wherever they are	33. We must embrace the fact ecosystems now incorporate many alien species and not try to achieve the often impossible goal of controlling their abundance	46. It is good to see wall lizards appear to be thriving here	56. I would make special trips to see wall lizards	37. Having a local colony of wall lizards is great	72. Wall lizards are killing off our native lizards	39. There is a bias against alien species	50. It's great for the kids to have wall lizards in the garden	10. Wall lizards really shouldn't be here	21. The presence of species which did not arrive here under their own steam is a concern	24. I'm concerned about Wall Lizards affecting native Sand Lizards and Common Lizards both in terms of competition and pathogens.	
		3. If wall lizards are in our garden then they become like our pets	30. Just leave the wall lizards alone	14. Wall lizards co-exist quite happily with common lizards on the continent so there's no reason why they wouldn't here.	69. Reptiles are so rare I'm excited to see any lizard, native or not	65. Many non-native species have become established here, wall lizards are just another	76. As average temperatures rise it is to be expected that wall lizards are thriving here	18. Wall lizards seem harmless enough.	74. If wall lizards are breeding they are obviously happy to be here	44. As long as wall lizards don't upset local ecology then I enjoy their presence		
			6. I hope wall lizards thrive in the UK	5. I'm happy to have wall lizards here	17. I cannot see that wall lizards are likely to become a problem	32. The authorities should do something about wall lizards spreading	62. It's really nice to have this wildlife (wall lizards) in our garden	54. The wall lizards always give a topic of conversation when they come out in the warmer weather	48. I find wall lizards intriguing and interesting.			
			38. We should be grateful wall lizards are here to enjoy	36. It's like being on holiday with wall lizards here	55. It's a shame people don't consider wall lizards when repairing/pointing walls	11. These wall lizards are invading the UK	25. I do wonder if global warming is a factor to wall lizards being here	9. Wall lizards feel almost out of place here	35. The public must be vigilant of such introductions and support management efforts			
					71. I know summer has arrived when wall lizards first start to appear on a sunny day	63. No strong feelings about wall lizards one way or another	7. I don't want to see the wall lizards killed					
						70. Wall lizards cause a loss in conservation value of sites planned for reintroduction of sand lizard						
						57. Don't know how I feel about wall lizards being here						