Risk, Habitat Use, and Behavioural Variation in Urban Grey Squirrels.

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Abstract

Behavioural differences between urban and rural wildlife have been widely reported, however, how these differences relate to individual differences in behaviour and the expression of personality variation remains less well understood. In a review of studies exploring personality variation in urban wildlife, this thesis finds that many of these studies appear to consider behavioural variation (repeatable among individual differences in behaviour) within the context of quite broad classifications of urban verses rural populations. Using these broad classifications may lead to difficulties in understanding and predicting how urban habitats might shape behavioural variation. Maintaining behavioural variation is likely to be an important factor in populations undergoing rapid human induced habitat change, thus being able to compare between studies in terms the relationships between behaviour and habitat features, could be important for making predictions about potential impacts.

Using grey squirrels as a model system, studies in this thesis attempt to address this issue by including habitat characteristics at the local habitat level into experimental field studies that investigate relationships between behavioural variation and habitat features associated with urbanisation. Firstly, it applies giving-up density (GUD) methodology to test for differences in risk perception and patch use in squirrels experiencing varying levels of urbanisation. This found that squirrels foraging near buildings and roads utilised ‘risky’ patches more readily than squirrels living further away from fixed features of potential disturbance risk. In addition, noise variability was found to be an important factor in squirrels perceived risk, with squirrels feeding under highly variable noise conditions leaving higher GUDs at ‘riskier’ feeding sites. To investigate the relationships between local habitat and personality variation, individual squirrels, at different sites, were measured on responses to handling and behaviours within an open-field test. This found that escape and exploration behaviours were repeatable for individuals, however, significant differences in personality variation between sites were not found. Local microhabitat features did not appear to significantly predict individual behaviours, although a trend for faster escape responses in individuals caught near roads was found at the urban site. Overall, differences in the mean levels of escape and exploration behaviours were found, with faster levels of escape responses and faster rates of exploration, although less total exploration, found in urban sites. These findings mirror those from other studies of personality variation in urban dwelling species, where levels of urbanisation experienced by populations were defined more broadly.

Like many successful urban species, urban grey squirrels live at higher population densities than their rural counterparts. The final study in this thesis uses auditory playbacks of conspecific calls to test if features of the urban built environment influence behavioural responses during foraging under an auditory cue of potential competition risk. Results suggest that squirrels foraging closer to roads and buildings appeared to be less attentive to conspecific playbacks. Further, local habitat quality level and noise were also found to impact time invested in social signalling behaviours, vigilance and feeding intake rate. Together these results show that foraging trade-offs under potential conspecific risk vary with local habitat features associated with proximity to human disturbance. Foragers under variable noise conditions and those feeding close to urban features appear to prioritise resource-acquisition over attending to conspecific risk.

Overall, the studies included in this thesis provide some insights into the behavioural differences between urban and rural grey squirrels in terms of resource-acquisition trade-offs, and the local habitat features affecting these. Integrating this approach into future studies of behavioural variation could aid in understanding of how urbanisation could impact behavioural variation in wildlife occupying these areas.

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Authors declaration and acknowledgements

I can confirm that the material presented in this thesis is my own work designed, conducted, and written up by me. My supervisors Dr Sasha Dall and Professor Robbie McDonald provided advice on methodology. Sasha Dall provided advice on analysis and drafts of the chapters. Data and methodology from parts of this thesis have also been submitted by students at the University of Exeter as part of their theses in BSc (hons) Zoology. Under supervision by Sasha Dall, students Louise Whale, Bali Posner-Tal, Lucy Jacobs and Naomi Lands used parts of the data and methodology in chapter 5 for their dissertation projects. The open-field test designed for Chapter 4 was used by Dr Lisa Leaver and dissertation students in Psychology for another study. However, I can confirm that the design and methods used in this thesis were designed before working with these students, with student involvement consisting of working on data collection and not conception or design of these studies.

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Chapter1: General Introduction

Urban environments, usually characterised by high human density, increased artificial structures, fragmented habitats, rapid habitat change, and novel sources of disturbance, place unique selective pressures on wildlife (Alberti, 2015; Thompson, Rieseberg, & Schluter, 2018). As a result, urban landscapes are usually associated with reduced biodiversity, however, there are a few species that appear to thrive under these conditions (Goddard, Dougill, & Benton, 2010; Shochat et al., 2010; Weston et al., 2014). What makes some species able to rapidly adjust to urbanisation and human disturbance is a key issue in Conservation biology and appears to be a rapidly growing area of interest within Behavioural Ecology. Behaviour is the first line of response an animal has to its environment and under rapid, novel ecological change, the behavioural options and behavioural responses available to organisms determine whether they can survive, or fail to cope, under changing conditions (Sih, 2013; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Comparisons between rural and urban wildlife suggest that successful urban dwelling animals might exhibit a number of behavioural adaptations to living alongside humans (reviewed in: Sih, 2013; Sol, Lapiedra, & González-Lagos, 2013). These changes in behaviour could be a result of learning, habituation, or could represent microevolutionary changes (Miranda, Schielzeth, Sonntag, & Partecke, 2013). As such, the investigation and interpretation of animal behaviour in urban habitats could reveal how anthropogenic activity can shape the wildlife populations living alongside humans in an increasingly urbanised world. For example, considering foraging behaviours can provide information about which parts of the urban landscape animals consider safe, risky, or profitable (Searle, Stokes, & Gordon, 2008; Verdolin, 2006), understanding the distribution of individuals could inform about disturbance impacts (Lowry, Lill, & Wong, 2013), and quantifying the expression of behavioural or genetic traits could help make predictions about the future of a species (Garroway & Sheldon, 2013; Johnson & Munshi-South, 2017; Selonen, Fey, & Hämäläinen, 2018). Understanding and observing these could help to identify some of the agents shaping the ability of some species to cope, or some to struggle, with living alongside humans; and could potentially provide information for mitigation in regard to sources of human-wildlife conflict.

This thesis attempts to address two main themes relating to behavioural variation in urban wildlife. Firstly, it considers if features of urban landscapes, including noise disturbance and the urban built environment, might affect the levels of behavioural variation in urban wildlife compared to rural populations. Secondly, it considers how these features of urban habitats can influence perception of risk during resource-acquisition. These themes are connected via the hypothesis that urban habitats change the structure of risk, and therefore behavioural risk-taking, compared to rural and ancestral landscapes. Urban habitats may offer several paradoxical risk associated problems for wildlife, for example, urban landscapes can have reduced predation rates and reduced predator diversity (Fischer, Cleeton, & Timothy, 2012), however predators in cities may be novel, and an animals ability to assess predation risk may be affected by anthropogenic activity and disturbance. Further, human dominated habitats can provide a buffer from seasonal and temporal fluctuations in resources. Yet, resources many be novel, aggregated and contain higher risk of competitive interactions or exposure to humans (Shochat, 2004).

1.1 Living in a landscape of disturbance – habitat use and risk perception

Studies considering the behaviour of urban wildlife suggest that urban dwelling wildlife has a tendency to be less risk-adverse to those living in rural settings (Martin & Fitzgerald, 2005; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2016; Sol et al., 2013, 2017; Stillfried et al., 2017). This may be in part because urban habitats contain high human population densities, therefore facing greater exposure to humans and disturbance from human activity. As such, successful ability towards living alongside humans might require behavioural adjustments to risk, including perceived risk. Human activity, even where it represents indirect and non-lethal disturbance, can shape wildlife behaviour through their presence alone, much like apex predators in natural predator-prey systems (Beale & Monaghan, 2004; Clinchy et al., 2016). The non-lethal impacts of fear, or perceived risk of predation, can affect wildlife in a number of ways, such as avoidance of certain features of the landscape

(Ciuti et al., 2012) and changes to reproductive and feeding behaviour (Fernández-Juricic, 2002; Fernández-Juricic & Tellería, 2000). Research into the impacts of anthropogenic disturbance has revealed that urban wildlife show temporal and spatial changes in terms of in distribution and behaviour according to human activity, for example increasing nocturnal activity to shift activity to periods of low human activity (Gaynor, Hojnowski, Carter, & Brashares, 2018), as well as physiological differences in stress responses due to chronic exposures to disturbance stimuli (Partecke, Schwabl, & Gwinner, 2006).

Whilst humans can represent a source of risk in similar ways to predation, other predator species can occupy urban environments, potentially increasing predation risk for prey species. However many of these predators may also fear humans, and increased human activity can potentially impact the ability of predators to detect and hunt their prey (Clinchy et al., 2016; Suraci, Clinchy, Zanette, & Wilmers, 2019). This means that for some species, urban habitats and sites of human activity will offer a release from natural predation regimes and its associated mortality risk. For example, female brown bears (*Ursus arctos*) and female moose (*Alces alces*) in Grand Teton National Park were found to occupy places closer to human recreation activity, preferring to give birth near to roads, suggesting that for these species roads can offer shielding from neonate predators (Berger, 2007). Urban habitat features could also influence risk perception through the presence of artificial structures and built features, such as buildings, roads, which can potentially impact predator detection, available shelter, and escape routes (Embar, Kotler, & Mukherjee, 2011; Tadesse & Kotler, 2012; Wheeler & Hik, 2014). Roads cause habitat fragmentation, and vehicular traffic may represent a high mortality risk (Bateman & Fleming, 2012; Berger, 2007; Nadège Bonnot et al., 2013; Murray & St. Clair, 2015), open spaces cleared of vegetation, such as managed lawns and recreational areas, may increase perception of predation risk through the loss of vegetation and canopy cover (Fernández-Juricic & Tellería, 2000; Flamand et al., 2019; Hume, Brunton, & Burnett, 2019). Fear and increased perception of risk also interact with resource-acquisition through increasing the need for anti-predator behaviours such as vigilance, which come at a cost to acquiring key resources (Brown, Laundre, & Gurung, 1999; Clermont, Couchoux, Garant, & Réale, 2017; Embar et al., 2011; Poudel, Spooner, & Matthews, 2016; Sarno, Parsons, & Ferris, 2014a). Research in to the behavioural ecology of individual behavioural variation, also sometimes referred to as animal personality variation, has indicated that individuals can vary in these physiological and behavioural responses to risk (Dall & Griffith, 2014; Wolf & Weissing, 2012). This is now emerging as a possible factor in the ability of a population to survive under anthropogenic disturbance and human rapid induced habitat change (Sih, 2013; Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

1.2 Personality variation under human rapid induced habitat change and urbanisation

Behaviour is the first line of response an animal has to its environment (West-Eberhard, 1989). In human dominated environments, such as urban habitats with increased levels of human disturbance, animals may face particularly novel and fast-paced challenges and conditions (Sih, 2013; Sol et al., 2013). As such, behavioural responses to these may be an important determinant of an animal's ability to cope in this environment. One of the key behavioural factors thought to influence the ability to cope with novel and fast-paced challenges is behavioural flexibility. Flexibility in terms of behavioural responses is likely to allow animals to habituate quickly to forms of disturbance, shift habitat and feeding preferences in response to novel resources and find solutions to novel problems(Bonier, Martin, & Wingfield, 2007; Diquelou, Griffin, & Sol, 2015; Lowry et al., 2013; Sol et al., 2013). However, habituation and behavioural flexibility may not offer a full explanation as to why some animals are better than others in ability to cope under urbanisation(Lowry, Lill, & Wong, 2011; Sprau & Dingemanse, 2017). There may be some intrinsic properties of species, and some individuals, that allow them to better cope under human induced habitat change.

Research into between species and between individual behavioural differences has suggested that there are limits to behavioural flexibility, and that some individuals may be less flexible (more consistent) in behaviour than others. This may be relevant to the understanding of behavioural responses to urbanisation, as it seems some individuals may be better able to adjust to urban habitats than others(Miranda et al., 2013). Between individual differences in levels of behavioural flexibility and behavioural consistency, has been studied in terms of individual differences in coping styles(Koolhaas, 2008), temperament (Gosling, 2001)and now increasingly in terms of animal personality. This increasingly body of research has revealed that individuals can exhibit consistency in levels of behavioural traits such as aggression, sociality, and activity, with these levels of behaviour being expressed consistently across different contexts.

This thesis will refer to between individual differences in behavioural consistency as variation in personality, or personality variation. Variation in personality is generally defined as the consistent differences in behaviour between individuals within a population (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Dall & Griffith, 2014). This level of behavioural variation is thought to arise, and be maintained, through shifting ecological pressures including predation levels, variation in resources, competition and social conditions (Bergmüller & Taborsky, 2010; Boon, Réale, & Boutin, 2007; Dall & Griffith, 2014; Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016; Wolf, van Doorn, Leimar, & Weissing, 2007). For some species, there appears to be strong links between personality variation and fitness (Dingemanse & Réale, 2005). This is because variation in personality generally reflects variation in behaviours associated with risk, for example, variation in 'boldness' can reflect an individual's willingness to risk exposure to predation.   Risk-taking behaviour, or the amount of risk an individual is willing to take, is likely to reflect individual trade-offs between current and future fitness. For example, individuals who adopt high risk-taking behaviours, such as foraging in the presence of high predation risk, may benefit from increased foraging and mating opportunities, however, they are likely to be exposed to increased mortality risks compared to more risk-adverse individuals (Stamps, 2007; Wolf, van Doorn, et al., 2007). Individual differences in factors such as age, state, and sex are also likely to mean that individuals differ in the 'optimum' behavioural strategy for a given situation. For example, males and females may experience differing selection pressures in terms of risk-taking behaviour due to differing levels of investment in parental care, or individuals may face differing cost and benefits of risk-taking across their development and lifetime. Further, the cost and benefits of behaving a certain way is also likely depend on the frequency of behavioural strategies expressed by other individuals within a population (Bergmüller & Taborsky, 2010; Dall, Houston, & McNamara, 2004).

Although urban wildlife appears to show a general tendency towards increased risk-taking, such as increased aggression, reduced flight initiation distances, and decreased neophobia (Parker & Nilon, 2008), it is remains unclear to what extent these represent flexible behavioural adjustments to living under urbanisation, non-random sorting of individuals who are more likely to move into urban areas, or selection pressures for particular behavioural 'types' in urban habitats. Studying animal personality variation in urban wildlife could offer potential insights into these factors and provide some clues about the long-term effects and potential evolutionary consequences of human disturbance on wildlife populations. Population variability in 'personalities' are likely to impact the sustainability of a population under rapid environmental change, rather like genetic diversity (Dingemanse, Both, Drent, & Tinbergen, 2004). Elevated levels of anthropogenic disturbance and rapid habitat change, are likely to result in altered selection pressures for urban wildlife, compared to those in rural populations (Johnson & Munshi-South, 2017). However, it currently remains unclear if, overall, urban environments reduce or increase behavioural variation expressed in wildlife populations.

Whilst a growing number of studies have found repeatability in behaviour in urban dwelling wildlife (see Chapter 2), and an increase in the mean levels of risk-related behaviours, such as exploration and aggression (Parker & Nilon, 2008), few of these studies reveal if the actual structure of personality variation (the levels of between and within individual variation in behaviour) is impacted by urbanisation. For example, urbanisation could create populations of homogenous individuals adopting the same behavioural 'strategy', or it could increase personality variation through the novelty or complexity of risks individuals could be exposed to during resource-acquisition. Here, individuals could benefit from diverging from one another in terms of risk-taking behaviours due to increased costs of resource competition (Bolnick et al., 2017; Dall & Griffith, 2014; Wolf & McNamara, 2012). It is highly likely that various urban habitat factors will impact behavioural variation differently for different species. Therefore, investigating how ecological factors associated with urbanisation may alter the pressures for or against certain behavioural types across different taxa is likely to aid in identifying the populations more vulnerable to human disturbances, as well as offer potential solutions for conservation and wildlife management.

There could be several factors acting as ‘filters’ affecting behavioural variation in urban wildlife. Drawing on the literature examining ecological and evolutionary explanations for the existence of animal personality variation (reviewed in Adriaenssens & Johnsson, 2013; Dall, Bell, Bolnick, & Ratnieks, 2012; Dall & Griffith, 2014; Wolf & Weissing, 2012), these filters are likely to include: individual tolerance to risk, individual differences in resource-acquisition trade-offs, and whether humans represent a predation threat to a particular species. For example, eastern chipmunks, *Tamias striatus* (Martin & Réale, 2008) and burrowing owls, *Athene cunicularia* (Martina Carrete & Tella, 2013, 2017) have been found to distribute themselves according to individual docility and tolerance to human disturbance, suggesting that there is reduced personality variation at locations close to human disturbance, with less disturbance tolerant, more risk-adverse individuals moving into other locations away from human disturbance. However, this trend may not appear for all species as risk-aversion close to human sites may have consequences for mortality. For example, for many species, anthropogenic food resources might present high quality, yet novel, feeding resources. High fear of novelty could impact access to these resources, yet for wildlife vulnerable to conflict with humans, or those regraded as pest species, novel foods, or novel items, could represent a risk of poisoning or trapping (Greggor, Clayton, Fulford, & Thornton, 2016; Griffin, Netto, & Peneaux, 2017; Sol, Griffin, Bartomeus, & Boyce, 2011).

Urban landscapes can contain a greater number of introduced and non-native species sometimes occurring through deliberate introduction by humans. These species may also fair better in urban environments because many are generalist species, likely to show greater behavioural flexibility than non-generalists. Generalists are likely to show a greater degree of behavioural flexibility because they occupy a wider range of habitats and utilise a wider range of resources (Martin & Fitzgerald, 2005; Williamson & Fitter, 1996). Introduced species that become invasive may offer an interesting model system for understanding how personality variation could be structured by rapid habitat change since it may be possible to monitor these from initial colonisation stages through to establishment. It is expected that high exploring and high risk-taking individuals could lead the colonisation of new areas, with newly colonised populations showing reduced behavioural variation (Sih et al., 2012), although overtime, this possible that variation in individual behaviour could increase relative to the time since urbanisation. Currently it remains unclear if, or how, urbanisation affects the expression of personality variation, however the body of studies on a range of difference species is increasing. Although generalisability may not necessarily be possible, understanding impacts on a range of species is important for understanding the consequences of urban living on wildlife.

1.3 Study species – Eastern grey squirrel (Sciurus carolinensis)

Birds have been the focus of a majority of studies of urban wildlife personality variation (see Chapter 2), with mammals appearing underrepresented. However, several species of mammals occur in urban habitats, with many occurring at high densities in cities compared to rural areas (Baker, Ansell, Dodds, Webber, & Harris, 2003). This may be due to the benefits of increased availability of anthropogenic food sources, and for some species, humans may purposefully offer supplementary feeding. Many mammal species living alongside human populations may also come into conflict with humans if they are perceived negatively, for example where they are considered as pests, associated with damage to property, or linked to zoonotic diseases (Baker et al., 2003; Bateman & Fleming, 2012). In this regard, eastern grey squirrels (hereafter, grey squirrels) can make an interesting study system to consider behavioural variation in a successful urban mammal in the UK. In the UK, grey squirrels are a non-native invasive species introduced in the early 19th century (Middleton, 1930). Since then they have become established across a range of urban and woodland habitats, and are now found in abundance across a a range of habitats that may vary in levels of human disturbance (Bonnington, Gaston, & Evans, 2013). In the UK they are considered an invasive pest, damaging trees and property (Sandro, 2008), and spreading zoonotic disease to native red squirrels, *Sciurus vulgaris* (Rushton et al., 2006), however, they are also considered a popular and charismatic mammal by many members of the public (Dunn, Marzano, Forster, & Gill, 2018), being fed by hand in some urban parks (personal observation). Their popularity with humans and their ability to utilise anthropogenic food resources may be some of the reasons for them appearing to live at higher densities in urban environments compared to woodland (Bonnington et al., 2013). Recent research also suggests that urban habitats could offer grey squirrels a refuge from natural predators, such as the re-introduced pine martin, *Martes martes* (Twining, Montgomery, Price, Kunc, & Tosh, 2020)

For the grey squirrel reproductive life-history traits are influenced by quality and availability of food resources (Thompson, 1977). Squirrels depend heavily on masting tree species as a food source, which show great seasonal and annual fluctuations in mast (Boutin et al., 2006). With these seasonal fluctuations in food resources, the energetic costs of reproduction and obtaining food will vary considerably with season and between years. For example, during autumn there is usually an abundance of food available for only a few months, followed by a period of scarcity during winter(Boutin et al., 2006). Many of the tree species important to grey squirrels in the UK, such as European beech*,* *Fagus sylvatica*, show annual fluctuations in seed production, with weather conditions in the spring determining quantity and quality of resources available for summer and autumn (Hilton & Packham, 2003). For grey squirrels, over-winter survival can depend on the ability to gain enough fat reserves during Autumn, with foraging and feeding activity highest at this time (Gurnell, 1996). To deal with these fluctuations in food availability, grey squirrels cache high energy food items during the autumn when tree mast resources peak, which they then relocate during winter and spring when resources are more scarce (Thompson & Thompson, 1980). So far, there appears to be little research on grey squirrel food resource use in urban environments. It is possible that urban habitats could buffer against the resource fluctuations that tree squirrels face in their native ranges, with urban squirrels benefiting from the food resources provided by direct and indirect feeding by humans (Bonnington et al., 2013). Living alongside humans appears to have these benefits for other squirrel species. Urban dwelling female eastern chipmunks (*Tamias striatus*) have been found to have increased body condition and body fat levels compared to rural chipmunks (Lyons, Mastromonaco, Edwards, & Schulte-Hostedde, 2017), suggesting that suitable food supplies in urban habitats may be plentiful.

Grey squirrels are generally regarded as non-social, although dominance hierarchies can form around food resources. These dominance hierarchies are thought to be based around size, sex and age, with older and larger males tending to dominate (Koprowski, 1996; Pack, Mosby, & Siegel, 1967). There is also some evidence to suggest that around human supplied supplementary feeding they may form dominance hierarchies with heterospecifics (Bonnington, Gaston, & Evans, 2014; Newson, Leech, Hewson, Crick, & Grice, 2010). Grey squirrels have a scramble competition mating system where males compete intensively for females who come into oestrous for only a few days, therefore, for males, aggressive interactions, peak during mating seasons which tend to occur in the UK between January-February and May-June (Thompson, 1977). During other times, tolerance towards the presence of conspecifics may vary according to food availability, with conspecifics representing a potential competition risk while foraging. However, conspecifics can also provide a source of information about patch quality and predation risk (Hopewell & Leaver, 2008; Jayne, Lea, & Leaver, 2015). Although not strictly territorial, individuals show site fidelity, holding home ranges, with males dispersing from natal habitat and females tending to hold home ranges within their natal territory (Koprowski, 1996).

There have been a number of studies utilising tree squirrels (including grey squirrels) as a model species for investigating foraging economics, patch use, and anti-predator behaviour (Hopewell & Leaver, 2008; Jayne et al., 2015; Lilly, Lucore, & Tarvin, 2019; Lima, Valone, & Caraco, 1985; Partan, Fulmer, Gounard, & Redmond, 2010; Wauters, Lurz, & Gurnell, 2000) so much is already known about many of the behavioural strategies squirrels use to manage the balance between foraging and safety, as well as the environmental factors influencing these. For grey squirrels, static habitat cues are used to make assessments about risk, for example grey squirrel perception of predation risk increases with distance for canopy cover (Parker & Nilon, 2008). This is likely to reflect the risk of exposure to terrestrial and aerial predators (Verdolin, 2006). Grey squirrels are sensitive to visual, auditory and olfactory cues of predator presence, and while foraging they show increased alert and vigilance behaviours where these cues are detected (Partan, Larco, & Owens, 2009). Vigilance responses may differ according to risk levels, with grey squirrels able to remain attentive to low level risk during feeding by increasing food handling times and maintaining ‘head up vigilance’, to compensate for some of the costs vigilance incurs to feeding (Makowska & Kramer, 2007). Grey squirrels in urban habitats have been shown to adjust several aspects of anti-predator behaviour in response to human presence, suggesting that part of their success in living alongside humans may be due to the ability to appropriately manage the risks to foraging posed by anthropogenic disturbance. For example, reducing flight initiation distances according to pedestrian behaviour (Bateman & Fleming, 2014), and switching conspecific communication cues according to levels of anthropogenic noise (Partan, Fulmer, Gounard, & Redmond, 2010). As well as reduced fear of humans, urban grey squirrels have also been found to show increased average levels of conspecific aggression, perhaps as a result of living at higher population density (Parker & Nilon, 2008). So far, variation in these behaviours at the individual level have not been studied in urban grey squirrels, although recent studies found that ‘trappability’,the number of times an individual is trapped over a set time, and diversity of traps caught in (used as measures of behavioural risk-taking) was found to be associated with increased gastro-intestinal parasite load (Santicchia et al., 2019).

1.4 Thesis preview

Whilst grey squirrels may now be a common mammal in UK urban habitats, there has been limited research into its behaviour in urban locations. Although, grey squirrels have been reported to show differences in behaviour in urban settings (Parker & Nilon, 2008) it is unclear whether this species demonstrates personality variation, and if the expression of this level variation changes according to levels of urbanisation. Grey squirrels may provide a good model species in terms of investigating how behavioural risk-taking may change in an urban mammal as their relative tolerance to humans and abundance in urban sites may make observational studies of behaviour and behavioural risk-taking fairly accessible. Risk and risk-related behaviour has been proposed as a key element in the structure of personality variation within populations, however empirical studies of this in wild mammals still remains sparse (although see: Boon, Reale, & Boutin, 2008; Boon et al., 2007).

This thesis begins with a systematic review of published empirical studies examining personality variation in urban wildlife **(Chapter 2).** It finds that, whilst differences in average levels of behaviour in relation to risk-related behaviours such as aggression and exploration are reportedly higher in urban wildlife, there are few studies examining if this behaviour shows variation in individual repeatability. In the studies that quantified this level of behavioural variation, few tend to compare across populations that vary in levels of the urban features assumed to influence personality variation. It was also found that few studies used multivariate methods to classify sites by urbanisation levels, which potentially makes it difficult to compare across studies in terms of how differences in urbanisation and human disturbance could shape behavioural variation. Following these findings, the review discusses three potential scenarios affecting the expression of personality variation in urban habitats: firstly, the role of behavioural variation in dispersal and initial colonisation of urban habitats, secondly, the potential for relaxation of resource-acquisition trade-offs in reducing personality variation, and finally, the potential of urban landscapes to contain spatial and temporal variation in risk that could maintain, or increase, the structure of behavioural variation under urbanisation. It then discusses how applying the a landscape of fear (*sensu* Laundré, Hernández, & Ripple, 2010) approach as a framework could aid in making testable predictions about how urban landscapes could impact the structure personality variation.

Following this, the thesis proceeds to use a landscape of fear approach by considering the landscape features that could contribute the perception of risk in foraging urban grey squirrels and examines how these could impact behavioural variation. **Chapter 3** considers if patch use is affected by proximity to urban built features, and if these features influence perception of foraging risk. Pairs of standardized food patches, containing a mix of sand and granulated peanuts, were placed across several sites varying in urbanisation levels. Using methodology from studies of giving-up density (Brown, 1999), food patches were placed in pairs across six sites that varied in squirrel population density, vegetation cover, road and building cover. Each pair consisted of one feeding patch placed under canopy cover close to a mature tree, representing a ‘safe’ patch, and one placed further away in open habitat, representing a ‘risky’ patch. For each patch, distances from roads, buildings and footpaths, and noise levels were measured. Patch use was determined by weighing the quantity of remaining peanuts after foraging, providing a giving-up density (GUD) for each feeding location. It was found that at sites closer to roads and buildings the difference between GUD in safe and risky patches was lower than at sites further away from these features. This suggests that foraging grey squirrels might perceive these locations as ‘safer’. Further, this study provides the novel finding for the effect of noise on GUD in urban wildlife. It found a significant interaction effect between noise variability and distance from roads and buildings, finding that with increased variability in noise levels there was an increased difference in GUD between safe and risky patches. This suggests that, whilst foraging close to human associated habitat features may not represent increased risk alone, noise variability, rather than mean noise levels, represented a source of higher perceived risk, perhaps due to its impact on risk assessment.

With squirrels foraging closer to urban habitat features leaving lower GUDs, it can suggest that these locations are perceived as safer and it could reveal that urban squirrels face different food-safety trade-offs compared to those foraging in rural habitats. Chapters 4 and 5 seek to explore if squirrels using parts of their habitat close to human disturbance vary in behavioural responses to risk, in an attempt to discover if individuals distribute themselves across urban habitats according to their behavioural ‘approaches’ to risk. Using a modified version on an open-field test **Chapter 4** investigates if individual squirrels show variation and repeatability in their behavioural responses to handling and the open-field test. Here we found that average levels of exploration and escape behaviours vary according to site levels of urbanisation. The study also provides the novel finding that these behaviours are repeatable in grey squirrels.

As well as the risk of exposure to human disturbance, many successful urban dwelling species, including grey squirrels, live at higher population densities than in rural sites. This is thought to increase the risk of competition for some species, with grey squirrels found to show increased conspecific aggression in urban locations (Parker & Nilon, 2008). To consider this further, **Chapter 5** tests if squirrel responses to the presence of conspecifics vary according to location within urban habitat. Here we found that behavioural responses to conspecific cues of social risk varied according to location, with squirrels feeding closer to buildings, roads and footpaths showing lower levels of behavioural responses to a cue of conspecific presence. These behaviours varied according to local patch quality and variability in noise levels, suggesting that these features are important for foragers balancing resource-acquisition with competition risk in urban locations.

Finally, **Chapter 6** provides a general discussion of the findings from each chapter and attempts to integrate this into the current literature on patch use and behavioural variation in responses to risk in urban wildlife. It discusses how the new findings from this thesis may help to develop methodology and questions for further research.

Chapter 2: Ecology of fear and personality variation under urbanisation

2.1 Introduction.

Currently over half of the world's human population are thought to be living in cities, and by 2030 this number is predicted to increase to over 60% as an increasing number of human societies move to industrial economies (Cohen, 2003). Urbanisation represents a particularly fast-paced form of habitat change generally associated with decrease in biodiversity (McKinney, 2006). However, whilst habitat destruction and conditions produced by urbanisation cause many species to decline, several species seem to be thriving under urban conditions, perhaps taking advantage of these novel conditions, including reduced predator diversity, altered competition regimes, and increased anthropogenic food resources (Sol et al., 2013).

Studies attempting to understand the traits allowing some species to persist, and others to fail, have found that urban wildlife differs from its rural counterparts in behaviour, morphology, and physiology. Some of the most notable and immediate differences observed between urban and rural wildlife are the behavioural responses to human disturbance and activity (Ditchkoff, Saalfeld, & Gibson, 2006). Behaviour is the first line of response an organism has to its environment, and is likely to adjust before many other phenotypic traits. Therefore monitoring behavioural responses can offer early insights into the ecological implications, and the possible evolutionary consequences, of fast-paced environmental changes such as urbanisation (West-Eberhard, 1989). Although, traditionally, behavioural responses have been thought of as being highly flexible, thought to allow individuals to quickly optimise their responses according to context, more recent research into behaviour at the individual level shows that individuals can behave consistently across time and context suggesting that the degree of behavioural flexibility is often bound by the individual. Across the literature this is referred to as personality variation (Dall, Houston, & McNamara, 2004), behavioural syndromes (Sih, Bell, & Johnson, 2004), coping style (Koolhaas, 2008) and temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), and has now been described for a diverse and wide variety of taxa. Such personality variation, which combines inter-individual differences with intra-individual consistency in behaviour within animal populations, has been found to be heritable (van Oers & Mueller, 2010), have consequences for individual fitness (Smith & Blumstein, 2008) and is likely to be maintained through natural (Adriaenssens & Johnsson, 2013) and sexual selection (Wiebke Schuett, Tregenza, & Dall, 2010), making the investigation of personality variation an increasingly popular area of research within behavioural ecology.

Due to the expected role of behavioural flexibility in the ability to adjust quickly to varying environmental conditions, urban ecologists and behavioural ecologists are progressively turning attention to the study of personality variation under human-induced rapid environment change (HIREC) and urbanisation (Sih, 2013). These studies are beginning to reveal that wildlife in urban environments might show differences in the expression of personality variation (the expression of the degree of behavioural flexibility) within and between populations inhabiting varying levels of urbanisation, particularly regarding risk-related behaviours, such as exploration and aggression (for examples see: Atwell et al., 2012; Hardman & Dalesman, 2018; Thompson, Evans, Parsons, & Morand-Ferron, 2018). The purpose behind many of these studies is to understand how urbanisation and human induced habitat change may shape animal behaviour and to inform predictions about the potential evolutionary consequences of urbanisation (Sih, 2013). As these studies begin to increase, it is becoming more apparent that there are contradictory and fragmented findings as to how and why urbanisation might shape consistent individual differences in behaviour (see appendix: 'Summary of studies'). There may be numerous reasons for this, not least because of the difficulty monitoring personality variation in wild populations, furthermore, some of the frequently used methods used to assess and interpret individual behaviour and 'animal personality' are being called into question despite cautionary advice from several discussion papers (Carter et al., 2013; Dall & Griffith, 2014; Montiglio, Sih, Mathot, Wolf, & Dingemanse, 2015; Perals, Griffin, Bartomeus, & Sol, 2017). An additional complication in urban studies, is that there are many various ways of defining levels of urbanisation in a particular habitat (Seress, Lipovits, Bókony, & Czúni, 2014). In studies of behaviour in urban wildlife there seems a tendency to compare behaviour from a rural population with urban ones based on often broad assumptions about what constitutes as an urban habitat. Researchers are, broadly, quantifying urban habitats in one dimension, rather than considering possible features of varying levels of urbanisation that might be selecting for differences in in the degree of personality variation. A possible solution to this is to measure urbanisation and human disturbance on microhabitat scales, as well as macrohabitat scales, and for studies to report levels of urbanisation and human disturbance in a way that allows for researchers to make comparisons across studies. One of the frameworks offering potential for insights into the way individuals differ in behavioural responses and use of their habitat is the 'landscape of fear' approach (Bleicher, 2017; Laundré et al., 2010). This approach involves quantifying an animal use of its habitat based on is perception of risk, or fear, assuming that animals attempt to avoid parts of a habitat where the perceived risks are higher than the perceived benefits. Foraging and feeding behaviour is usually the focus of these studies, for example the use of giving up density (the amount of food remaining in a standardised food patch after a forager has ceased feeding (Brown, 1988)). These methods of measuring habitat use by foraging animals can be used to create maps of how a species uses its landscape, in particular, habitat features can be compared to investigate if they offer static cues of risk. These approaches are usually employed to investigate the landscape of fear for a species or population, however, it is possible that an individual-based landscape of fear approach can work alongside the measurement of personality variation to provide greater understanding of the features within landscapes that could drive the expression of consistent individual behavioural variation, or at least address whether individuals with certain behavioural 'types' could use habitats differently.

Although there have been a number of discussion papers focusing on the potential for the study of personality variation to provide insights into the influence of human disturbance and urbanisation (Martin & Réale, 2008; Réale et al., 2007; Smith & Blumstein, 2008), this review is concerned specifically with the role of the ecology of fear in the structure of consistent behavioural differences among individuals within populations of the same species. Here, the key features linking the ecology of fear with personality variation are discussed, with the suggestion that these can enhance understanding of the expression of this class of behavioural variation under urbanisation and be practically incorporated into field studies of free-ranging wildlife.

2.2 Behavioural differences in urban wildlife.

Humans are highly effective niche constructers, and this is particularly evident in urban areas where the environment has been extensively modified to meet human needs, creating altered and novel conditions for many other species (Fletcher, Orrock, & Robertson, 2012). Urban habitats can generally be defined as areas with dense human population, high energy consumption and dominated by built environment such as roads and building cover (Gehrt, 2010). Human activity and urbanisation cause changes in the biotic and abiotic features of habitat, including an increased light, noise and air pollution, habitat fragmentation, and an increase of non-native flora and fauna, generally resulting in a loss of biodiversity (Garroway & Sheldon, 2013; Pickett et al., 2011; Smith & Bernatchez, 2008). As a result, differences in behaviour and physiology have been observed in urban wildlife in comparison to rural habitats. These differences vary between species, urban areas and across urbanisation gradients; however, typical differences observed in urban wildlife include altered life-history, altered fear responses and altered behavioural patterns (Ditchkoff et al., 2006).

A few species dominate the urban landscape, these have generally been regarded as behaviourally flexible and innovative, allowing them to monopolise this new urban ecological niche , out competing those less responsive to rapid habit change and disturbance (Ducatez, Clavel, & Lefebvre, 2015; Sol et al., 2011, 2013). A few species thrive under in urban conditions, becoming dependant on anthropogenic resources, undergoing synurbization – the process of becoming associated with, and dependent on, urban habitats (Francis & Chadwick, 2012). Many species undergoing synurbization appear to display similar trends in behavioural characteristics. These include reduced anti-predator responses, decreased home range size, increased population density and increased aggression. These correlated traits or ‘symptoms’ of synurbization have been coined the ‘Urban Wildlife Syndrome’ (Parker & Nilon, 2008). Although ‘Urban Wildlife Syndrome’ was used to refer to the general trends in average behaviour observed in urban wildlife, the study of behavioural consistency in individuals over time and context (animal personality variation) is revealing that there may be similar behavioural tendencies at the individual level. In a review of 29 studies comparing the behaviour of urban individuals to those in rural populations of the same species, it was found that 27 of these studies reported significant differences in average levels of behaviour, with urban wildlife having higher levels of aggression, boldness, and reduced escape behaviour (Miranda et al., 2013). In this review Miranda *et al* (2013) found that individual repeatability in behaviour was assessed in only two out of these 27 studies. Although these studies found that these behavioural characteristics could be liked to individual behavioural consistency, it is unclear if this represents a difference in the level of personality variation contained in urban populations compared to rural ones.

Behavioural adjustments, flexibility or personality?

Coping with urban habitats is likely to involve behavioural adjustments, as for many species urban environments are expected to differ from ancestral habitats. There are likely to be a number of routes and mechanisms involved in adjusting to urbanisation, with one of the key issues being how organisms behaviourally adjust to novel conditions and situations(Sih, 2013). Generalist species (those that occupy a broad range of habitats) are thought to cope better in urban environments because the behavioural responses required to respond to novel conditions may involve adjustments that are already available within their behavioural range, for example, adjusting life history events to ‘optimal’ environmental conditions, such as temperature(Sih, 2013; Sol et al., 2013).

With behavioural flexibility potentially being a key factor in responding to novel or varying conditions, such as those found in urban environments, the study of personality variation has caught the interest of several authors examining the role of behavioural flexibility in coping with human induced habitat change. This is because personality variation represents the limits and the breadth of behavioural flexibility within individuals and populations, and through examining ‘personality’ in this way it may be possible to examine some of the ways urban environments select for certain species or individuals(Miranda et al., 2013). Key to the definition of ‘personality’ variation is that 1) an individual’s behavioural responses are, to some extent, repeatable over different contexts 2) and that these behavioural responses are repeatable, or correlated, over time(Bell, 2005; Carter et al., 2013). This means that for a particular behaviour to be defined as ‘personality’ it should remain relatively stable over an animal’s life-span and development, or during different states and conditions. The less flexible the behaviour in question, the higher the levels of repeatability.

To consider to what extent investigations of animal personality in urban environments have revealed the structure of this level of variation under different levels of urbanisation, here I review empirical studies that have measured and compared repeatability in behaviours between urban and rural populations.

2.3 Review of published studies:

Building on the review conducted Miranda *et al* (2013), here the assessment of personality variation in urban wildlife is reviewed seeking to address the following: 1) What consistent individual behavioural traits have been examined in urban wildlife and what, if anything, do they reveal about the pressures urban animals face? 2) What measures of urbanisation have been used in the study of urban animal personality variation? 3) How have additional measures of an animal's habitat been quantified in these studies?

Following the literature search and evaluation protocol outlined by PRIZMA: the preferred reporting items for systematic reviews and meta-analyses (Moher, Liberati, Tetzlaff, Altman, & Group, 2009) ISI Web of Science was used to search for published empirical studies on animal personality in urban habitats using the search terms *individual differences* behaviour*urban, Animal Personality * Urban, * Urbanisation (last search conducted May 10th 2019).* Each study was assessed on three criteria 1) studies were primary research, 2) measures of behavioural consistency were recorded on one or more time point for individuals and analysed for repeatability, 3) individuals were from wild caught populations occurring in both urban and rural habitats. Initial search yielded 278 studies, however after application of the three criteria, 15 studies remained (see appendix summary of studies).

A majority of studies were conducted on birds (N = 8). Insects were represented in 33.3% (N =5) of studies, and reptiles were tested in 13.3% (N = 2). There were no studies on urban mammals that met all the three criteria. 'Boldness', usually representing risk-taking under a predation like event, appeared to be the behavioural trait most tested in these studies (N = 9), this was typically measured using flight initiation distance (FID) to approaching human and/or response to predator cues. Behaviours defined as ‘Activity’ and ‘exploration’ within a novel arena assay were assessed in seven of the studies reviewed, and five studies considered individual aggression within the context of conspecific contest cues or responses to predator cues. The least investigated behavioural trait thought to be associated with success in urban environments was ‘neophobia/neophilia’, which as examined in two studies. Here neophobia/neophilia was measured using latency to approach novel food or object.

Definitions of urbanisation varied across studies, with seemingly four main approaches to defining the level of urbanisation at a site or study population 1) Categorical labelling of sites into urban and rural based on whether site was located in a city or town, (N = 6 studies) 2) human population density or building density at site (N = 1)), 3) Euclidean distance from city centre (N= 5), and 4) multivariate methods used to compute an urbanisation index, for example, using principle component analysis (N = 3).

2.4 Significance of consistent individual differences in risk-related behaviour for urban wildlife.

Although there is much ongoing debate surrounding the factors maintaining the existence of consistent individual differences in behaviour, central to many of the explanatory models of animal personality variation is the idea that it reflects differences in the way individuals behaviourally manage risks relative to individual differences in life history characteristics, social environment and/or ecological conditions (Adriaenssens & Johnsson, 2013; Dall et al., 2012; Morgan David & Dall, 2016b; Luttbeg & Sih, 2010; Réale et al., 2007). For example, individual variation in life-history strategies can explain consistent individual differences through the differing trade-offs individuals face in relation to future and current fitness (Hall et al., 2015; Quinn, Cole, Bates, Payne, & Cresswell, 2012; Réale et al., 2010). Individuals with low-residual reproductive value are thought to benefit from consistent aggressive and bold behaviours, that although are ‘risky’ as they incur higher mortality costs, may be beneficial in order to acquire resources that maximise current, rather than future, reproduction. On the other hand, individuals investing in future reproduction are likely to prioritise safety (long term survival), adopting a risk-adverse behavioural strategy (Réale et al., 2010; Wolf, van Doorn, et al., 2007). Thus, consistent individual behavioural variation should be underpinned by individual differences in intrinsic state (physiological and/or morphological), for example, age, body-condition, body size and metabolic rate, and extrinsic state such as the social and environmental conditions in which the individual inhabits, for example, local population density, predation pressure, and the 'traits' of conspecifics (Dall et al., 2004; Montiglio et al., 2015). The reasoning behind the relationship between individual variation in behaviour and state is that state affects the costs and benefits of a behaviour. For example, in contests over territory, individuals who are in better condition have higher resource holding potential, so may be more aggressive and bold, whereas individuals in lower condition should be less aggressive because the energetic cost and mortality risks of fighting may outweigh the rewards of gaining access to a defended resource(Arvidsson & Matthysen, 2016; Biro, Post, & Parkinson, 2003; Luttbeg & Sih, 2010; Réale et al., 2007).

In populations of wild organisms, the expression of this personality variation is likely to vary due to differences in selection pressures, such as predation level (Magnhagen et al, 2012) and resource availability (Boon, Réale, & Boutin, 2007; Dingemanse et al., 2004). Furthermore, behavioural variation among individuals has important implications at the population level by influencing the dispersal, distribution and demographics of a population (Dall et al., 2012; Sih et al., 2012). The stability of consistent individual behavioural variation expressed within a population reflects limits on the degree of behavioural flexibility by at least some individuals, so may constrain population level responses to rapid or novel changes in the environment (Bolnick et al., 2011). This is likely to be of significance in populations undergoing human induced rapid habitat change (Sih, 2013). Research into the relationship between personality variation and population stability and rapid habitat change is a much-needed area of investigation, as it could offer an early insight into how rapid habitat change could impact animal behaviour in the longer term. Personality variation studies looking at individual differences in habitat use suggest behavioural consistency could represent individual behavioural specialisms in resource use (Bonnot et al., 2014; Rockwell, Gabriel, & Black, 2012; Wolf & Weissing, 2012). It is thought that these differences within a population help to reduce competition between individuals, ultimately leading to a population that could have higher productivity through more efficient use of resources (Sih et al., 2012) . Furthermore, several empirical studies have demonstrated that individual behavioural consistency is moderately heritable and stable over an individual’s lifetime, suggesting that genetic variation is a component of animal personality variation. Much like genetic diversity, the maintenance of behavioural diversity may reduce the likelihood of extinction where populations undergo rapid changes in environmental conditions, as such, there is concern that urbanisation and rapid human-induced habitat change can lead to novel directional selection pressures that reduce both behavioural and genetic diversity (Bolnick et al., 2003; Garroway & Sheldon, 2013; Lowry et al., 2013).

Urbanisation is expected to effect individual differences in behavioural consistencies in several ways: Individuals first colonising novel habitats are thought to show greater behavioural flexibility, as well as higher average levels of boldness and exploration tendencies (Atwell et al., 2012; Canestrelli, Bisconti, & Carere, 2015). If higher levels of boldness and exploration represent individuals that are consistent in these behaviours. newly colonised habitats could become a homogenous population of behavioural ‘types’, with the level of personality variation in these behaviours being lower than in established populations. With increased exposure to human activity and, perhaps, relaxed predation levels, the expression of these behavioural traits could increase further, therefore, the mean level for certain behavioural traits such as boldness and exploration will be higher in urban populations than that of ancestral populations. However, it is likely that within urban habitats there could be differing costs and benefits of behavioural consistency meaning that the degree of personality variation could change over time since a population becomes urbanised, and according to the risk-related trade-offs faced by individuals within that habitat. Where costs and benefits between behavioural ‘types’ vary, we could expect to see repeatability of behaviours within individuals and increased levels of variation in behavioural consistency between individuals in urban environments. On the other hand, repeatability and correlations between behavioural traits could weaken if resource acquisition trade-offs are relaxed, for example, through lower predation rates, greater stability of food availability via anthropogenic food provisions (Bókony, Kulcsár, Tóth, & Liker, 2012; Dall & Griffith, 2014; ; Hasegawa, Ligon, Giraudeau, Watanabe, & McGraw, 2014; Senar, Conroy, Quesada, & Mateos-Gonzalez, 2014). As such, there can be three main expectations regarding the expression of personality variation in urban environments. These are unlikely to represent all possible outcomes, nor are they mutually exclusive, however they may offer a simplified approach to the initial understanding of why measures of local habitat and ecological factors, as experienced by individuals, may be needed to further unravel the relevance of individual differences in behavioural flexibility within urban environments, and the differences in personality variation under urbanisation:

2.4.1) Scenario one: Risk tolerance and behavioural flexibility facilitates dispersal into urban habitat.

Behavioural flexibility (lower levels of personality variation), particularly in relation to fear responses, may facilitate species, or populations, ability to expand their range, exploit novel resources, and tolerate novel and unpredictable habitats (Bonier, Martin, & Wingfield, 2007; Martin & Fitzgerald, 2005). It is still unclear to what extent urban environments do represent greater unpredictability, novelty or uncertainly, furthermore it is likely this effect will vary according to species (Griffin et al., 2017). For example, in some cases, urban habitats may provide a buffer from seasonal fluctuations in food availability through increased stability of anthropogenic food resources (Newsome, Garbe, Wilson, & Gehrt, 2015; Uchida, Suzuki, Shimamoto, Yanagawa, & Koizumi, 2015). However, these food resources are likely to be novel and coupled with increased human disturbance, representing greater levels of complexity and risk for some species (Lowry et al., 2013; Tryjanowski et al., 2016). Heterogenous (complex) habitats with greater variance in spatial and temporal structure and composition (Kovalenko, Thomaz, & Warfe, 2012) are thought to select for a greater degree of behavioural flexibility (Delarue, Kerr, & Rymer, 2015), therefore we might expect to find increased behavioural flexibility in urban populations where urbanisation represents greater habitat complexity for a particular species. Studies in some bird species have found that urbanisation does lead to lower repeatability and weaker associations between behaviours that are usually found to represent behavioural syndromes (Bókony et al., 2012; Hardman & Dalesman, 2018; Scales, Hyman, & Hughes, 2011), suggesting that, in some cases, individual responses in urban inhabitants are relatively more flexible.

The effects of urbanisation on the expression of behavioural flexibility may also differ over time since a population has become urbanised. Bolder and more ‘fear-tolerant’ individuals are generally thought to be the first to first colonise new habitats, including urban spaces (Moller, 2010; Sol, Lapiedra, & González-Lagos, 2013). Studies across taxa have found that active and more exploratory individuals tend to disperse further than more risk-averse individuals (Canestrelli et al., 2015; Sih et al., 2012). Furthermore, a number of personality variation studies have linked individual consistency in boldness to individual variation in physiological stress responses (Bonnot et al., 2015; Martin & Réale, 2008; Minias, 2015) with the implication that these bolder behavioural ‘types’ may less responsive to environmental stressors, and habituate more rapidly to human disturbance (Rodríguez-Prieto, Martín, & Fernández-Juricic, 2010; Viblanc, Smith, Gineste, & Groscolas, 2012). Where bolder and less risk adverse individuals have been the first colonisers, we may expect early urbanised populations to contain these qualities, perhaps showing lower levels of personality variation in regard to these behaviours. As time passes, selection for or against risk-tolerance and behavioural consistency may vary according to the qualities of an urban habitat, leading to varying outcomes for different populations, potentially resulting in the scenarios outlined in two or three.

2.4.2) Scenario two: Relaxed resource acquisition trade-offs in urban environments reduce fear, perception of risk, and the levels of behavioural consistency across contexts.

It is has been generally thought that, for most species, urban habitats contain reduced predation pressures due to reduction in predator diversity and density (Fischer et al., 2012). Many urban populations may also benefit from resource predictability through supplementary anthropogenic food sources (Anderies, Katti, & Shochat, 2007; Stears & Shrader, 2015). This suggests urban populations, in some cases, are buffered from the pressures of predation and starvation – key components of behavioural trade-offs under risk that are thought to maintain individual behavioural consistency (Luttbeg & Sih, 2010; Quinn et al., 2012).

Where predation pressure is decreased, we might expect that populations within urban habitats will contain a higher proportion of risk-taking behaviours, such as exploration, as the mortality risks associated with predation risk exposure are reduced, and the benefits, such as access to resources (Short & Petren, 2008), may be enhanced. Benefiting from the reduced predation pressures, successful urban species often live at higher population density than their rural counterparts (Prange, Gehrt, & Wiggers, 2003), therefore, at the individual level there may be increased competition, resulting in competitive advantages for bolder individuals who can gain dominance over resources. In many studies, risk-related behaviours such as exploration and aggression, correlate together to form a 'boldness syndrome'(Carter et al., 2013; David & Dall, 2016; Dingemanse & Réale, 2005), however, with relaxed predation pressures these behavioural associations may breakdown in favour of more flexible context-dependent behaviours (Bókony et al., 2012; Kralj-Fišer, Hebets, & Kuntner, 2017; Sih et al., 2012). Correlations between behaviours such as aggression and exploration which make up behavioural syndromes are likely to represent differences in the balance between competition, predation risk and resource acquisition, therefore the expression of the relationships between these are likely to give an indication of the important trade-offs occurring within a population, as well as how constrained behavioural responses are (Bell, 2005). Although, on average, urban populations are bolder, several studies have found that the boldness syndrome breaks down under conditions of low predation pressure and high population density in urban populations (Kralj-Fišer et al., 2017). A possible explanation for this is that under high population density there will be increased costs of aggression and sociality, for example, injury and mortality risks during aggressive encounters (Duckworth, 2006) or increased exposure to parasites and disease during social encounters (Santicchia et al., 2019), therefore selecting for exploratory, but less aggressive/social behaviours. However, high population density may also drive increased personality variation as the payoffs for stable behavioural strategies are likely to be frequency dependant (Maynard-Smith, 1976). This is likely to vary according to the social system of a species, for example, those with stable social groups may contain greater personality variation where individuals may specialise in behavioural strategies (Dall & Griffith, 2014; Dall et al., 2004; Wolf & Weissing, 2012)

Whilst predation rates and predator diversity may be lower in urban habitats, human disturbance is usually high. To some organisms human activity and disturbance can be perceived as a predation risk (Beale & Monaghan, 2004). Managing predation risk can incur high energetic costs through missed feeding opportunities and increased anti-predator activities such as vigilance or fleeing (Frid & Dill, 2002; Houston, Prosser, & Sans, 2012; Petrelli, Levenhagen, Wardle, Barber, & Francis, 2017; Siemers & Schaub, 2011). Some animals are thought to reduce the costs of disturbance by shifting behavioural routines to periods of low human activity (Ciuti et al., 2012; Gaynor, Hojnowski, Carter, & Brashares, 2018). However, these adjustments in behaviour and habitat use can be costly in themselves as they potentially reduce opportunities for encountering prey/food or mates (Frid & Dill, 2002). Therefore, reduced fear responses and tolerance to human disturbance are thought to be an important behavioural predictors of a species ability to successfully colonise in urban environments (Bonier, Martin, & Wingfield, 2007; Moller, 2010). As a consequence many urban populations, on average, appear to be more tolerant of human disturbance and activity than rural ones (Engelhardt & Weladji, 2011; Lin et al., 2012; Valcarcel & Fernández-Juricic, 2009). Individuals with greater behaviourally flexibility toward novel non-threatening disturbance, or those that are less sensitive to human disturbance are likely to have reduced disturbance costs, so may fair better under urbanisation.

2.4.3) Scenario three: Urban environments show spatial and temporal variation in risk (landscape of fear) that may maintain consistent individual differences in behaviour.

Like other habitats, urban landscapes are unlikely to be homogenous regarding the structure of resources and risk, showing spatial and temporal variation in resource distribution, predation risk and human disturbance. Individuals distribute themselves and use their habitat in a non-random way, for example, there are often differences in habitat distribution by sex and age classes, which may also include distribution by behavioural differences (Brown, 2014; Martina Carrete & Tella, 2017; Morosinotto, Thomson, & Korpimäki, 2010). In a study of urban dwelling burrowing owls *(Athene cunicularia),* individuals displayed repeatability in flight initiation distance (FID) to human approach. Individuals with consistently short FIDs tended to hold territories closer to areas of high human disturbance (Carrete & Tella, 2010). As FIDs were shown to be consistent within individuals, and vary significantly between individuals, it was argued that this reduced fear response towards humans may not simply be a result of habituation, but it may be due to individuals holding territories matching individual differences in tolerance to human disturbance.

Different areas of the urban landscape may offer varying risks and benefits for individuals with different phenotypes (including behavioural phenotypes). For example, urban habitats may contain aggregated food resources, either by supplementary feeding or by proximity to human food waste, such as landfill sites (Lowry et al., 2013). Here individuals can benefit from consistent and predictable food availability, however, these sites may contain a higher population density and attract a higher number of other species, including predators, increasing the potential for conflict, competition and increased predator exposure (Lowry et al., 2013). As such, we might expect to find individuals with behaviours related to higher resource holding potential, such as dominance and aggression, to occupy these areas. In contrast, at the edge of urban habitats food resources may be less predictable and contain increased predator diversity (Donovan, Jones, Annand, & Thompson, 1997). Here we may expect more risk-averse individuals to benefit from reduced population density and competition, whilst experiencing reduced vulnerability to predation, through increased predator avoidance behaviours and as such, reduced mortality costs to their 'bolder' counterparts.

Empirical research linking animal behavioural consistency with habitat selection is still sparse, despite the calls from several theory driven papers (Adriaenssens & Johnsson, 2013; Dall et al., 2012; Dall & Griffith, 2014; Dingemanse & Réale, 2005; Wolf & Weissing, 2012). However, some studies have demonstrated that consistent individual behavioural variation is reflected in habitat use and is likely to represent behavioural risk-management strategies at the individual level (Bonnot et al., 2015). A widely applied concept linking landscape ecology and behavioural responses to risk is the 'Landscape of Fear' (Laundré et al., 2010). In the landscape of fear, habitat use by populations and individuals is affected by an organisms perceived level of risk, rather than the actual predation rate. Human disturbance has been found to contribute to the landscape of fear for wildlife, suggesting that anthropogenic activity can increase perceived predation risk (Ciuti et al., 2012; French, González-Suárez, Young, Durham, & Gerber, 2011; Gaynor et al., 2018; Stillfried et al., 2017). A few researchers have begun to apply the landscape of fear concept to the study of individual behavioural differences, and are revealing that perceived risk varies for individuals and is likely to represent differences in consistent individual behavioural variation (Bonnot et al., 2015; Mella, Ward, Banks, & McArthur, 2015; Stillfried et al., 2017; Van Dongen, Robinson, Weston, Mulder, & Guay, 2015). The landscape of fear concept offers several practical methods for researchers to record and quantify risk across habitats, as it is perceived by animals. Incorporating these into empirical research designs for investigating individual differences in behavioural consistency within populations could provide useful insight into the selection pressures faced for wildlife under urbanisation.

Table 2.1: Behaviour examined in urban animal 'personality' studies:

The core focus of many studies into consistent individual behavioural variation are risk-related behaviours: boldness, exploration, aggression, and response to novelty. These are all labels of behaviour pertaining to the degree of risk exposure an individual may be willing to take to acquire resources. These behaviours are not necessarily mutually exclusive, however, often they are discussed under these sub-headings. It is also worth noting that the way these behaviours are assessed, defined, and measured can vary across studies despite the use of the same behavioural label.

Behaviour	Predicted relevance in urban wildlife	Predicted effect on personality variation	References
'Boldness'/general risk-taking	Boldness is used as a general term to describe behaviours, or suites of behaviours, that reflect a willingness to take risks, usually in a novel context, for example activity in a novel enclosure or the latency to examine novel environment. Research into boldness in urban animals has linked individual variation in behaviour with individual variation in physiological stress responses. With those individuals liking close to humans having reduced stress responses.	1)Founding populations could contain reduced personality variation in 'bold' behaviours, for example, consisting of a homogenous population of high exploring individuals. 2) As urban populations establish there may be increased variation for boldness, for example, where bold behaviour infers high mortality costs whilst also providing access to high value resources. Individuals may distribute themselves according to risk-taking, with less risk adverse individuals	(Atwell et al., 2012; Carrete & Tella, 2010; Carrete & Tella, 2013)

		living closer to sites of human disturbance.	
Aggression	Individual variation in aggression is thought to benefit individual territory holding ability and ability to dominate resources. Aggression is thought to increase in urban wildlife due to resource aggregation and increased population density/ increased competition. Aggressive behaviours are usually correlated with other risk related behaviours such as increased activity, forming a boldness syndrome, however, of the limited urban personally studies examining aggression in urban wildlife, it appears that this boldness-activity-aggression syndrome breaks down under urbanisation, perhaps due to the costs associated with contests under high population density.	Urban habitats may lead to reduced variation in aggression, where resource availability is high reducing competition. However, where population density is high and competition for resources is high there may be increased personality variation for aggression through the emergence of dominance hierarchies.	(Evans, Boudreau, & Hyman, 2010; Hardman & Dalesman, 2018; Kralj-Fišer et al., 2017; Lapiedra, Chejanovski, & Kolbe, 2017; Scales, Hyman, & Hughes, 2013)
Exploration/Activity	Thought to be important in dispersal and early stages of colonising urban habitats and therefore the first behavioural 'filter'. Exploration can be regarded as information-seeking behaviour, for example, providing information on the availability of key fitness-enhancing resources, such as food and mates. It is usually quantified through an individual's movement within a novel arena, usually an open-field test. Individuals are expected to explore this environment on a slow-fast continuum, with faster explorers spending more time moving throughout an	Early stages of urbanisation may lead to homogenisation of exportation strategies, where high explorers colonise these habitats first. Fast explorers may benefit through faster information gathering about novel environments. However, human disturbance and novel resources could lead to increased personality variation where exploration incurs high mortality costs. Habitats high	(Halpin & Johnson, 2014; Kaiser, Merckx, & Dyck, 2018; Moule, Michelangeli, Thompson, & Chapple, 2015; Prasher, Thompson, Evans, El-nachef, & Bonier, 2019; Schuett et al., 2018; Thompson et al., 2018; Tüzün, Müller, Koch, & Stoks, 2017)

	enclosure and investigating unfamiliar objects, in comparison to slower explorers. Urban wildlife is predicted to benefit from ‘fast’ exploration tendencies. It is assumed that fast exploring individuals can locate resources quickly, and therefore monopolise novel resources. Although fast exploration can be a high reward strategy, it also carries high risk, for example increased exposure to predation and competitive interactions, and active exploration can have high energetic cost.	in fragmentation, for example containing more roads, may cause reduced variation in behaviours associated with risk-taking during dispersal. Individuals more willing to disperse over roads and open spaces may leave behind a population overrepresented by less exploratory individuals.	
Neophobia/Neophillia	Referring to responses to novelty and usually measured by behavioural responses to novel objects and novel food. Often it is predicted that animals in urban environments will have reduced neophobic responses due to the abundance of novel resources. However, some studies have shown that neophobia is higher in urban dwelling wildlife. This might be related to resource stability where there is continuous supply of food available, yet potentially an increase in risk from several anthropogenic factors, including chemical pollutants and poisons. It is possible that were information about food supply becomes less valuable, attraction to novelty decreases, and combined with increased risks (e.g. from poison, pollution) neophobia increases.	Colonising populations may show reduced variation in neophobia, however, novel resources are likely to involve both high costs and high reward, Over time this may increase personality variation for this trait. However, for species highly persecuted by humans, such as those that may be trapped and poisoned, we may find that variation is reduced as costs of neophilla become too high.	(Audet, Ducatez, & Lefebvre, 2015; Bókony et al., 2012; Prasher et al., 2019)

2.5 Using an individual ‘landscape of fear’ approach to understand costs and benefits of personality variation under urbanisation.

Some of the most notable features of urban environments are the increased level of human presence and disturbance from anthropogenic activities; such as road traffic, noise, and novel predators in the form of domestic pets (Frid & Dill, 2002; Gaynor, Brown, Middleton, Power, & Brashares, 2019; Gaynor et al., 2018). For many species, exposure to human activity and human related disturbances are thought to have similar energetic costs to that of indirect predation (Frid & Dill, 2002). For example, much like the threat of predation, it increases time invested towards vigilance and avoidance strategies, reducing time invested in fitness-enhancing opportunities such as feeding and mating (Brown, 1999; Houston et al., 2012). In studies of wildlife in rural habitats, animals demonstrate similar responses to human activity as prey under high predation stress, suggesting that human disturbance is analogous to predation risk (Beale & Monaghan, 2004; Ciuti et al., 2012). Furthermore, many of the behavioural adjustments found in animals inhabiting high-predation environments are also observed in urban wildlife, such as shifts in habitat use, altered foraging and activity patterns and disruptions to growth and reproduction (Ditchkoff et al., 2006), further suggesting that anthropogenic activity can be perceived as source of risk or predation pressure.

Capacity to habituate to human disturbance is often cited as quality of successful urban species (Steyaert et al., 2014; Viblanc, Smith, Gineste, & Groscolas, 2012), however it is unlikely to offer a full explanation as to why some populations are more successful than others under these conditions. Habituation requires stimuli to be predictable and repeatable (Rankin et al., 2009) which may not necessarily be the case with many forms of human disturbance. Furthermore, habituation to predator like cues could be costly, particularly were cues of predation risk could be novel, unreliable, or unpredictable. Some species are likely to be quicker to habituate, or faster to learn about novel predators than others(Moller, 2010; Moller, Grim, Ibanez-

Alamo, Marko, & Tryjanowski, 2013). These species tend to be generalists, having an evolutionary history of occupying diverse habitats, and as a result, tend to display a greater degree of flexible behavioural responses. These species are usually found in higher numbers in urban habitats (Moller, 2010). Studies of flight initiation distances (FIDs) reveal that more generalist species have shorted FIDs in response to human disturbance compared to specialists, perhaps due to their ability to rapidly learn, or flexibly respond to novel or diverse predation risks (Martina, Carrete & Tella, 2010; Petrelli et al., 2017; Uchida, Suzuki, Shimamoto, Yanagawa, & Koizumi, 2015). However, many of the studies suggesting habituation tend to consider population average response levels (Martina, Carrete & Tella, 2011), rather than individual responses. Research into individual consistency in FIDs have not found support for habituation as primary mechanism, rather, they suggest individuals with reduced fear of humans are more likely to colonise urban habitats and inhabitant areas of high disturbance (Carrete & Tella, 2010). As such, the expression of personality variation is likely to depend on the variation in human disturbance levels and types of disturbance experienced by a population. For example, under high and consistent levels of human disturbance personality variation may be reduced as only the individuals who are ‘bold’ in the face of disturbance may persist.

Levels of human disturbance and activity within the urban environment is likely vary across space and time. This may mean that animals living in these habitats are exposed to temporal and spatial variation in disturbance and risk. Risk levels, both actual and perceived, are likely to vary according to individual differences such as sex and state and is likely to include among-individual differences in behavioural consistency (Luttbeg & Sih, 2010; Stankowich & Blumstein, 2005; Wheeler & Hik, 2014). Fear generated by the perception of risk is likely to allow organisms to allocate costs to their day-to-day activities that have potential to incur mortality risks, therefore, this perceived risk shapes the allocation of animal activities across a habitat (Brown, 1988; Gaynor et al., 2019). In field studies of anti-predator behaviour, behavioural management of risk has been quantified in a variety of ways, such as vigilance behaviour, foraging and resource exploitation, and activity budgets (Bergvall, Schäpers, Kjellander, & Weiss, 2011; Lamanna & Martin, 2016; Makowska & Kramer, 2007; R. a. Mccleery, 2009). Few researchers incorporate these into designs investigating personality variation, however, this approach may be particularly insightful when monitoring behaviours in novel and rapidly changing habitats, such as urban environments.

The ‘landscape of fear’ concept (Laundré et al., 2010) provides a number of ways to measure the ecology of fear - the food-safety trade-offs animals make (Brown, 1999). With feeding and avoiding mortality risk being key determinants of individual fitness, incorporating individual differences in perceived ‘risk landscape’ can help provide information on the likely key trade-offs being made by individuals living at different levels of human disturbance and urbanisation. Free-ranging individuals are likely to experience a wide range of environmental conditions, with these varying over time and space, therefore quantifying all of these can represent a huge challenge. Methods traditionally used in ecology of fear and landscape of fear studies can provide a feasible way to measure some of the local habitat factors influencing individual’s behavioural responses and perception of risk (Bedoya-Perez, Carthey, Mella, McArthur, & Banks, 2013; Gaynor et al., 2019). Furthermore, these can then be linked to more general behavioural ecological concepts and processes, such as optimal foraging theory or niche separation (Bleicher, 2017; Laundré et al., 2010). Key landscape of fear concepts: predation risk, foraging economics and energetics, and population density and community structure are also key concepts in explanatory models of individual behavioural consistency. Additionally, they form core questions in the broader understanding of animal behaviour in urban habitats, therefore a combination of these approaches is likely to add insightful and ecologically relevant dimensions to the understanding of structure and expression of individual variation in behavioural consistency under urbanisation.

2.5.1) Predation paradox: Is the urban environment safer?

Whilst for some species urban habitats may offer some safety from predation, the addition of novel predators and exposure to human disturbance may increase perceived predation risk for others (Fischer et al., 2012). Furthermore, only a few studies of consistent individual differences in behaviour have acknowledged the role of humans and human related disturbance as a key sources of perceived predation risk in urban environments. Whilst many types of human disturbance are non-lethal, they may carry disturbance costs due to increased perceived predation risk, for example, through pedestrian activity, presence of domestic predators such as dogs and cats, habitat fragmentation by roads and increased vehicle activity. Even where actual predation rates are reduced, perceived predation through the mere presence of predators can have significant impacts on foraging behaviour, habitat use, and breeding behaviours (Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Lowry et al., 2013; Newsome et al., 2015).

One of the key methods used in mapping animals' perception of risk variation across habitat is the giving up density approach(Bedoya-Perez et al., 2013; Brown, 1999). This approach can provide temporal and spatial map of foraging-safety trade-offs using experimental artificial feeding patches and measuring the quitting harvest rate, or 'giving-up density' (GUD), the measure of resources left at the point at which an animal ceases foraging at a patch (Brown, 2016; Brown, 1988; Charnov, 1976). This provides a quantifiable currency for perceived predation risk as it reflects the amount of marginal profit (energy gained from feeding) a foraging animal is willing to 'give up' in order to balance the marginal costs of foraging (of which mortality risks make up a substantial proportion). Another widely applied field method of quantifying foraging-safety trade-offs in free-ranging animals is the use of flight initiation distance (FID) – the distance at which an animal flees from an approaching predator stimulus. Researchers investigating consistent individual differences in behaviour have begun to use this approach and it has offered some interesting insights into how individuals distribute themselves across habitats, as well as how they manage and adapt to non-lethal anthropogenic stimuli (see summary of studies for some examples).

Interpreting habitat use and risk perception in urban habitats can be difficult for several reasons. Firstly, human activity may produce false cues of predation risk, which could lead to avoidance of certain areas of habitat that do not contain high 'actual' risk. Secondly, human activity, disturbance and forms of pollution may also mask predation risk, providing inaccurate cues of safety. Therefore, foragers may perceive areas as safe, where they are in fact risky. However, these methods could help to interpret and assess consistent individual differences in behaviour in the field, under ecologically relevant conditions.

2.5.2) The influence of anthropogenic resources on energy costs and state

A recent meta-analysis of urban birds has suggested that birds living in urban habitats live longer that their rural counterparts (Sepp, McGraw, Kaasik, & Giraudeau, 2018), this may be the case for mammals too, as some studies have found similar survival rates (Lehrer et al., 2016). This increased survival is likely to be due to a combination of factors including increased resource availability through supplementary feeding, or unintentional feeding (for example, waste sites), and lower actual predation rates. With reduced predation risk and increased, perhaps more predictable, food resource input it can be easy to assume that urban wildlife would be in better condition that their rural counterparts. In a study of urban eastern chipmunks, females were found to have increased body condition and reduced cortisol suggesting the increase in predictable food sources enable these animals to hold increased energy reserves, however this effect was not found in males in this species possibly reflecting the sex differences in energy requirements for this species (Lyons et al., 2017). Integration of optimal foraging theory into the ecology of fear provides useful ways in which to conceptualise and quantify how individual state can influence behaviour and decision making under risk in free ranging wildlife. Whilst foraging, an animal must trade-off energy intake with risk of predation. The use of cues relating to predation risk may vary between individuals., Animal personality variation theory predicts links between individual differences in life-history strategy and intrinsic state dynamics with levels of behavioural consistency(Montiglio et al., 2015; Wolf & Weissing, 2012). This may imply that some individuals have more to lose than others if they assess risk inaccurately. Although the cost of under-estimating mortality risk has the potential to be large (i.e. injury or death), the willingness to trade of food for safety will be impacted by individual state (Brown, 1999).

Studies employing foraging behaviour into the study of consistent individual behavioural differences in urban environments could benefit from quantifying both the state of the individual forager (e.g., body condition) and the properties of the environment (for example the perceived and actual predation risk, and patch quality) that can influence the balance of these food-risk trade-offs. As individuals in the wild are likely to vary in state across time, this is an important component of considering behavioural repeatability over time and context. GUD studies have been useful for quantifying food-safety trade-offs in relation of static habitat features, such as distances from vegetation cover (Abu Baker & Brown, 2010). However this use of GUD appears to have only been utilised in a handful of studies comparing urban habitats. These have found that urban populations tend to have lower GUDs than rural populations, appearing to forage in a less risk averse manner and demonstrating little variation in GUD between food patches placed in open (supposedly high risk) habitat and low risk patches close to cover (Bowers & Breland, 1996b; Tsurim, Abramsky, & Kotler, 2008). This indicates that, despite the frequency of human disturbance in urban habitats, many species successfully living in urban habitats perceive predation risk as low. Given the abundance of research demonstrating the negative impact of human disturbance on wildlife, at first glance this seems unexpected. However, a closer consideration of the population dynamics and differences in the energetic costs of living under urbanisation could offer some insights. For example, urban species tend to live at higher population densities, so could GUDs in urban populations reflect the consequences of intraspecific competition risk rather than predation risk? Could the physical features of urban habitats, such as roads or the decrease in vegetation cover, create differences energetic costs during feeding and locating food patches?

2.5.3) Effects of Competition and population density.

Where urban populations benefit from reduced predation rates and increased food input, many urban species can live at higher population density than they might do under rural conditions. Theoretical work on competition and population structure under urbanisation suggests that living at high population density, lack of predation, and reliable resource input can change the selection pressures experienced by urban dwelling animals, thus changing population structure from that of rural populations. For example, living at a high population density is likely to increase competition for food and other resources, which although abundant and more predictable than those in rural habitats, tend to result in ‘over-matching’ (over exploitation of areas perceived to be rich in resources) and high competition at the individual level (Anderies et al., 2007; Tsurim et al., 2008). Therefore, the lower

GUDs found in urban populations may be explained in terms of intra-specific competition, with urban habitats perhaps selecting for individuals highly efficient foraging at aggregated food patches (Shochat & State, 2007; Valcarcel & Fernández-Juricic, 2009). Shochat (2004) argues that living at high population density with low predation risk and stable resource input allows foraging animals in urban environments to 'live on credit' obtaining just enough energy to live day-to-day, resulting in populations with a high abundance of low-quality individuals which would normally be removed through predation and starvation in rural systems. Although there is mixed support for this (see Lyons et al., 2017), urban populations of many avian species, have been found to have reduced body condition and produce more low-quality offspring compared to rural populations(Liker, Papp, Bókony, & Lendvai, 2008; Sepp et al., 2018; Viblanc et al., 2012; Weaver, Ligon, Mousel, & McGraw, 2018). Buffered by the pressures exerted by predation and seasonal fluctuations weather and food supply, many urban populations mature earlier, exhibit longer breeding seasons and demonstrate reduced migratory behaviours (Sepp et al., 2018). Higher adult survival and longer breeding seasons allow many urban populations to show higher rates of reproduction, although for some populations, increased population density can lead to increased individual competition for quality mates, territory and nesting sites, perhaps resulting in only a few individuals having access to sufficient resources to reproduce (Anderies et al., 2007). Stress from human disturbance, particularly noise disturbance, further impacts reproductive behaviours such as mate choice and investment in parental care in some species, adding to the differences in population community dynamics between rural and urban wildlife (Barber, Crooks, & Fristrup, 2010). As a result, tolerance for living under conditions of high competition and high population density seems likely to be an important criterion for successful habitation of urban habitats. How this might impact expression of personality variation has not been widely tested, however, a handful of studies looking at behavioural syndromes (correlated suites of behaviours that are repeatable over time) have suggested that there may be stronger selection for behavioural flexibility in aggressive behaviours due to increased likelihood of social interactions (Charmantier, Demeyrier, Lambrechts, Perret, & Grégoire, 2017; Hardman & Dalesman, 2018; Minias, 2015). Experimental studies using individual GUD could help to reveal the role of individual resource acquisition ability through measuring individual differences in foraging efficiency in connection with habitat use and population density. For example, do individuals with different behavioural types exploit patches differently? How do these individuals balance competition risk-feeding trade-offs? Do individuals living at high population density opt for high perceived predation risk foraging patches due to the perceived benefits of group vigilance?

With a greater number of individuals living ‘on credit’ (*sensu* Shochat & State, 2007) there may be differing consequences for the sexual selection of personality variation in urban environments. Although there are few studies explicitly examining this, a few have indicated that males in urban environments show reduced competitive and aggressive behaviours than rural populations (Bonier, Martin, Sheldon, et al., 2007; Hasegawa et al., 2014; Lintott et al., 2014). In a study of urban house finches this effect on behaviour was apparent, even when accounting for the influence of other phenotypic indicators of competitive/dominance ability, such as of plumage colouration (Hasegawa et al., 2014). The expression of personality variation under urbanisation may be difficult to fully understand in many species without consideration of the role of sexual selection in the maintenance of consistent individual differences in behaviour. Furthermore, engaging a landscape of fear approach can reveal how risk-related behaviours in urban habitats are influenced by individual reproductive value, for example, individual GUDs could be used to test some of the risk-safety trade-offs predicted by life-history strategy explanations of animal personality variation.

2.5.4) Habitat features influencing risk perception

Published research into the possible effects of urbanisation on the structure of individual differences in behavioural consistency appear to vary in how urbanisation is measured and recorded (see appendix: review of studies). A crucial problem with this is that it can create difficulties in making comparisons between studies, perhaps adding another layer of complication into the understanding of the pressures driving consistent behavioural differences, making it difficult to generalise findings in a meaningful way. Common approaches are the use of categorical differences (compare urban Vs rural site), measuring distance of a site from a city centre, quantify human population density/activity within site, the use of satellite imagery to calculate percentage of build environment, or less commonly used, but perhaps more informative, is the use of combined multivariate methods (e.g. taking different measures and use principle component analysis to create an urban index). Landscape of fear and ecology of fear approaches emphasise the relevance of variance in habitat features in the of perception of risk. For example, an urban park may contain high disturbance and human activity levels yet contain vegetation and tree canopy cover which offer refuge (Haigh, Butler, O'Riordan, & Palme, 2017). This can mean that a population living in an urban park will show a differing landscape of fear to that living in another type of urban site with less vegetation cover, but the same level of human disturbance. As such, habitat features are in important aspect of understanding the fear-safety decisions being made by individuals.

Urban populations often live in fragmented habitats, the degree to which a habitat is fragmented is likely to influence the expression of risk-related behaviours. Fragmentation is likely to increase the physical gaps between key resources, for example roads pose a mortality risk, and large gaps between trees carry increased energetic costs associated with travel between food patches (Hinsley et al., 2008), therefore we may find that individuals will differ on their tolerance for level of habitat fragmentation. Open areas with reduced vegetation cover may mean individuals with risk-taking tendencies have an advantage (Short & Petren, 2008), whilst, areas with a complex array of alternative resources might be beneficial for individuals with high information gathering tendencies.

2.5.5) Applications for managing wildlife in urban areas.

Increasing urbanisation, and the encroachment of urban habitat into rural habitat, can lead to potential for human-wildlife conflict where wildlife is associated with negative effects, such as predation on domestic animals/pets, feeding from waste, entering houses, spread of zoonotic diseases, and traffic accidents (Bateman & Fleming 2012), understanding how urban habitat structures shapes the relationship between individual risk perception and personality variation could help inform wildlife management strategies in urban areas. For example, if urban habitat selects for the expression of bold and aggressive individuals, we may be able to understand how to induce a landscape of fear that reduces the willingness of individuals to occupy parts of a habitat where human-wildlife conflict is likely.

Urbanisation is also of conservation concern where it leads to reduced biodiversity and potential extinction for species unable to live under high human disturbance(Pickett et al., 2011; Smith & Bernatchez, 2008). Understanding the behavioural processes involved the perception of risk in these more vulnerable species could help aid the design of urban habitats in a way that reduces the likelihood of extinction and maintains behavioural variation within populations enough so that that it may buffer populations from the effects of rapid human-induced habitat change (Sih et al., 2012).

2.6 Summary and conclusions:

Gradients of urbanisation can offer opportunities to test some of the explanatory models of consistent individual behavioural variation in free-ranging individuals, such as how the expression of behavioural ‘types’ can be impacted by individual state, population density and dynamics, risk management behavioural strategies, and resource predictability. However, currently, how urbanisation impacts the expression of personality variation remains unclear due to some of the challenges in terms of understanding the ecological factors shaping such behavioural variation under these conditions, as these factors are not often measured in published studies of animal personality variation in urban wildlife. The ecology of fear, and the experimental approaches used to quantify the landscape of fear, may offer practical field-based methods that allow the mapping of risk as perceived by both populations and individuals. This may aid behavioural ecologists in reducing the need to monitor behaviour in the lab and captivity and move toward understanding risk-resource related behaviours within ecological settings, as well as improve links with more general ecological theory. Understanding the differences in the expression of behavioural consistency in urban and rural populations may require researchers to quantify urbanisation in several dimensions, including, the measurement of habitat variables that impact food-safety decision making that is relevant to their study system.

In the research that has been carried out so far, it seems that urban environments are likely to reduce repeatability in behaviour (animal personality variation), or at least favour behavioural flexibility. In initial stages of colonisation of urban habitats, it is likely behaviourally flexible species (and perhaps individuals) are more likely to be attracted to, or remain in, these habitats. As time since colonisation progresses, the degree of behavioural flexibility (degree of personality variation) may change according to the conditions faced. These are likely to include the degree of complexity and novelty of problems urban animals face, such as increased resource competition, novel food resources, persecution by humans, supplementary feeding by humans, and novel predators such as domestic pets. Further research incorporating measures of these ‘problems’ in the study of personality variation across a wide range of urban dwelling species could help us to understand how generalisable these findings are, and perhaps if anything can be done to support species with reduced behavioural flexibility as they face an increasingly urbanised world.

Chapter 3: Foraging Risks in Human-Altered Landscapes: Giving-up density in response urbanisation in grey squirrels.

Abstract:

Risk influences the decisions of foraging animals meaning that they do not use their habitat in a homogenous way, with activity and feeding usually biased towards areas of a habitat where the benefits of feeding outweigh the risks. Human activity and its associated disturbance are thought to be perceived as a source of risk analogous to predation in wildlife. Due to the increase of human presence and disturbance, altered habitat, and novel resources in urbanised areas, urban wildlife may face differing problems associated with foraging and patch use compared to their rural counterparts. This study measured giving-up densities (GUD) at artificial food patches placed at varying levels of urbanisation, to investigate differences in patch use of foraging grey squirrels. It was found that differences in GUDs between 'safe' and 'risky' patches were reduced in foragers feeding near roads and buildings. These results suggest that the costs of foraging away from cover may be reduced in locations close to these features. There was a significant interaction effect between proximity to these features and noise variability, with higher GUDs and larger differences between safe and risky patches found under higher levels of noise variance, suggesting that this might be an important factor for influencing risk perception t in this species.

3.1 Introduction:

Balancing the costs and benefits associated with food acquisition is key for survival for a foraging animal, therefore, decisions of where, when, and how long to forage is shaped by the animal's assessment of risk at a patch (Brown, 1988; Brown, 1999). Feeding and searching for food leaves a forager exposed to predators, yet forgoing opportunities to feed can also be 'risky' in terms of reduced survival and reduced fitness through starvation (Olsson & Molokwu, 2008). Information about predation risk and food availability at a patch could vary in quality in space and time, therefore foragers often must make decisions about the costs and benefits of feeding based on incomplete information (Brown, Laundre, & Gurung, 2006). Fixed habitat characteristics, such as vegetation structure, influence perceived predation risk and could have a greater influence on foraging behaviours than more direct cues of predation, such as predator presence or density, perhaps because these are more stable, but not necessarily more reliable, predictors of risk (Orrock, 2004; Verdolin, 2006). This study aims to investigate if habitat features associated with urban environments and human presence differentially influence the foraging decisions of grey squirrels living at varying levels of urbanisation.

The relationship between foraging, habitat use, and fear is conceptualised via the ‘landscape of fear’. The landscape of fear suggests the way in which animals use their habitat is based on fear and perceived risk of predation (Laundré et al., 2010). Therefore, the way in which an animal uses its habitat can reveal much about the problems it faces in its day-to-day activities. Fear is a foraging cost as it requires foragers to increase investment of time to vigilance and avoiding predators, thus reducing time invested in feeding and finding food (Brown, 1999). In order to optimise energy gains acquired from feeding at a patch, foragers should feed for as long as the energy obtained from feeding is greater than the costs of foraging and locating food (Charnov, 1976). However, foragers assess more than the energetic value of a food patch, they also need to balance this with the costs of being predated and the costs of missed opportunity to engage in other fitness enhancing activities, such as finding mates and defending territories (Brown, 1988). As the forager depletes the food in a patch, these costs of foraging will begin to outweigh the benefits of feeding. The point at which this occurs can be quantified using the giving-up densities (GUD) in standardised patches, where the amount of food left behind when the forager decides to stop feeding representing a measurable GUD (Brown, 1988). Developed by Brown (1988) the GUD method has been employed to quantify perception of risk during foraging and feeding, and the landscape of fear in a variety of species, across a diverse range of habitats and contexts, for example, the thermoregulatory costs of foraging (Kilpatrick, 2003), competition and niche separation (Brown, Kotler, & Mitchell, 1997) and responses to the presence of novel predators (Kovacs, Crowther, Webb, & Dickman, 2012). Giving-up density is a reflection of the foragers quitting harvest rate: the point at which the energy gained from food is no longer profitable because the survival and fitness costs of feeding begin to outweigh energy gains (Brown, 1999). As such, this point reveals a number of factors about the individual forager and the foraging patch, including: the level of predation risk at the patch, the current energy state of the forager, the foragers current fitness value, and the energetic value of the food at a patch (Brown, 1988). As a consequence, GUD is expected to be high where predation risk is high and/or energy state and fitness value of forager "assets" are high, because foragers with a positive energy budget should be less willing to take foraging risks which could impact their future fitness (*sensu* the asset protection principle: Clark, 1994; McNamara, 1990).

With feeding and foraging behaviour revealing much about the survival and fitness consequence of habitat use, examining the foraging decisions in urban wildlife can play an important role in understanding the impact of living in human-altered environments on distribution and abundance of wildlife. Mapping the landscape of fear in urban wildlife can also aid in the development of urban wildlife management practices, for example, by identifying methods of artificially increasing the perceived predation risk in order to control impacts of pest species, or species likely to come it to conflict with humans, as they forage in certain areas (Baker, Emerson, & Brown, 2015). It is now widely accepted that human activity and related disturbance can significantly alter the behaviour of other species, with this is being most apparent in urban habitats (Johnson & Munshi-South, 2017; Lowry, Lill, & Wong, 2013; Sol, Lapiedra, & González-Lagos, 2013). Much of this change in behaviour might reflect differences in the perceived risk humans represent for a particular species. Humans can represent both an indirect and direct predation risk, similar to other apex predators, with their presence generating a landscape of fear in similar ways (Ciuti et al., 2012). For example, human activity and can increase mortality rates directly through vehicle collisions with wildlife, destruction of habitat, or management of species regarded as pests. There are also indirect mortality costs associated with avoiding humans and living under high disturbance, including the energetic costs of increased physiological stress and exposure to disturbance (Ditchkoff et al., 2006). In some species, human activity may be perceived similarly to predation, yet human activity may actually reduce mortality for some, through reducing the density of other predator species, providing a ‘safer’ habitat for some prey species compared to their natural range (Fischer et al., 2012)

Whilst there have been limited studies employing GUD methodology to assess human induced landscapes of fear within urban habitats, other methods have revealed that spatial and temporal habitat use are shaped by human activity, or cues of human presence. In response to experimental playbacks of human voices, both large and medium-sized carnivores have demonstrated physiological and behavioural fear responses to the sound of human presence, and show behavioural avoidance of areas near auditory cues of human disturbance (Clinchy et al., 2016). In a recent study of mammal responses to human disturbance, Suraci, *et al* (2019) manipulated cues of human presence with human voice playbacks throughout two 1km areas within the Santa Cruz mountains, USA. The movements of mountain lions (*Puma concolor*) occupying this area were monitored via GPS collars, and camera traps and supplementary food patches were used to monitor medium sized and smaller mammals including skunks (*Mephitis mephitis*), bobcats (*Lynx rufus*), opossums (*Didelphis virginiana*), deer mice (*Peromyscus* spp.) and woodrats (*Neotoma fuscipes*). Whilst mountain lions and medium-sized carnivores showed avoidance of areas with human playbacks, foraging by small rodents increased in these areas. This implies that, for these large and medium sized carnivore species, humans create a landscape of fear, which in turn can provide predation release for some smaller prey species. Furthermore, this study provides an example of how human disturbance can alter and shape habitat use in whole communities of species, much like apex predators (Suraci et al., 2019).

A number of landscape of fear studies conducted in a range of habitat types, demonstrate that it is not only predator species that avoid human activity (Bonnot et al., 2013; Rösner, Mussard-Forster, Lorenc, & Müller, 2014). Human recreational activity was found to impact patch use and GUD in Nubian ibex, *Capra nubiana,* (Tadesse & Kotler, 2012), revealing that human disturbance can represent an significant foraging cost. Similar costs of human disturbance have been highlighted by studies investigating the behavioural impacts of anthropogenic noise, where increased noise disturbance can lead to increased investment in vigilance behaviours (Klett-Mingo, Pavón, & Gil, 2016; Sarno, Parsons, & Ferris, 2014), spatial and temporal avoidance of foraging in certain areas according to the spatial and temporal fluctuations in human activity levels (Luo, Siemers, & Koselj, 2015), and additional impacts on other fitness-enhancing activities, such disruption of mate selection cues and changes in investment towards territorial defence, that have been associated with making behavioural adjustments to disturbance (Barber, Crooks, & Fristrup, 2010; Fuller, Warren, & Gaston, 2007; Herborn, Heidinger, Alexander, & Arnold, 2014; Morris-Drake, Bracken, Kern, & Radford, 2017; Petrelli et al., 2017).

Here we investigate the patch choices in free ranging populations of eastern grey squirrels (*Sciurus carolinensis*) living at sites of varying human disturbance. A common exotic species in the UK, grey squirrels are abundant across several landscape types and live at high density in many urban parks (Bonnington et al., 2013; Parker & Nilon, 2008). Behavioural differences between urban and rural squirrels have become apparent, with urban squirrels showing reduced flight initiation distances towards human (Bateman & Fleming, 2014; Dill, 1989), living at higher population density (Sarno et al., 2014) and increased population differences in intraspecific aggression (Parker & Nilon, 2008). Their success in urban habitats is thought to be due to their behavioural flexibility, which may enable them to obtain food from a wide selection of novel resources, such as bird feeders and waste resources (Bonnington et al., 2014; Kays & Parsons, 2014), which is likely to buffer them from the seasonal fluctuations in food supply usually experienced by woodland populations (Gurnell, 1996). Grey squirrels have been widely used in studies of foraging ecology and giving-up density (for examples see: Lima, Valone, & Caraco, 1985; Makowska & Kramer, 2007; Newman & Caraco, 1987; Wauters, Lurz, & Gurnell, 2000), so much is known already about their habitat preferences, however, research into their habitat use in urban environments appears to be limited, particularly in the UK, where their status as an alien invasive species means that further understanding of the factors influencing their distribution and abundance is important for wildlife management (Bonnington et al., 2013, 2014).

In their native range of North America, eastern grey squirrels inhabit densely forested habitat, preferring to feed and forage close to dense vegetation cover where they are protected from aerial predators (Newman & Caraco, 1987). They are usually associated with habitats containing masting tree species, where their over-winter survival is impacted by the abundance of cashable food sources available in autumn

(Fox, 1982). They coexist with other species of tree squirrel (e.g. fox squirrels *Sciurus niger*) particularly in large urbanised parkland where a combination of anthropogenic food sources and mature masting tree species are thought to support high populations of squirrels (Van Der Merwe, Brown, & Jackson, 2005). Habitat use and foraging behaviour of grey squirrels is likely to depend on variation in food availability, distribution of conspecific and intraspecific competitors, and distribution of predators. These factors may be temporally and spatially variable, therefore foraging squirrels have been found to use stable cues for assessing risk. Whilst grey squirrels are sensitive to dynamic cues, such as social cues of risk(Jayne, Lea, & Leaver, 2015; Lilly et al., 2019), stable/static cues provide ‘rules of thumb’ for reducing exposure time to potential predation events(Hopewell & Leaver, 2008; Leaver, Jayne, & Lea, 2017; Newman & Caraco, 1987; Newman, Recer, Zwicker, & Caraco, 1988). Several studies of squirrel foraging behaviour have demonstrated that these key cues relate to distance from cover. As a rule, squirrels show preference for feeding close to the base of trees and shrubs, and where there is good overhead cover such as dense canopy. This is likely to reflect the ability to escape from predators by quick retreat up a tree, and the ability to limit visual detection ability of predators through the restricted visibility provided by vegetation or canopy cover(Brown, 2016; Embar et al., 2011; Newman & Caraco, 1987).

These static cues not only influence decisions of where to forage, but also influence other features of feeding behaviour, with several studies demonstrating that squirrels make behavioural adjustments to handling times, caching, and travel time between patches according to these cues(Jayne et al., 2015; Lima et al., 1985; Newman & Caraco, 1987). Overall, these studies also demonstrate that grey squirrels provide an interesting model species for examining how habitat features influence patch use and foraging decisions. Urban habitats may contain differences in both static and dynamic cues for foraging squirrels. For example, the built environment including buildings, roads and footpaths may offer static cues of human presence. However, they may also offer cues of reduced exposure to other predators. Currently, there appears to be limited research verifying the value of these cues in urban wildlife. Urban squirrels may also face a number of dynamic cues of risk, such as human activity, traffic, and differences in levels of social risk.

In a study of urban squirrel foraging, Bowers and Breland (1996) used citizen science to measure the summer GUDs of grey squirrels at 78 artificial food patches placed at individual points across an urbanisation gradient in Virginia, USA. They found a higher rate of locating artificial food patches and lower giving-up densities at artificial food patches placed near areas of human habitation, suggesting that food patches near areas of human activity are readily exploited by squirrels, perhaps offering abundant feeding opportunities and protection from natural predators (Bowers & Breland, 1996). Following on from this research, this study also asks whether the 'landscape of fear' differs for grey squirrels across and urban-rural gradient, and if so, do static cues associated with urbanisation influence this? Building upon previous findings from GUD studies in grey squirrels, it is expected that perceived foraging risk will increase with distance from trees and vegetation cover, therefore this study provides foragers with a choice of 'safe' (close to trees) and 'risky' (further from cover) patches. Whilst following a similar line of enquiry to Bowers *et al*, rather than investigating single points across the gradient, this study provides foragers with a choice of alternative food patches within the same site allowing individual foragers to accept and reject patches, whilst experiencing similar missed opportunity costs across patches. This can allow patch selection to reveal finer level insights into differences between the value of 'safe' and 'risky' patches for squirrels feeding at different levels of exposure to potential cues of human presence. If urbanisation decreases perceived risk for grey squirrels, then we should expect the difference between safe and risky patches to be lower than in locations further from urban features.

In this study, we collect giving up density data during winter when natural sources of food are scarce across sites and squirrels show a greater willingness to forage at ground level (Parker, Gonzales, & Nilon, 2014). We also habituate squirrels to feeding from artificial trays prior to data collection, to reduce the impact of neophobic responses to artificial food patches across sites, as we might expect urban squirrels to be more familiar with obtaining food from novel anthropogenic food sources than forest dwelling squirrels. We also include estimates of squirrel population density to consider if conspecific competition might be an impacting factor. To examine the role of a dynamic urban cue of potential risk we measure variability in noise levels. Whilst population density is not often included in GUD studies (although see: Carthey &

Banks, 2015), the density of conspecifics is likely to increase competition for food resources, and may generate lower GUDs . Noise levels were also measured at each pair of food trays, to consider if variability in noise levels relating to proximity to human settlement represented a foraging cost for grey squirrels. These variable noise disturbances are predicted to disrupt foraging, for example through startle responses, or through distraction (Chan et al., 2010; Gil, Klett-mingo, & Pav, 2016) and animals may be less likely to habituate to stimuli that are variable or inconsistent (Rankin et al., 2009).

We tested the hypothesis that proximity to habitat cues of the urban built environment could increase perception of risk at standardised feeding patch (resulting in higher GUDs), and that site level of urbanisation could change the balance between feeding and safety resulting in smaller differences in GUD between ‘safe’ and ‘risky’ patches at more urban sites.

3.2 Methodology

Ethics statement

This research was carried out with approval from the University of Exeter Biosciences Ethics Committee (reference 2015/892).and conforms to the Association for the Study of Animal Behaviour (ASAB) guidelines for use of animals in behavioural research (2014). Permissions to conduct research was also obtained from the relevant landowners of each site.

Study sites

The study was conducted during winter (December 2014-Febuary 2015 for museum, garden, park, and Naphill forest sites, and December 2015 – February 2016 for the Arboretum and Pepperboxes Woodland sites) at six sites across Buckinghamshire, UK, varying in levels of urbanisation. Daily temperatures during data collection ranged between -4˚C to 9˚C. Attempts were made to ensure temperature and weather conditions were similar on the days prior and during GUD data collection in order to keep temperature related energetic costs of foraging as similar as possible across sites. Each GUD experimental plot consisted of a plot 100m X 100m placed within the wider site. These locations were selected based on accessibility (ability of the researcher to carry equipment to the location), landowner permissions, and that they might represent a different level of urbanisation. The forested sites consisted of a plot within a 33.11 acre and a 155 acre ancient woodland. Here, dominant tree species include European Beech (*Fagus sylvatica)*, Ash (*Fraxinus excelsior*) and Oaks (*Quercus robur)*. Urban sites included a location within an 53 acre public park and a museum garden based in High Wycombe, Buckinghamshire UK. Both locations contained beech trees as well as limes (*Tilia europaea)* and yew (*Taxus baccata)*. The suburban locations consisted of five adjacent private gardens, and an Arboretum in Little Kingshill, Buckinghamshire, UK. Bird feeders were observed at the garden sites, and members of the public were often observed feeding squirrels at the urban park and museum site. Across all sites potential predator species included red fox (*Vulpes vulpes)*, red kites (*Milvus milvus*), and buzzards (*Buteo buteo*) were also reported at the woodland site. Although abundance of domestic dogs (*Canis familiaris)* and cats (*Felis catus)* were not measured in this study, it is likely that they are found at higher density in urban and suburban areas (Baker, Bentley, Ansell, & Harris, 2005; Weston et al., 2014). Sites were greater than 10 km from each other, therefore it is likely that these represent independent populations. Daily home range sizes for grey squirrels are reported to cover 1.20 acres (~4856.32 m^2) with a maximum linear distance of 136.7 m (Doebel & McGinnes, 1974), however, there have been cases of dispersal distances up to 64 km (Rushton, Lurz, Fuller, & Garson, 1997).

Three main features of land cover type: roads, buildings and vegetation cover were used to provide an index of urbanisation for each site. Using digital images in Google Earth Pro, sites were divided into 10X10 grid (100 squares 100m X 100m), covering an area of 1-km^2 around each site. Each square was scored according to building cover (0 if ratio of buildings is 0%; 1, if < 50%; 2, if >50%), vegetation cover (0, if 0%; 1, if < 50%; 2, if >50%) and if solid road was present (0, if absent; 1, if present). An urbanisation score for each site was created from the first principle component score calculated using the summary statistics of the 100 squares at each site (Czúni, Lipovits, & Seress, 2012; Liker et al., 2008). This revealed that the most urban site, based on road and building cover was the Museum site, with the least urban site (based on mean vegetation density) was the Woodland and Forest sites.

Table 3.1. Land cover scores for each site based on building, road cover and vegetation cover..

Site	Mean building density	No. squares >50% build	Mean vegetation density	No. squares >50% veg	No. road squares	PC1 (Urban index)
Pepperboxes Wood	0.25	3	2.02	100	28	-36.19
Naphill Forest	0.06	0	1.99	98	4	-48.81
Arboretum	0.75	16	0.96	96	34	-23.69
Park	0.48	17	1.36	44	24	7.28
Gardens	0.79	20	1.4	40	27	13.11
Museum	1.7	72	0.73	16	89	88.28

Land cover scores for 100 squares (100mX100m) covering grid of 1-km^2 area around each site. PC1 values calculated from principle component analysis on the five variables for each site using methodology described in Czúni et al. (2012). Larger scores indicate higher building and road cover and less vegetation cover.

Squirrel population density

Grey squirrels were observed regularly at all six sites and their local abundance in the South East of England has been noted since at least 1916 (Middleton, 1930). Fixed-duration point counts were used to provide an estimate of squirrel abundance at each site. These counts were conducted at points within the experimental plot and the surrounding area. Point counts were used as they provided a way to calculate an index of population density in these fragmented sites where line transects are not possible (Bonnington et al., 2013; Parker & Nilon, 2008). Following similar methodology to that described in Flyger (1959), 15min point counts were made from 10 observation points at each site, with each of these points being a minimum of 150m apart to account for home range sizes (Doebel & McGinnes, 1974) as an attempt to reduce the likelihood of repeated counts of the same individual. Individual points being selected via an initial walking transect stopping every 150m, and locating the nearest suitable observation point with a 360-degree visual field. . Counts were conducted at least four times at each site prior to collection of GUD data, and were carried out on dry calm days (<4 Beaufort scale) within five hours of sunrise when squirrel activity is usually highest (Parker & Nilon, 2008). Squirrel counts begun as soon as the observer approached the observation point. Using a range finder (Viking monocular laser range finder, Viking Optical, Suffolk, UK) the radial distance of each squirrel from the observer was estimated. Using the following equation, an index of relative population density (N) was calculated from the total area of the site (A), total number of squirrels counted (Z), the number of 15min observation sessions (n) and the average radial distance to squirrels counted (r) (Flyger, 1959; Parker & Nilon, 2008):

$$N = \frac{AZ}{n\pi r^2}$$

Table 3.2 *Squirrel Population Estimates for each site based on point counts.*

Location (listed in order of most to least urban)	**Squirrels (individuals/acre)**
Pepperboxes wood	0.19
Naphill Wood	0.80
Suburban gardens	0.85
Arboretum	0.85
Public park	4.14
Museum gardens	1.07

Squirrel densities ranged from 0.19 – 4.14 individuals per acre, with largest estimates for population densities occurring at the urban park site (Table 3.2).

In their native range densities of grey squirrel populations typically range from 0.3 – 0.8 individuals/ha (0.75 – 2 individuals/acre) (Williamson, 1983). With UK urban populations found to range from 0.46 – 8.29 individuals/ha (1.15 – 20.7 per acre) (Bonnington et al., 2013).

Measuring giving-up density

At each site, eighteen food patches were placed in pairs across 3X3 grid over an area of 100m^2, creating nine feeding locations spaced approximately 30m apart (N = 108 patches across all sites). Trays were placed in pairs with one tray at the base of a mature tree with a minimum diameter at chest height of 45cm (Parker & Nilon, 2008), and the other tray placed 3-7 meters away in open habitat, at least 3 meters from vegetation cover. For seven days squirrels were habituated to feeding from the trays before data collection begun. Feeding signs, such as footprints and peanut skins and sunflower shells, as well as camera traps were used to assess whether squirrels were encountering the trays. If trays were not fed from for more than 3 days, they were moved to a new location.

Giving-up density was measured using the amount of food left behind at artificial food patches. These patches consisted of green plastic trays (38cm L x 24cm W x 5cm high) each containing 15 grams of granulated peanuts buried in 2.5 litres of sand. Granulated peanuts were used because squirrels consumed these at patches, rather than cashing single nuts. A grid constructed of plastic mesh with 5cmX5cm squares was placed on the top of each tray to further increase diminishing returns as squirrels foraged (Image 3.1). Preliminary trials using 2 litres of sand, found that patches were depleted rapidly by urban squirrels, with most patches being depleted to zero after 8 hours foraging. To reduce foraging by birds the trays were also covered with a cage of wire mesh allowing squirrels to enter and exit on two sides, during preliminary trials camera traps were used to confirm that other species were not foraging from these patches. Patches were opened at sunrise and closed at sunset (approx. 0800 – 1600) during this study, therefore the weight of peanuts left in the tray reflected 8 hours of foraging. Trays were sieved to separate the peanuts from the sand substrate, and the weight of peanuts remaining was recorded as the giving-up density.

Image 3.1: GUD food patch including grid to increase diminishing returns and wire surround to prevent more than one forager from feeding at a time.

Measures of anthropogenic disturbance

GPS coordinates for each tray were entered into EDINA DigiMap (EDINA DigiMap, Edinburgh, UK) and measurements from the mid-point of each pair of trays to the nearest building, road, and footpath were taken using the distance '*Roam*' measurement function. An index of 'distance to urban features' was computed from these measures using principle component analysis. The first principle component, PC1, explained 94.9% of the variance, and had a strong positive correlation with the distance to buildings (r = 0.75), distance to roads (r = 0.66) and weak positive correlation with distance to footpaths (r = 0.01). As PC1 explained the highest amount of variance, these scores were used to represent distance to urban features with higher scores indicating increased distance from these features. Distance to footpaths, buildings and roads were also treated as separate fixed effects for analysis.

At each pair of food patches, noise levels were monitored from a point equidistant between each tray. Noise levels were sampled every 15 seconds at three time points (morning ~0800 – 0930, afternoon 1200 – 1400, evening 1600-1800) over three days using a hand-held Benetech digital sound level meter (A-weighted, range 30 – 130 dB). This resulted in 135 sampling points for each tray pair. The mean and variance in noise levels were calculated for each pair in an attempt to capture differences between patches in both average levels of noise as well as exposure to intermittent noise disturbances.

3.3 Analysis & Results

Descriptive statistics suggest that on average squirrels foraged in a pattern similar to those found in other studies, leaving higher GUD at food patches further from cover for each site. Squirrels feeding at urban sites left lower mean GUDs overall.

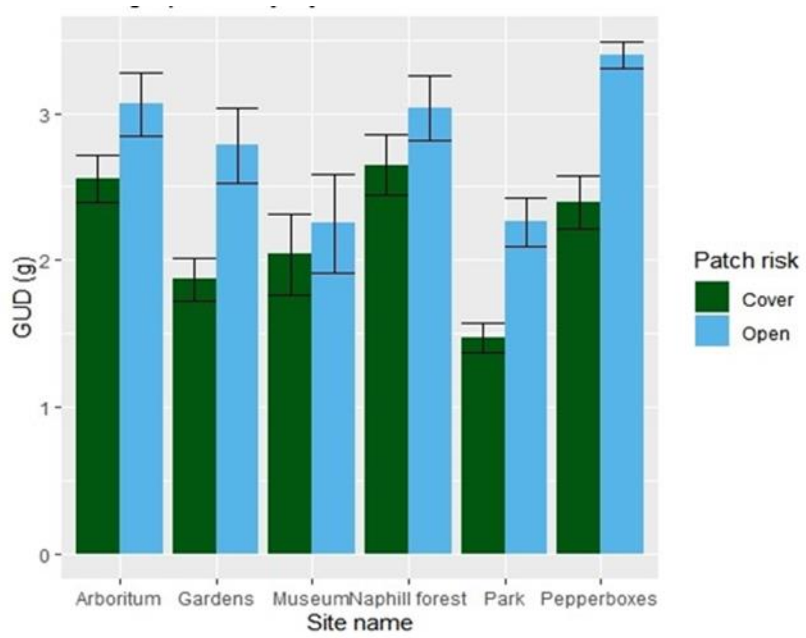
***Table 3.3 Mean GUDs at each site**.*

Sites ordered from least to most urban.

Site	Mean (SD) GUD Safe patches (g)	Mean (SD) GUD risky patches (g)	Urban Index
Naphill Forest	7.346 (3.141)	9.593 (3.744)	-2.1967
Pepperboxes Wood	5.457	11.753 (	-1.65122

	(2.964)	1.719)	
Arboretum	6.756 (2.639)	8.647 (3.738)	0.002873
Park	2.252 (0.870)	5.771 (1.924)	0.12371
Gardens	3.663(1.688)	8.851 (4.304)	0.24547
Museum	4.766 (4.009)	5.956 (5.159)	3.729041

***Figure 3.1**: Differences in GUD at open & cover patches according to site*



Generalised linear mixed models with gaussian distribution were used to test for the effects of proximity of urban features on the differences in GUD between open and cover patches in each pair. GUD difference was calculated by subtracting the GUD at the patch further from cover (open) from the GUD at the patch close to the base of a tree (Cover). Higher positive scores from GUD difference indicate that risky (open) patches had higher GUDs compared to the safe patch in the pair. Negative scores represent that safe patches yielded higher GUDs than the risky patch in the pair. Model assumptions were validated by visual inspection of plots (Appendix) and strength of correlations between predictor variables were examined using Pearson correlations. The variables distance from roads and distance from buildings were found to be highly correlated. Prior to analysis, predictor variables proximity to urban features, mean and variability in noise levels were rescaled and mean centred.

The maximal model contained continuous predictor variables: distance from roads, buildings and footpaths, urban score (PC1), site squirrel population density, noise variance, noise level and their two-way interactions. Site was included as a random effect. Model selection for fixed effects was carried out using stepwise elimination. All analyses carried out using R version 3.5.2. Linear mixed models were carried out using the *lmer* in the package '*lme4*' (Bates et al., 2015), model selection were carried out using backwards stepwise regression using the *step* function in the *car* package (Fox & Weisber, 2019). Terms were excluded based on whether their exclusion increased each models Akaike Information Criterion (AIC). Confidence intervals associated with each fixed effect was calculated using the *confint* function. PCA was carried out using *prcomp* function.

The minimal model (Table 3.4) found a significant effect of distance from buildings, t (48) = 2.911 , p < .005, and roads, t(48) = -2.865, p <.006 , on the differences between safe and risky patches. Foragers feeding closer to roads and buildings were found to have significantly smaller differences in GUD between safe and risky patches. Differences in GUD between safe and risky patches was not significantly predicted by noise variance, t (48) = 0.914, p = 0.36. However, there was a significant interaction with noise variance for distance from roads, t(48) = 2.432, p = .019, and distance from buildings, t(48) = - 2.229, p = .03, suggesting that higher noise variability increases perception of risk (increases GUD), and increases the difference in GUD between safe and risky patches.

Table 3.4 Summary of fixed factors in LMM minimal adequate model influencing GUD difference between safe and risky patches. Site included as random factor.

Variable	*Estimate (±SE)*	*df*	*t*	*p*	*CI 2.5%*	*CI 97.5%*
(intercept)	2.654 (0.853)	8.7	3.111	0.013	1.144	4.162
Building distance	6.897 (2.369)	48.49	2.911	0.005	2.716	12.204
Road distance	-6.583 (2.298)	48.36	-2.865	0.006	-11.792	-2.527
Noise variance	0.0255 (0.027)	48.99	0.914	0.365	-0.029	0.077

Building distance X Noise variance	-0.25265 (0.11333)	48.99	-2.229	0.030	-0.492	-0.05
Road distance X Noise variance	0.26705 (0.109)	48.96	2.431	0.018	0.072	0.505

Figure 3.2: Interactions between noise variance and distance from buildings on differences in GUD.

Noise variance was split into categories based on a median split.

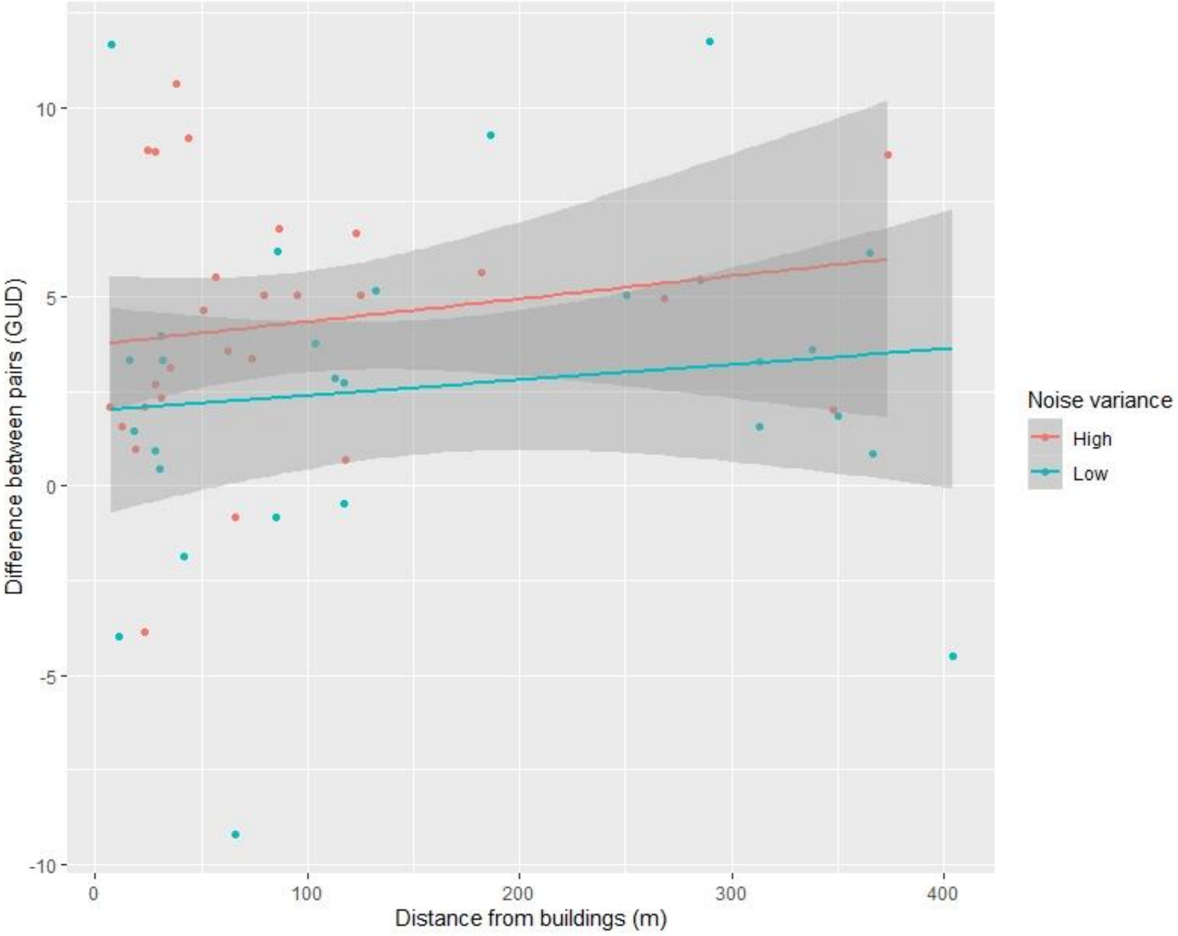
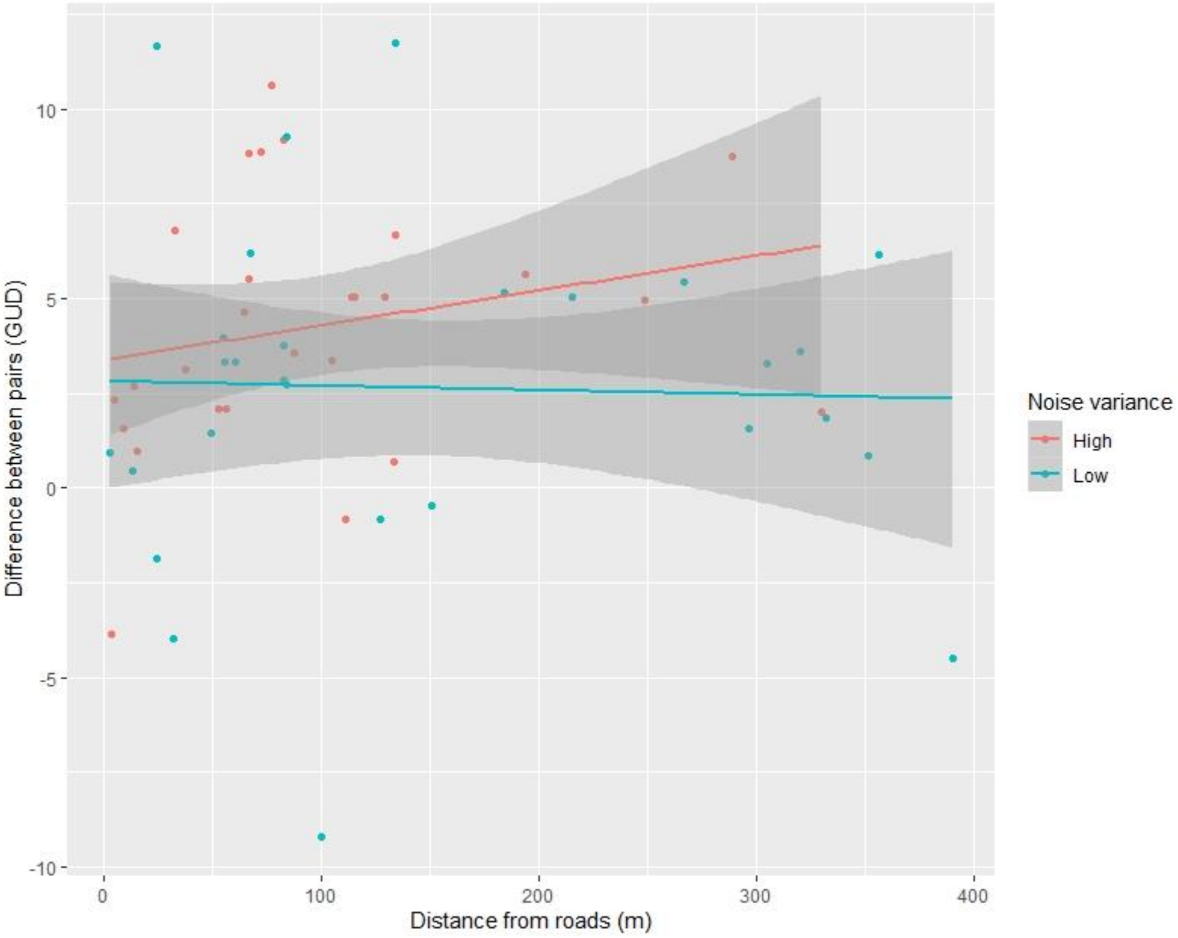


Figure 3.3: Interactions between noise variance and distance from roads on differences in GUD.

Noise variance was split into categories based on a median split.



3.4 Discussion

In this study squirrels across all sites showed selective patch use leaving lower GUDs, on average, closer to trees than in open (risky) habitat, reflecting the microhabitat preferences found in previous GUD studies conducted within their native range (Lima et al., 1985). For grey squirrels, foraging near the base of large trees offers both an escape route from terrestrial predators and canopy protection from predatory birds (Newman & Caraco, 1987). We used the difference in GUD between pairs of standardized food patches to assess if urban built features can alter the perceived risk between these safe and risky patches. It was found that there was a significant decrease in the difference between these safe and risky patches in relation to proximity to roads and buildings, with pairs of feeding patches closer to these features having smaller differences in GUDs. This suggest that these features do not increase perceived risk, rather, they may reduce it. Noise variability, but not average noise levels, were found to interact with distances from roads and buildings to increase risk perception. Under higher levels of noise variability, the differences between ‘safe’ and ‘risky’ patches increased, suggesting that higher noise variability squirrels are more likely to stay within foraging patches closer to cover where they feel safer. This may be due to the impact of sound on ability to assess other forms of risk, for example social cues from conspecifics and heterospecifics. These results suggest that it is the variable quality of sound, rather than overall noise, that may increase perception of risk, as variability may, perhaps, impact reliability of this signal to act as a risk cue (Gill, Job, Myers, Naghshineh, & Vonhof, 2015; Warren, Katti, Ermann, & Brazel, 2006).

Whilst these results suggest grey squirrels may perceive sites close to urban built features as having lower perceived risk, this may not necessarily imply that living close to human disturbance is risk free. Urban habitats may contain altered and novel predation pressures, although actual predation rates in urban environments appear to be lower (Fischer et al., 2012). Sites near human settlement and disturbance may offer a refuge from natural predators for some species, whilst encounters with humans are likely to be non-fatal in general, and this may explain why, in this study, squirrels were able to forage for longer close to static cues of human disturbance, such as buildings. Previous studies of urban grey squirrels have found that urbanised squirrels become less wary of human activity showing reduced flight initiation distances as humans approach (McCleery, 2009; Parker & Nilon, 2008), although the level of predictability, type and frequency of human disturbance appears to cause variability in the vigilance behaviours of grey squirrels, suggesting that not all forms of human disturbance are perceived equally in terms of risk (Sarno et al., 2014). Furthermore, in urban settings, the ‘safe’ patches, close to vegetation and trees used in this study may not necessarily represent a safer foraging option, as it would in grey squirrels’ native range. Urban gardens may contain higher densities of domestic pets, altering predation risk. For example, domestic cats are ambush predators (Baker et al., 2005), therefore foraging in open habitat may be safer for prey species where cats are present.

Lower GUDs observed in urban sites could also reveal differences between sites in terms of resource quality and missed opportunity costs. Foraging models based on missed opportunity costs predict that GUDs should be higher in environments with high food availability and short travel distances between patches (Olsson & Molokwu, 2008). This may provide an explanation for the higher GUD observed in forest sites, where an abundance of masting trees, such as beech and oak, may provide plentiful alternative foraging opportunities at the time data was collected. In contrast, urban sites may require further, energetically costly, travel distances between aggregated food patches (Hinsley et al., 2008), resulting in increased foraging efficiency (lower GUDs) and increased perceived value of a patch when it is encountered. In a habitat containing high food availability, the differences in GUDs between safe and risky patches are predicted be greater as foragers are less likely to take risks (Olsson & Molokwu, 2008). Conversely, where food availability is limited or patchy, and/or where the foragers are in a low energy state, food becomes a higher value resource and foragers more may be more willing to take greater risks to acquire it (McNamara, 1990). Therefore, the reduced differences in GUDs between safe and risky patches close to urban features may reveal that, in urban habitats, squirrel foraging behaviour shifts from being predator-limited, to being food-limited (Bowers & Breland, 1996).

Contrary to predictions, the model did not find a significant effect of squirrel population density at each site on patch differences in GUD. It was expected that in sites with higher population densities, GUD would be lower, perhaps reflecting the effects of limited access to food resources on foraging behaviour in urban sites, or the benefits of group foraging. Grey squirrels are not regarded as particularly social or territorial in comparison to other sciurids (Koprowski, 1996), however, they demonstrate dominance hierarchies in the context of resource access (Allen & Aspey, 1986), and forage in the presence of conspecifics (Hopewell & Leaver, 2008). The increased presence of conspecifics in habitats of higher population density may allow squirrels to use social information, rather than habitat features, to make assessments about risk (Lima, 1995). Foraging grey squirrels are known to respond to feeding, vigilance, and alarm call behaviour in both conspecific and heterospecific foragers (Getschow, Rivers, Sterman, Lumpkin, & Tarvin, 2013; Jayne et al., 2015; Partan et al., 2010). In a study of urban grey squirrel responses to conspecific alarm calls, it was found that urban squirrels were more reactive to alarm signalling than less urbanised squirrels, and were found to attend most strongly to visual alarm signalling, such as tail flagging, perhaps due to the impact of anthropogenic noise disturbance on attention to auditory signals (Partan et al., 2009). As such, foraging within a group may reduce perceived predation risk for grey squirrels through the benefit of the information provided by 'many eyes' (Lima, 1995). This could allow individuals to reduce vigilance behaviours and invest more time in foraging and feeding, resulting in lower GUDs. Furthermore, it may allow foragers to exploit 'risker' patches more readily if conspecifics are present. Although the effects of social foraging on GUD has not been as widely studied , in a study of the GUD in black rats (*Rattus rattus*) and bush rats (*Rattus fuscipes*), it was found that solo foragers left higher GUD than those foraging in a group, suggesting that social context may be an important factor to consider in GUD studies (Carthey & Banks, 2015).

Whilst reducing perceived predation risk, the presence of other foragers can represent additional foraging costs including patch defence and the risk of aggressive interactions (Jayne et al., 2015). It is possible that in urban sites squirrels are faced with living at high population density and limited access to resources, either because resources are aggregated (e.g. bird feeders, refuge/waste sites) or that resources are limited. These factors combined may lead to higher levels of competition for resources. Perhaps through exploitative competition, individuals in urban sites may be driven to forage more rapidly to obtain a greater share of a high value resource. Further research could consider competition levels at each individual GUD patch to investigate how competition levels may be altering food-safety trade-offs in the context of urban habitat features at each standardised food patch. Furthermore, it may be that the individuals more willing to risk antagonistic interactions with conspecifics are those willing to forage at patches close to areas anthropogenic disturbance. Further work would benefit from taking an individual based approach to find which individuals are foraging at these patches. For example, it might be that bolder individuals, less sensitive to human disturbance, dominate these food patches. We may also find that it is individuals in a low energy state (due to higher competition for resources) in urban habitats (Shochat & State, 2007), that are more likely to exploit patches near sites of human disturbance and engage in riskier foraging. Data collected in this study took place just within typical breeding season: January-June for UK grey squirrels (Middleton, 1930), therefore the value of mating opportunities is likely to be high during some of the time data was collected. According to the asset protection principle (Clark, 1994), the value of safety becomes higher in individuals with high reproductive potential. Squirrels living in sites further from human disturbance could be in a higher energy state, or better body condition, so may be less willing to take foraging risks. However, further studies are needed to assess differences in body condition, reproductive success, and survival rates of grey squirrels across the urbanisation gradient in order to put these findings in this context.

Overall, the results in this study suggest that foraging costs and perception of risk in foragers are altered by proximity to buildings and roads: key urban features related to human activity. This can be interpreted as there being lower predation risk close to these features, or that the marginal value of food is higher for foragers at these sites. It is likely that the differences in GUD across sites in this study reveal a variation in the balance between predation risk, food value and missed opportunity costs across different levels of urbanisation. Future research into foraging and patch use across urbanisation levels should examine the variations in food supply, body condition, reproductive and survival differences in squirrels across the gradient, areas that appear understudied in UK populations of grey squirrels, as this could aid in a better understanding and interpretation of differences in behaviour, distribution and abundance of squirrel populations living at varying levels of human disturbance.

Chapter 4: Does urbanisation influence individual levels of boldness and exploration during escape in grey squirrels?

Abstract

Wildlife living in urban environments are often reported to be ‘bolder’, having higher risk-taking tendencies than their rural counterparts, however, the drivers of individual variation in levels of these behaviours is still largely unexplained in urban environments. This study investigates individual differences in behavioural responses towards handling and towards a novel environment in grey squirrels living at different levels of urbanisation (N = 53, across 3 sites) to test whether these responses were consistent over time (personality variation or plasticity). Due to increased exposure to human disturbance in urban sites, it was predicted that urban squirrels would, on average, be ‘bolder’ during handling, and would be more exploratory in a novel environment than less urbanised squirrels due to the likely relationship between exploration and ability to utilise novel resources. As predicted, handling responses and responses to novel environment were repeatable over time for individuals, although urban squirrels showed slightly lower levels of repeatability than woodland squirrels, suggesting greater behavioural plasticity in urban squirrels in response to these assays. There was a significant effect of site on handling response, with urban and suburban squirrels showing faster escape responses to handling than woodland squirrels. Contrary to the prediction, urban squirrels were less exploratory than squirrels from other sites when faced with a novel environment which included an escape route. Under these conditions, urban squirrels were faster to escape and spent less time exploring. Body index was found to have a significant effect on exploration time, with lower body index being associated with longer exploration durations. The secondary aim of the study was to consider these individual behavioural differences at a smaller spatial scale than is usually employed in studies of behavioural consistency in urban wildlife. Here, trapping locations were used to investigate the association between individual habitat occupancy and behaviour. A trend was found between individual trapping distance from roads and

faster escape responses in urban squirrels, however no significant effect was found across all sites.

4.1 Introduction

Individuals of the same species have been found to differ consistently in their behavioural responses, with this level of variation now thought to shape key ecological processes (Adriaenssens & Johnsson, 2013; Canestrelli et al., 2015; Dall et al., 2012; Sih et al., 2012a). Over the past decade, research into individual behavioural variation that is consistent over time and situation, often referred to as personality variation (Dall & Griffith, 2014), temperament (Réale et al., 2007) and behavioural type (Koolhaas, 2008), has increased within behavioural ecology. This is because, rather than being 'noise' in the data, the level of consistent individual behavioural variation expressed within populations could have important consequences for evolution and ecology (Dall et al., 2012; Dingemanse & Réale, 2005; Réale et al., 2007). More recently this level of variation is being considered within the context of responses to human induced habitat change and disturbance, with the hope that it could provide insights into the ability of some species to survive and cope in an increasingly urbanised planet (Lapiedra et al., 2017; Miranda et al., 2013; Sih, 2013).

The rate at which humans are modifying the environment means that observations of animal behavioural responses to human disturbance and habitat change can provide direct means to monitor the potential ecological and evolutionary impacts of these changes, as the pace of behavioural change occurs faster than many other forms of phenotypic adaptation (West-Eberhard, 1989). Urbanisation represents a significant and particularly fast-paced form of human-induced habitat change and is likely to play a significant role in reduced biodiversity and the extinction of many species(McKinney, 2006). Novel conditions and evolutionary traps created in human-dominated urban landscapes mean that many species fail to cope (Garroway & Sheldon, 2013; Robertson, Rehage, & Sih, 2013; Thompson, Rieseberg, & Schluter, 2018). However, for some species, these environments create opportunities, including a release from natural predators and resource limitation

(Shochat, 2004). Due to the novel ecological and evolutionary conditions found in urban environments , species that flourish here are thought to be behaviourally flexible generalists, able to scavenge or utilise the novel resources encountered in these habitats (McKinney, 2006).

There is rapidly growing evidence that urban wildlife behaves differently from rural and ancestral populations of the same species (Ditchkoff et al., 2006; Miranda et al., 2013). On average urban wildlife is thought to be more aggressive (Foltz et al., 2015), less vigilant (Mccleery, 2009; Sarno et al., 2014; Uchida, Suzuki, Shimamoto, Yanagawa, & Koizumi, 2019) and explore more than rural wildlife (Sol, Griffin, Bartomeus, & Boyce, 2011; Thompson, Evans, Parsons, & Morand-Ferron, 2018). How these behavioural differences arise is not completely understood, although likely drivers of these differences include changes in abiotic conditions including pollution, changes in ambient temperature and light, as well as the differences in biotic conditions, such as increased population density and novel predators (Alberti, 2015; Bonier, 2012; Sepp et al., 2018). To further understand how these urban conditions change behaviour, a number of studies have begun to consider and compare behavioural differences at the level of the individuals occupying these habitats. Several of these studies have found that, in comparison to rural individuals of the same species, individuals in urban habitats are observed to be more aggressive (Foltz et al., 2015), have greater exploration tendencies (Thompson et al., 2018), and demonstrate a higher proportion of neophilic responses (Candler & Bernal, 2014). Broadly, urban environments are thought to contain ‘bolder’ individuals appearing to have higher risk-taking tendencies. One of the key explanations for this is that risk-taking is important for dispersal into new habitats, with ‘bolder’ individuals more likely to disperse further and into more novel habitats, than their ‘shyer’ counterparts (Lowry et al., 2013). Urban habitats are likely to contain high levels of disturbance, including increased exposure to humans, roads, noise and light pollution, and novel predators, which may elevate perception of risk, or increase direct mortality risk, meaning that under some circumstances urban environments could be considered more ‘risky’ than less urbanised ones (Carrete & Tella, 2017; Ciuti et al., 2012; Clinchy et al., 2016).

Boldness under risk, usually predation risk, and exploration of a novel environment have become widely used as measures of individual variation in behavioural risk-taking in studies of animal personality variation. Exploratory behaviour and activity are usually quantified using the open-field test, a novel environment which has been modified in various ways to measure behaviour in both captive and wild individuals (for examples see: Boon, Réale, & Boutin, 2007; Martin & Réale, 2008; Perals, Griffin, Bartomeus, & Sol, 2017). In urban wildlife, levels of exploration behaviour are thought to be higher than in rural wildlife due to the association with dispersal tendency, neophilia and the ability to locate and utilise novel resources. However, tests of exploration behaviour in urban populations have found mixed results, possibly because, whilst dispersers and early settlers to urban environments may benefit from being high explorers, each population is likely to experience different selection pressures as the population establishes (Sol et al., 2013). For example, in urban environments with predictable patches of food resources there may be reduced selection for exploration than in environments where resources are fluctuating or less predictable (Lowry et al., 2013). However, broadly, exploration is expected to benefit urban wildlife where it is associated with information gathering and acquisition of novel resources (Arvidsson & Matthysen, 2016; Ferrer, Thompson, & Morand-Ferron, 2019). Eastern chipmunks living near sites of high human activity were found to show higher durations in exploratory behaviour (Martin & Réale, 2008), and when presented with a novel environment, urban anole lizards (*Anolis sagrei)* explored more than less urbanised individuals (Lapiedra et al., 2017). Black-capped chickadees (*Poecile atricapillus*) caught in urban sites were found to explore faster and have higher levels of repeatability in initial exploration than forest caught chickadees, furthermore, urban caught individuals were found to have higher among-individual variation compared to forest birds, suggesting that divergence between individuals in exploration styles may be beneficial under urban conditions (Thompson, Evans, Parsons, & Morand-Ferron, 2018).

Another commonly employed measure of individual variation in risk-taking are behavioural responses to a predation related threat. This is usually measured via responses to simulated predators (Jones & Godin, 2010), flight initiation distance to approaching human (Atwell et al., 2012; Carrete & Tella, 2010; Sol et al., 2017) or responses to human handling during field tests (Atwell et al., 2012; Careau et al., 2015; Charmantier et al., 2017). Predation is regarded as one of the key selective mechanisms shaping personality variation and distribution of behavioural types (Bell

& Sih, 2007; Dingemanse et al., 2007). Therefore, we might expect, where urban environments contain risk similar to predation risk, personality variation in these environments may follow a similar pattern. Human disturbance and activity can represent both direct and indirect predation risk (Clinchy et al., 2016), furthermore, urban wildlife are likely to face novel predators and novel predation regimes(Fischer et al., 2012). However, these risks in urban environments may be complex to assess as urbanisation may also offer release from direct predation in some species (Fischer et al., 2012).

A key explanation for the existence of animal personality variation is the ‘trade-off hypothesis’, where consistent individual behavioural variation is thought to reflect individual differences in the trade-off between starvation and predation (Montiglio, Sih, Mathot, Wolf, & Dingemanse, 2015; Wolf, Doorn, Leimar, & Weissing, 2007).It is predicted that under high risk conditions, such as high predation risk, there will be more intense trade-offs between mortality and starvation, or resource acquisition, leading to increased personality variation in risk-taking behaviours (Dall & Griffith, 2014; Wolf & McNamara, 2012). Therefore, insights into individual risk-taking under risk in urban wildlife could offer further understanding into the predation (and perceived predation) risks and foraging/resource acquisition demands of urban living, perhaps revealing how ‘risky’ urban life really is. If urban habitats offer relaxed predation and relaxed competition for food resources, then we might expect less variation between individuals in risk-related behaviours. However, there may be a ‘predation paradox’ in urban habitats where, whilst direct mortality risk is low, perceived risk of predation may be high due to human disturbance (Fischer et al., 2012).

Whist several studies have begun to compare differences between animal personality variation expressed in urban and rural populations, many of these take a broad approach to quantifying urbanisation of sites (see Chapter 2). However, a few studies have begun to take a fine-scaled spatial approach to categorising the differences in exposure to urban features experienced by individuals (for example, Carrete & Tella, 2010; Carrete & Tella, 2017). Much like other landscapes, urban habitats are likely to contain spatial and temporal variation in disturbance levels, resource distribution, predation levels, competition levels and other factors likely to influence an individual’s perception of risk. Animals in urban environments may distribute themselves according to these risk factors, and at the individual level there is likely to be differences in habitat selection and habitat use based on behaviour and risk perception. For example, using flight initiation distance (FID, the distance to flee from an approaching human), burrowing owls (*Athene cunicularia*) were found to distribute themselves within habitat according to consistent individual variation in FIDs. Owls with shorter FIDs were found holding territories closer to areas of human disturbance, suggesting that tolerance of humans was a factor shaping distribution of individuals (Carrete & Tella, 2010).

In order to examine some of these ongoing questions regarding differences in behavioural responses in urban wildlife, this study investigates behaviour of grey squirrels in commonly used assays of personality variation: handling responses and a novel environment, open-field test, and asks if those living in more urbanised habitats demonstrate differences in risk-related behaviours under two contexts: 1) boldness during handling and 2) exploration and escape behaviour within a novel environment. Further, we ask if there are individual differences in the consistency of these behaviours over time, and if individuals might distribute themselves within urban habitats according to these behaviours. Trapping locations for each individual was used as a proxy for habitat occupancy, and it is predicted that individuals trapped in close proximity to features related to human settlement including buildings, roads and footpaths, will be ‘bolder’ in their responses to handling and exploration of the novel arena. During handling, behaviours associated with ‘boldness’ including time taken to move into a handling cone, vocalisations, and breath rate are measured. These behaviours are thought to relate to squirrel anti-predator responses. It is predicted that, due to possible familiarity with humans, squirrels living close to humans will be faster to move into a handling cone and show less vocalisations and lower breath rates in the presence of a human.

In the open-field test, duration taken to enter the novel arena, duration to time taken to move through the arena, number of holes investigated are measured. Due to their possible increase in exposure to novel objects and situations in urban environments, it is predicted that urban squirrels with investigate holes more but move into the arena faster than less urbanised squirrels. It is predicted that average levels of risk-taking will be higher in more urban sites, which will be shown with faster escape responses during handling and increased exploration behaviours in an open-field test. Urban sites that are close to disturbance are predicted to show greater behavioural flexibility (lower levels of behavioural repeatability) than squirrels at less urban sites, due to the potential for urban locations to contain higher diversity of risks and novel situations, including human disturbance and exposure to domestic predators.

4.2 Methods

Study species

Grey squirrels are diurnal tree squirrels, and a common exotic mammal in the UK found in both rural and urban habitats containing trees (Bonnington et al., 2013; Williamson, 1983). Within urban habitats in the UK they can be found living at higher population densities (Bonnington et al., 2013) and although they not regarded as a social species, grey squirrels form dominance hierarchies with individuals often defending ‘home patches’ (Thompson, 1978). This species may be useful to explore questions about impacts of urbanisation on mammals due to its abundance across urban, suburban, and woodland areas. Although grey squirrels have not been the focus of many studies of personality variation (although see: Haigh, O’Riordan, & Butler, 2017), they have been widely used in behavioural field studies, in particular studies of foraging and anti-predator behaviours (for examples see: Hopewell & Leaver, 2008; Jayne, Lea, & Leaver, 2015; Makowska & Kramer, 2007; Newman & Caraco, 1987). However, little is still known about the factors influencing behavioural variation of this species in urban environments, particularly in the UK where they regarded as an alien invader, having the potential to come into conflict with humans and other wildlife (Bonnington et al., 2013).

Although in the UK grey squirrels have few natural predators, they manage several risks in their day-to-day lives that may be impacted by urbanisation levels. Urban squirrels live at higher population densities (Bonnington et al., 2013), therefore urban environments may contain increased competition and social risks via increased conspecific presence. They are also likely to face increase competition from heterospecific species, such as corvids. Actual predation rates for urban squirrels appears to be unreported, however, they may face increased predator presence near human settlements from domestic pets including cats and dogs. These species, and the increased presence of humans, may increase perceived risks of predation, a factor known to influence squirrel foraging and feeding behaviours, as well as habitat use. Further, higher levels of disturbance near humans may increase foraging costs through disruption to feeding and increased energetic costs associated with fleeing. Urban grey squirrels may also face several benefits from living alongside humans, for example, humans may provide supplementary food either through direct or indirect feeding, and provide refugia from natural predators (Twining, Montgomery, & Tosh, 2020).

Sites & urbanisation levels

During winter and summer 2015 – 2017, squirrels were trapped at three sites in Buckinghamshire, UK. During summer and winter 7-14 days of trapping was carried out at each site, each year. This included 3-5 days of habituation to traps, where traps were baited, but left closed. Sites included an urban park/school grounds based in the centre of High Wycombe, an area covering private suburban gardens, and a mature woodland based in Great Missenden Buckinghamshire. These sites varied in levels of urbanisation, human disturbance, and squirrel population density. In total 53 adult squirrels were captured across sites, 18 female and 35 males. Estimates of squirrel population density for each site were carried out using fixed-duration point counts (Bonnington et al., 2013; Flyger, 1959) during December 2015. Using the GPS coordinates for each trap location, distances to human settlements/building and roads were measured using the measuring tool in Digimap (EDINA Digimap, University of Edinburgh). From these measures, Principle Component Analysis was used to provide an index of proximity to human disturbance for each trap using the first principle component, PC1, with 95% of the variance explained by this component (contributions: distance from roads 0.65, distance to buildings 0.75).

On a broader scale, each site was evaluated for land cover characteristics by assessing digital images of each site and recording road, building and vegetation cover. Digital images for each site were produced in Google Earth Pro, with each site being divided into 10X10 grid (100 squares 100m X 100m), covering an area of 1-km^2 . Scores for each square were produced according to building cover (0 if ratio of buildings is 0%; 1, if < 50%; 2, if >50%), vegetation cover (0, if 0%; 1, if < 50%; 2, if >50%) and road (0, if absent; 1, if present). Using these summary statistics for each site, Principle Component Analysis was used to compute a score for each site based on the amount of built features and vegetation cover (Czúni et al., 2012). This first principle component accounted for 99.7% variance.

Table 4.1. Description of site characteristics computed from vegetation, road and building cover.

Site	Mean building density	Number of squares with >50% building density	Mean vegetation density	Number of squares with >50% vegetation density	Number of squares containing solid road	PC1 (built features score)	Squirrel population density (individuals per acre) *
Woodland	0.25	3	2.02	100	28	-40.06	0.14
Suburban gardens	0.79	20	1.40	40	27	22.29	0.85
Public park	0.48	17	1.36	44	24	17.76	4.14

Land cover scores for 100 squares covering grid of 1-km^2 area around each site. PC1 values calculated from principle component analysis using methodology described in Czúni et al. (2012). Larger scores indicate higher building and road cover and less vegetation cover.
[i]**** Squirrel population density is based on estimates from fixed-duration point counts taken in December 2015.***

Trapping and handling procedures

Squirrels were trapped during summer and winter 2015 – 2017. Traps were placed at the base of trees and baited with a mix of peanuts, sunflower seeds, maize, and apples to provide hydration. During colder temperatures, a handful of hay was included to provide warm bedding. Traps were covered with camouflage fabric, with additional leaf litter placed on top, and were pad-locked to trees to prevent theft or interference by both humans and dogs, which was a concern in the urban sites. Small twigs were placed vertically at the entrance of the trap to reduce the size of the entrance. This was to minimise the likelihood of non-target species entering the trap, including small domestic cats and pheasants. Within a 1-km^2 area, a trapping grid of 5X5 (squares of 200 m^2) was used to identify trapping locations. Traps were placed at locations within each square where squirrels had been observed to feed regularly and were placed a minimum of 150 meters apart in order to maximise chances of trapping different individuals. Closed traps were placed out a minimum of 5 days prior to trapping to habituate squirrels to their presence. Sunflower seeds were placed on top of these closed traps and feeding signs were used to establish if squirrels had located the trap. If no feeding signs were detected after 3-5days, the trap was moved to an alternative location. During trapping, traps were opened at 07.30 and checked every two hours until 1800. Traps were removed at night.

Measuring ‘personality’ variation

Once trapped, a handling cone was fitted to the entrance of the trap. The time taken for the squirrel to move into the handing cone was recorded. If squirrels vocalised as the researcher approached the trap, or during handling procedures, this was recorded as a categorical variable: yes/no. This data was collected as vocalisations may represent an anti-predator response in squirrels. Once in the handing cone the squirrel was weighed using a spring balance (weight of handling cone subtracted), hind foot length was measured from heel to the end of longest toe using Digital Vernier Callipers. Foot length was dived by body weight to provide an index of body condition relating to potential fat/protein reserves (Wauters & Dhondt, 1989), and reproductive condition was noted for the visibility of nipples in females (indicating pregnancy or lactation) or position and size of testes in males (Ferryman, Mayle, & Morgan, 2006). Based on these signs, squirrels were classified as either breeding or non-breeding. Breath rate was visually counted as the number of breaths taken over 10 seconds, observing rise and fall of the abdomen whilst squirrel was in the handling cone. Breath rate has been used in several of ‘personality’ studies as a measure of responsiveness to human handlers (for example see: Weaver et al., 2018) Squirrels were PIT tagged for individual ID. Only adult squirrels were used in the study, with young released immediately.

Following handling, squirrels were returned to a covered trap with the entrance placed at the opening of the novel open-field arena. Time taken for the squirrel to leave cover and enter the arena was recorded using a stopwatch. The design of the arena was based on the open-field tests employed in studies on wild *Sciuridae* including north American red squirrels (Boon, Réale, & Boutin, 2008), and eastern chipmunks (Martin & Réale, 2008). Although, unlike the standard enclosed open-field test, the design of the arena included an exit on one of the sides meaning that squirrels were not captive and could escape once they had located the exit. This was included as an attempt to reduce the activity behaviours possibly related to trapping responses and fear, rather than exploration. Several authors have noted that activity in an open field test may represent fear related behaviours, rather than active exploration as it is often described in studies of animal personality variation (Greggor, Thornton, & Clayton, 2015; Montiglio, Garant, Thomas, & Réale, 2010; Perals et al., 2017).

The novel arena design consisted of 1.22m X 0.6m enclosure made from white corrugated plastic. The roof of the arena was also made from white plastic with a hole for video recording behaviour. This solid roof was used rather than the clear plastic that is often used in open-field assays, as trials during design phase found that squirrels tried to jump up to the roof. Furthermore, as these tests were conducted in the field, using a solid roof may reduce possible behavioural variation due to the perception of risk caused by differences in canopy cover, a factor known to impact risk perception in squirrels (Bowers, Jefferson, & Kuebler, 1993; Bowers & Breland, 1996). It may also reduce the likelihood of the observer being seen by the squirrels during the trials. The floor was marked into four equal sized squares which were used to quantify activity via the number of squared sections squirrels crossed. Each square also contained a black plastic flowerpot approximately 10cm deep, sunk into the floor (see Appendix). The number of times squirrels placed their head into each flowerpot was recorded. This ‘head in the hole’ test was based on designs from lab based open-field tests, where holes are used to separate exploration from activity related movements that could represent fear (Perals et al., 2017). The total time squirrels spent in the arena (time taken to exit) was also included in the analysis. After each assay, the arena was cleaned using a solution of 70% alcohol. There was a minimum of 5 days interval between each assay for each individual. All procedures and video analyses were carried out by the same observer. Videos were analysed using BORIS software (Friard & Gamba, 2016) and behaviours were measured for frequency, latencies and durations, and defined based on behavioural descriptions for Eastern chipmunks, *Tamias striatus* (Martin & Réale, 2008) and north American red squirrels *Tamiasciurus hudsonicus* (Boon et al., 2007) (see Appendix)

Ethical note

All handling, experimental procedures and animal care was carried out in accordance with Association for the Study of Animal Behaviour Guidelines and were approved by the University of Exeter Biosciences Ethics Committee (2015/892).. A Natural England Licence for trapping and re-release of grey squirrels was held in accordance with schedule 9 of the Wildlife and Countryside Act (licence number 2018-34690-SPM-NNR-5). The researcher also obtained additional advice, mentorship and training from Home Office/FERA Wildlife training modules, and Forest Research (forestry commission) representatives who have experience with squirrel trapping, marking and handling procedures. Permissions from landowners to carry out trapping at each site was obtained.

4.3 Analysis

Analysis was conducted using R statistical software, with PCAs conducted using *FactoMineR* package (Le, Josse, & Husson, 2008) and LMMs fitted using *lmer* function in *lme4* and *lmerTest* packages (Bates et al., 2015). Adjusted repeatability was conducted using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017). Plots were created using *ggplot2* (Wickham, 2016).

Prior to analysis, principle component analysis was used to reduce the duration of behaviours into composite variables. Initially a PCA was run on all behavioural variables collected. Variables with weak contributions to the first dimension of the PCA were then excluded (Appendix D). Factor loadings and visualisations were used to separate remaining behaviours into exploration and anti-predator responses during escape from handling and the open-field test (Figure 4.1). Two behaviours appeared to relate to anti-predator response (referred to as ‘handling responses’). These included times to move from the trap to the handling cone in the presence of a human handler, and time spent still (a possible freeze response) in the novel arena. Exploration responses included time spent walking, time spent with head in holes, time spent visually scanning the arena, and time taken to escape from the arena (total time in arena).

Figure 4.1: Principal component analysis (PCA) plot showing contributions of each behavioural variable.

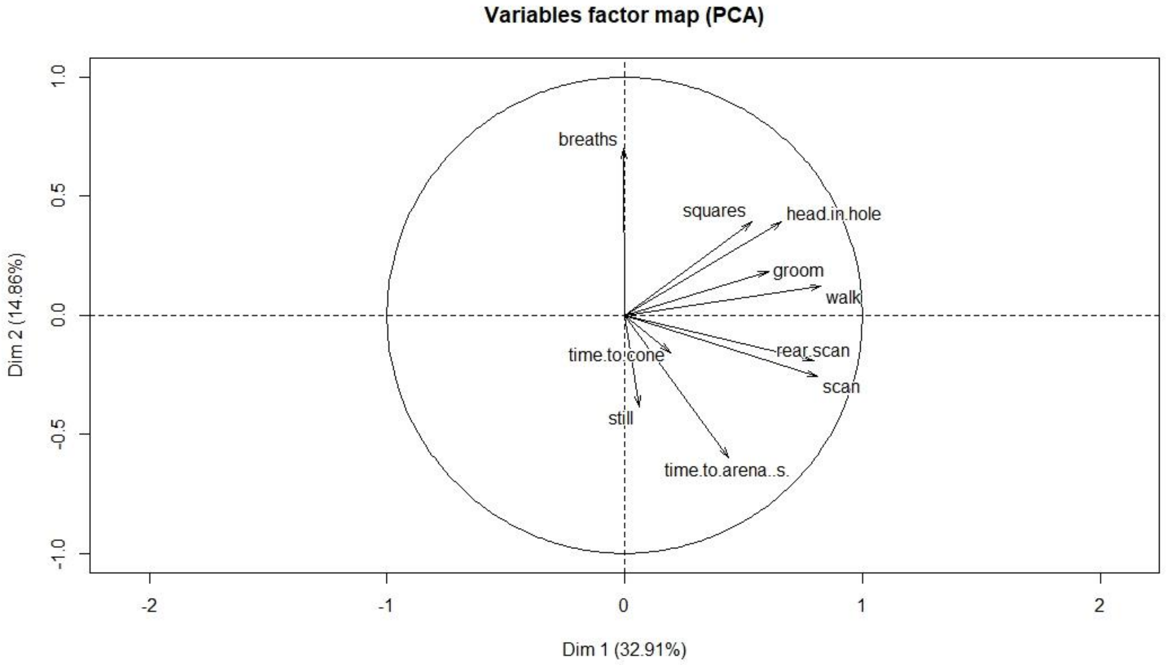


Table 4.2: Behavioural variables contributing to anti-predator/handling response and arena behaviour scores.

Handling responses (boldness in the face of human presence/anti-predator response)		Behavioural responses to arena (Exploration during escape)	
Variable	***Dimension 1 contribution***	***Variable***	***Dimension 1 contribution***
Time to move towards handling cone from trap	0.82	**walk**	0.77
Time spent still in arena	0.82	**Head in hole**	0.55
		Rear scan	0.91
		Scan	0.92
		Total time in arena	0.97

Variance explained	67.6%	**Variance explained**	70.4%
Eigenvalue	1.34	**Eigenvalue**	3.52

4.4 Results

A total of 53 adult squirrels were marked and recaptured across all sites (Gardens N = 13, Park N = 24, Woods = 15). Most were males (Males N = 35, Females N = 18). Squirrels in the Garden sites had higher overall weight and higher body condition scores than squirrels trapped at the other sites.

Table 4.3: Sex ratio, weight and body index of squirrels trapped across sites.

Site	N (sex)	Mean weight g (range)	Mean body index (range)
Gardens	13 (7 M, 6 F)	655.3 (525 – 721)	9.264 (6.908 – 10.565)
Park	24 (19 M, 5 F)	571 (480 – 690)	8.5228 (6.944 – 10.147)
Woods	16 (9 M, 7F)	599.2 (520 – 710)	8.591 (7.493 – 9.595)

Repeatability of behaviour

Individual repeatability in handling (anti-predator) boldness and arena behaviour was assessed with adjusted repeatability using linear mixed-effects models. The response variables, Handling boldness and arena (exploration) scores, were log10 transformed with the addition of a constant (exploration + 2; handling response + 5) to improve normality prior to analysis. Among-individual differences were controlled for using fixed effects for assay date (number of days since July 1st 2015), assay number, sex, body condition, trap distance from urban features, and random intercepts were included for individual ID. Repeatability was also analysed for each site separately. Confidence intervals around repeatability were generated using 1000 permutations using the rptR package in R (Stoffel et al., 2017). Linear mixed-effects models were used to assess sources of variation in arena behaviour and handling responses separately. For each data set, three null models with different random effect structures for individual ID and assay time were compared to find the model with the best fitting random effects structure (Appendix).

The maximal model for arena behaviour included assay time, sex, site, trap distance from urban features, distance from roads, buildings, and footpaths, body condition and their interactions with assay time and site as fixed effects. Continuous variables: body condition, trap distance from urban features (urban) and distance from roads, buildings and footpaths were mean centred prior to analysis. Assay number was re-coded into a categorical factor ‘Assay Time’ (0 first assay; second, third and fourth assays were recoded as 1) with this factor representing change in response from novel environment (first assay) to a more familiar environment (repeated assay). Models were fitted with random intercepts and slopes for individuals and for assay time.

To assess sources of variation in handling response, individual and assay were included as random effects. Assay number, sex, site, trap distance from urban features, distance from roads, buildings, and footpaths, body condition and their interactions with assay time and site were included as fixed effects. Continuous variables were mean centred prior to analysis, and assay number was re-coded into a categorical factor ‘Assay Time’ (0 first assay; 1 repeated assay). All models were stepwise simplified, starting with the maximal model and manually removing predictor variables to then compare with the more complex model. At each step the fixed effect term with the highest non-significant values were removed. Models were compared using likelihood ratio tests.

Table 4.4: Summary statistics for final LMMs with behaviour as the response variable.

Bold p-values indicate significant effects.

Final model	Random term	Var.	Fixed effect	estimate	SE	df	t	p
Arena behaviour	ID	0.0162081	Body Condition	-0.1743	0.0346	40.0444	-5.028	**<0.0001**
	Assay Time	0.0006005	Site (park)	-0.3466	0.0621	32.5274	-5.576	**< 0.0001**
	Residual	0.0084934	Site (woods)	-0.1278	0.0659	32.7996	-1.937	0.06135
			Sex (male)	-0.0856	0.0503	31.9484	-1.702	0.09852
			Body condition * Site (park)	0.1493	0.0497	36.4385	3.005	**0.0047**
			Body condition * site (woods)	0.1597	0.0786	34.5188	2.032	**0.0498**

Handling/anti-predator response	ID	0.17040	Site (park)	-0.2516	0.1740	36.1696	-1.446	0.15666
	Assay time	0.00000	Site (woods)	0.5187	0.2469	36.6900	2.101	**0.04255**
	Residual	0.04846	Distance from road	-0.1809	0.1083	36.2316	-1.671	0.10326

When adjusting for among individual differences, across all sites arena behaviour and handling response were found to be repeatable with exploration behaviour showing higher levels of repeatability than handling/anti-predator responses. For exploration during arena escape, woodland squirrels showed higher levels of repeatability (R = 0.533) than the urban park squirrels (R = 0.287). Squirrels caught from the urban park site also showed lower levels of repeatability for handling/anti-predator responses (R = 0.496) than individuals from woodland (R = 0.671) and suburban garden (R = 0.702) sites.

Table 4.5: Summary statistics for behavioural repeatability.

Adjusted repeatability	*R (CI) Arena behaviour*	*R (CI) Handling response*
All effects (N = 104 observations, 53 individuals)	0.619 (0.434 - 0.755)	0.412 (0.208 – 0.664)
Gardens site (25 observations, 13 individuals)	0.382 (0.104 – 0.736)	0.702 (0.241 – 0.877)
Park site (N = 49 observations, 24 individuals)	0.287 (0.0418-0.583)	0.496 (0.272- 0.728)
Woodland site (N= 30 observations, 16 individuals)	0.533 (0.206 – 0.79)	0.671 (0.302 – 0.864)

Predictors of behavioural responses to arena.

The fixed factors relating to trapping distance from urban features and their interactions were non-significant and were not retained in the final model (see Table 4.4). There was a significant difference between scores for behaviour within the arena for park squirrels compared to other sites, t = -5.576, df = 32, p < 0.0001. Squirrels trapped at the park site were found to have significantly lower exploration scores (spent less time in arena) than garden and woodland caught squirrels. Spending less time to escape from the arena and exploring less (Figure 4.2).

There was a significant effect of body condition on exploration time within the arena, t =-5.028, df = 40, p <0.0001. Broadly, squirrels with lower body index scores (lower body condition) were found to spend more time exploring the arena during escape.

This effect appears more pronounced for Garden squirrels (Figure 4.3). This interaction between body condition and exploration varied by site when both park and woodland sites were used as reference level (Table 4.4). Both squirrels in the Garden and Woodland sites appear to show a wider spread of body condition and exploration scores that those caught in the Park site (Figure 4.3)

Figure 4.2: Differences between sites in overall exploration

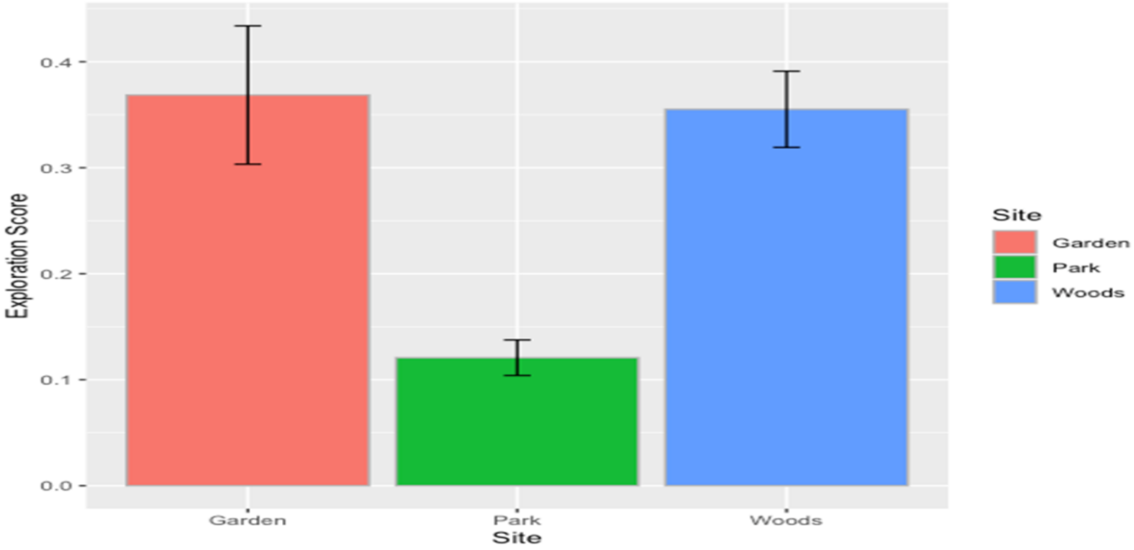
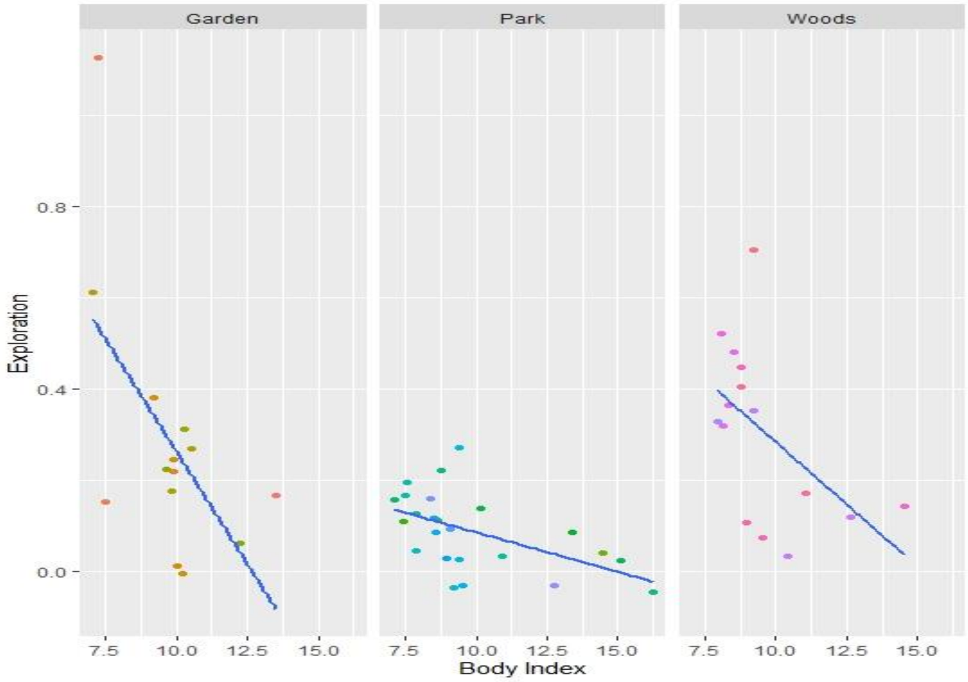


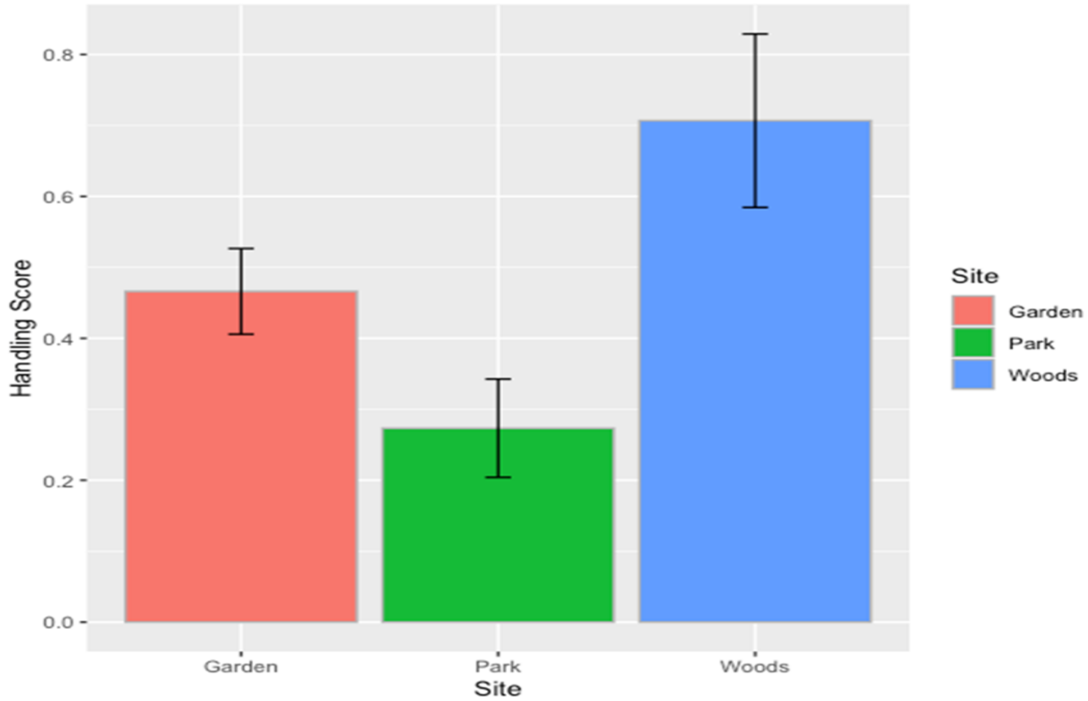
Figure 4.3: Relationships between mean body index and mean exploration scores (exploration during escape from novel arena) by site for each individual. *Exploration scores are log transformed.*



Predictors of behavioural responses to handling (anti-predator responses to human presence).

Non-significant factors including sex, body condition, urban distance scores and trap distance from buildings and footpaths were not retained in the final model. In the final model there was a significant effect of site on handling response with squirrels trapped at suburban garden and urban park sites showing significantly faster handling response scores (faster to move to handling cone and less time spent motionless in the arena) than woodland caught squirrels, t = 2.101 , df = 36, p = 0.04255**.**

Figure 4.4: Differences between sites in overall handling responses



4.5 Discussion

This study aimed to test if squirrels living at different levels of urbanisation demonstrated differences in levels of risk-taking behaviours, as measured by anti-predator responses in the face of human presence (responses to handling) and exploration of a novel arena.. Squirrels trapped across all sites were found to express repeatability over time for both handling and arena response behaviours.

However, repeatability levels were lower in squirrels at the Park site. This suggests that these squirrels may have more behavioural flexibility in terms of these behaviours, than squirrels at the Garden and Woodland sites. The levels of repeatability found across sites were found to be within the expected range for behaviour to be considered consistent or repeatable, with an average repeatability for studies of personality variation reported as being around 0.37 (Bell, Hankison & Laskowski, 2009), suggesting that responses to handling and behaviour in the open-field test could be considered aspects of personality variation in these populations. There have been few studies of personality variation in the eastern grey squirrel, although using trap-mark-recapture data, Santicchia *et al* (2019) found repeatability for trappability ('boldness', r = 0.25) and diversity of traps an individual was caught in ('exploration', r = 0.29).

Repeatability levels of a behaviour is likely to be affected by the methodological factors used to measure it, including the durations between assays and location/context in which they are conducted. For example, in a review of personality studies, durations between behavioural assays of less than a year were found to offer higher levels of repeatability, furthermore, behaviours measured in the field are found to be more repeatable than those measured in lab (Bell, Hankison & Laskowski, 2009). In this study a minimum of five days between assays was used to reduce habituation effects, although this can be considered a short duration between assays. It should be recommended that in order to capture true repeatability over time and context, longer durations between assays should occur, although unfortunately this can be impractical in the study of wild individuals. Therefore, whilst durations between behavioural assays ranged between five days to one year, the moderate to high repeatability found in this study should be treated with some caution as it may yield overestimates due to the short time between the assays.

Exploration during escape

As predicted, there were significant differences between sites in average levels of exploration, however contrary to the prediction, it was found that urban squirrels expressed the shortest durations of exploration, exiting the arena faster than woodland and suburban squirrels. It is possible that these results could be explained in terms of the design of the open-field test used. Due to the open-field arena not being enclosed, it may be measuring ability to locate escape routes, or cognitive differences in processing information about surroundings, in addition to exploration behaviour. Further, our open-field design incorporated a covered roof, in contrast to many other open-field designs where clear Perspex is used. This was employed to reduce fear responses, as squirrels are known to perceive open spaces as riskier, therefore, it is possible that squirrel leaving the arena faster are those that perceive exiting an enclosed space as either low risk or are more willing to take a higher risk. Those remaining for longer may be less willing to move quickly into a higher risk open space or may be more willing to place higher value on exploration or gathering information about their surroundings. Here, squirrels at the park site showed reduced exploration of the arena, having faster escape times. Studies of squirrel foraging in urban parks, suggest that perception of risk level for foraging further from cover may be reduced for squirrels living in urban parks (Bowers & Breland, 1996), therefore it is likely that these squirrels are perceiving the risk level of the open-field test differently.

Squirrels with faster latencies to exit the arena were found to engage in less exploration. The arena behaviours contributing to exploration scores consisted of active exploration related behaviours, and did not consist of freezing, motionless or grooming behaviours that can be related to fear and response to predators in mammals (Doyle & Yule, 1959), therefore, it is likely that duration of time in the arena did capture aspects of exploration. Whilst several studies have found that urban individuals have a tendency towards higher exploration, this may not be universal. Using the traditional enclosed open-field arena, in a study of eastern chipmunks (*Tamias striatus*), urban dwelling individuals were found to be less active. Furthermore, these urban chipmunks were found to have higher body fat, and lower levels of hair and faecal cortisol concentrations. As such, the reduced activity in the open-field test was interpreted as urban chipmunks having a reduced need for exploration due to higher abundance and predictability of resources through anthropogenic food subsidies (Lyons et al., 2017). We found a similar relationship between body condition and exploration for urban and suburban grey squirrels, finding a significant interaction between body condition and exploration, with this interaction varying by site.

Body condition scores can serve as a proxy of fat reserves, which may indicate an individual's access to food resources (Wauters & Lens, 1995). Our results suggest there was a negative relationship between body index and exploration, with squirrels scoring low in body condition showing increased exploration times. This effect was most pronounced in the garden site, although this site contained several outliers with a few individuals showing high exploration behaviours. These results could be interpreted as individuals with less access to food resources having increased motivation to explore in order to gather information about possible feeding opportunities. As this effect was most pronounced in garden caught squirrels, it is possible that squirrels here face slightly enhanced challenges compared to their park inhabiting counterparts, where the spread of body condition scores and exploration were less wide. For example, predation risk may be higher on edge habitats, due to increased predator diversity (Donovan et al., 1997). They might face a greater variety of food resources and habitat complexity through increased diversity of trees, plants and crops near garden (Chamberlain, Cannon, & Toms, 2004; Goddard et al., 2010). Furthermore, garden owners may be more likely to feed wildlife, for example through bird feeders, which might lead to differing levels of conspecific and intraspecific competition regimes over aggregated food patches compared to both rural and more highly urbanised habitats and public spaces (Bonnington et al., 2013; Hanmer, Thomas, & Fellowes, 2017). Perhaps squirrels with lower body condition are less likely to dominate key anthropogenic food resources in these areas such as bird feeders, and are therefore more likely to benefit from exploration for alternative novel resources

Individuals who explore more thought to be more likely to locate, exploit or dominate resources faster (Atwell et al., 2012; Sol et al., 2013).. Studies of the relationships between natural resource fluctuation and personality variation in the wild have found mixed results. For example, wild female great tits *(Parus major)* who were more exploratory were found to have higher survival success in years of low beech mast availability, whereas the effect was opposite for males where high exploratory individuals were found to have lower survival rates during years of low food abundance, perhaps due to changes in population density (competition levels) associated with food availability (Dingemanse, Both, Drent, & Tinbergen, 2004).

In red squirrels (*Tamiasciurus hudsonicus*), exploratory females had faster growing offspring than less exploratory females during years of high resource availability and were more likely to bequeath territory to offspring, enhancing offspring overwinter survival (Boon et al., 2007). Santicchia *et al* (2019) found body mass was positively correlated with trappability in female grey squirrels but no significant relationship was found in males. We found no differences related to sex, due to our sample consisting of mostly male squirrels. Currently, there is no published research into the fitness consequences of personality variation in the grey squirrel. However, there is likely to be sex differences in space use and resource acquisition (Thompson, 1977) that could drive sex differences in personality. Future research could examine the relationships between body condition, behavioural variation, and food resource availability in urban settings in greater detail via habitat mapping of natural and anthropogenic food resource distribution and simultaneous monitoring of habitat use in free ranging individuals, an area seemingly understudied in animal personality variation (Spiegel, Leu, Bull, & Sih, 2017).

Broadly, exploration behaviour is likely to be driven by an accumulation of social and environmental factors in the wild, therefore the differences in exploration found between sites are likely to reflect a number of site-specific differences, for example the urban site contained higher population density of squirrels, as well as increased anthropogenic disturbance. One main criticisms of the use of the open-field test here, is that we did not measure exploration outside of the predation risk context with the presence of a human observer and handler likely to represent a possible predator. This means that results do not capture individual exploration strategies independently from anti-predator strategy. However, it does provide the novel finding that, within this context, lower body condition was associated with increased exploration tendencies, with this effect being most pronounced for urban grey squirrels. Repeatability in exploration was lower in park and garden caught squirrels, compared to woodland squirrels, suggesting that those living in more human dominated habitats showed greater behavioural flexibility in exploration when presented with a novel arena.

Handling responses

In this study, handling responses represented the duration of time taken for a squirrel to move from a trap into a handling cone and the freeze response when entering a novel arena. These responses are likely to represent a response to the presence of a human handler, therefore this context is possibility synonymous to the presence of a predator. We found that squirrels in urban sites exhibited faster escape responses during handling and reduced freeze responses, compared to woodland caught squirrels. It is possible that due to the types of risks they encounter in these more urban habitats, for example crossing roads or open ground away from canopy cover or encountering humans and domestic predators such as dogs and cats, urban squirrels may require faster escape strategies in response to a predation threat. Although non-significant, the model suggested a positive trend between trapping distance from roads and latency to escape, with squirrels caught closer to roads exhibiting faster responses to move into the handling cone and reduced motionless responses to the novel arena.. Responses to handling have been used in a number of studies of personality variation in mammals, including eastern chipmunks, *Tamias striatus* (Martin & Réale, 2008), wood mice *Apodemus sylvaticus* (Hernández, Navarro-Castilla, Piñeiro, & Barja, 2018), and North American red squirrels *Tamiasciurus hudsonicus* (Boon et al., 2007). Handing is likely to simulate stress similar to a predation event in animals unfamiliar with human handling (Carere & Van Oers, 2004).

A number of behavioural responses were measured during handling, including vocalisations and breath rate, however from principle component analysis, time spent motionless in the arena and latency to escape from the handling cone were the two behaviours contributing to the ‘handling response’ measure in this study. These behaviours could be considered as escape related responses in a predation context. In one of the few studies examining personality differences under predation in the wild, Santos *et al* (2015) found that individual homing pigeons (*Columba livia*) that were consistently faster to escape from a confined space were more likely to survive a raptor attack compared to slower individuals. This illustrates that individual consistency in escape and anti-predator responses could have implications for survival (Santos et al., 2015).

Effects of urban habitat features

Urban habitats can provide ‘natural experiments’ where expression of personality variation can be compared across different sites of urbanisation. There is a growing body of research utilising this approach, however, these studies tend to use broad categorisations of urbanisation that may not fully capture fully the differences between sites (Moll et al., 2019). This study opted for taking this broad approach to classification, whilst simultaneously attempting to classify individual levels of urbanisation exposure by including some of the local microhabitat variables associated with the human built environment that may represent possible static cues of urbanisation and human disturbance levels. These consisted of quantifying trapping distance from roads, buildings, and footpaths to produce an urban score for an individual trapping location.

Whilst we did not find a significant effect of microhabitat urbanisation level on individual variation in boldness and exploration related behaviours, further work could benefit from using larger sample sizes covering several urban populations. Our results that demonstrate a possible relationship between body condition and exploration behaviour could also be considered in great detail by quantifying food resource distribution and quality in these different habitats. Although this study did not find a significant effect of static urban habitat variables, taking an individual microhabitat approach can still be recommended as it should help to unravel the selection pressures faced by individuals. Several review papers and empirical studies have discussed the role of animal personality variation in individual niche specialisation (Dall et al., 2012) suggesting that animals are likely to distribute themselves within their habitat in a non-random manner that is likely to reflect individual behavioural specialities under varying social contexts (Bergmüller & Taborsky, 2010; Laskowski & Pruitt, 2014). The hypothesis that individual behavioural variation can be linked to individual differences in risk perception and habitat use is further underpinned by a large body of research into individual variation in fear responses and behavioural energetics (Bleicher, 2017; Brown, 1999; Brown, Laundre, & Gurung, 1999) and can be conceptualised via an overarching framework of the ‘landscape of fear’ (*sensu* Gallagher, Creel, Wilson, & Cooke, 2017; Laundré, Hernández, & Ripple, 2010) .

There have been few attempts to incorporate this landscape of fear approach into the understanding of individual variation in behavioural consistency (although see: Bonnot et al., 2014; Van Dongen, Robinson, Weston, Mulder, & Guay, 2015) , however, it could provide useful insights to the mechanisms selecting for behavioural variation in urban wildlife, in particular how individuals may distribute themselves according to tolerance of human disturbance (Carrete & Tella, 2010). In this study we only considered microhabitat features relating to the built environment: roads, buildings, and footpaths. These were measured due to their potential of being locations with high concentrations of human presence and disturbance. They may also represent static cues of human presence. Grey squirrels are known to use static habitat cues, such as trees, to assess risk. Therefore, it is possible that these could offer relevant cues for squirrels regarding the risk of human encounters. Roads and footpaths could also represent barriers through increasing mortality risk or representing 'risky' spaces between habitats. In a recent study of gene flow in red foxes (*Vulpes vulpes*) these urban features were found to create behavioural barriers for dispersal, contributing to genetic differentiation between urban and rural foxes (Kimmig et al., 2019). In grey squirrels, canopy cover, vegetation, conspecific and intraspecific presence can all provide additional factors effecting perception of risk and dispersal within a habitat(Jayne et al., 2015; Newman & Caraco, 1987; Wauters, Lurz, & Gurnell, 2000). It may be that presence of these can act as a buffer against the risks of human disturbance in this species. Further research could benefit from including all these factors.

Conclusions and further research:

This study provides the novel finding that escape behaviours and exploration in a novel environment are moderately to highly consistent in eastern grey squirrels living outside their native range. Average levels of these behaviours varied between sites, with squirrels living at urban sites having faster escape responses, and reduced exploration during escape. Repeatability in these behaviours was lower at these sites, suggesting increased behavioural flexibility in these behaviours for squirrels living in the more urban locations. These sites varied in both urbanisation factors and squirrel population density factors, suggesting that these factors may drive differences in escape responses between urban and woodland squirrels. Squirrels caught in the urban park were found to show significantly faster escape behaviours under both assays, suggesting that speed of escape may be important in this type of urban environment. These differences could reflect the ability to move across roads and escape from traffic, and/or the ability to respond fast in response to predators including humans. Whilst we did not find a significant effect of trapping microhabitat on behavioural variation, further research could benefit from including additional habitat variables that potentially impact individual competition and anti-predator behaviours, including vegetation structure, food resource availability, and conspecific and heterospecific presence.

Chapter 5: Influence of urban habitat features on responses to competition risk (conspecific playbacks) during foraging.

Abstract

Urban wildlife faces many challenges, including living under increased levels of human disturbance, novel food resources, and changes in heterospecific and conspecific competition regimes. Many successful urban dwelling species may live at higher populations densities than rural counterparts. For foragers in urban environments this could potentially change the balance between managing risk and acquiring resources. Foragers under risk make behavioural trade-offs between acquiring resources and reducing risk, with these risks including exposure to predation and potential aggressive interactions with conspecifics. Habitat features are known to influence both perceived and actual risk levels in many foraging animals, changing the expression of foraging behaviours in relation to certain features. The expression of these behaviour during food acquisition and foraging can reveal an animal’s perception of the risks in its environment as well as the value of food and safety for individual foragers. This study considers the impacts of habitat features and disturbance effects relating to urbanisation on the responses of grey squirrels to a conspecific risk signal to investigate how certain features of urban environments might influence perception and responses to competition in a non-social species where conspecific abundance can occur at higher densities in urban habitats. Auditory playbacks of conspecific calls were used to simulate a cue of a potential foraging competitor, and changes in multiple behavioural responses recorded. Results indicate that certain features of the urban built environment modify responses to competition risk and, perhaps, competitive risk-taking behaviour during foraging. Squirrels feeding closer to roads and buildings, and those under high ambient noise variability, were less attentive to conspecific signals and showed less competitive signalling behaviours. They appear to invest more time to food intake, suggesting individuals living at highly urbanised locations may prioritise acquiring

food efficiently over attending to potential conspecific competition and human disturbance risks.

5.1 Introduction

The presence of humans and human activity can inflict substantial trade-offs for wildlife. For example, anthropogenic noise disturbance can mask the informative content of acoustic communication that provides important information about resource opportunities and predation risk for several species (Barber et al., 2010; Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Luo et al., 2015). Furthermore, disturbance from human activity can distract or divert attention away from attention that could be directed towards the acquisition of key resources (Chan et al., 2010) and can increase physiological stress through increasing the perceived risk of predation (Viblanc et al., 2012). A large proportion of research into the effects of disturbance on urban wildlife has focused on the impacts of noise disturbance on avian species within the context of mate selection and signalling (Kight & Swaddle, 2011), although a rapidly growing body of research is revealing that other forms of anthropogenic disturbance and activity impact a wide range of behaviours in urban wildlife (Lowry et al., 2013). Knowing how urban wildlife responds to disturbance and urbanisation can be key to understanding how urban landscapes could be managed in a way that supports biodiversity and reduces human-wildlife conflict, issues that are becoming more apparent in an increasingly urbanised world.

Whilst human disturbance and activity may cause reduced biodiversity, there are some species able to use anthropogenic resources and may occur at higher population densities in urban habitats (Shochat, 2004). Reduced predator diversity and increased predictability of food resources have been proposed as the key factors enabling these populations to live at higher population densities. Whilst these conditions can support higher population densities, at the individual level this is likely to lead to higher competition levels (Sol, Santos, Garcia, & Cuadrado, 1998). Therefore, it is likely that individuals living under urbanisation face several conflicting and paradoxical demands: increased exposure to human disturbance yet decreased predation risk, increased resource predictability yet increased competition levels.

How this could structure individuals and their behaviour still remains unclear and is likely to vary according to species and level of urbanisation. Shochat argues that the abundance of anthropogenic food resources in urban environments can result in relaxed selection pressures on individuals enabling a higher proportion of poor quality individuals to 'live on credit' compared to those in rural populations where poor quality individuals would not gain access to quality resources (Shochat, 2004). Under some natural conditions, strong competition levels can drive distinctive foraging strategies, with some individuals specialising in acquiring food efficiently under competition risk (Anderies et al., 2007), yet this may not occur in urban habitats if food resources are plentiful and individuals of varying quality have equal opportunity to gain access to food resources. However, if competition levels are high, and resources are aggregated (for example supplementary wildlife feeders or refuse sites), individuals may face high levels of competition near to these sites. Urban wildlife may also face a range of other potential sources of risk during feeding and finding food, these can include competition from other species and exposure to potential predators. They are also likely to face increased risk of disturbance from human activity. Human disturbance may represent a cost to foraging through increasing the time and energy required for vigilance and fleeing, thus reducing feeding intake (Frid & Dill, 2002).

This study attempts to quantify how individual foragers might balance the risk of conspecific competition risk against the risk of human disturbance whilst feeding at an aggregated food patch during a simulated conspecific intruder event. Experimental food patches with a known quantity of food are placed across locations varying in proximity to fixed urban features that are likely to be associated with human activity. Here we use eastern grey squirrels (*Sciurus carolinensis*), a mammal common to urban habitats in the northern hemisphere, found to be living at higher populations in urban landscapes compared to rural woodlands (Bonnington et al., 2013; Parker & Nilon, 2008). Grey squirrels have provided a model system in which to consider foraging risk trade-offs in a number of studies. Foraging squirrels are known to use static cues as 'rules of thumb' for assessing risk within their habitat (Leaver, Jayne, & Lea, 2016), these static cues include distance from trees/cover, features related to ease of escape and visibility to predators (Leaver et al., 2016; Lima et al., 1985). Grey squirrels may also use dynamic cues of risk including the number of conspecifics, heterospecifics, or predators within a location (Hopewell & Leaver, 2008; Jayne et al., 2015a; Leaver et al., 2016).

Foraging and finding food form key survival activities for most animals. Examining the behavioural strategies foragers use to balance risk and resource acquisition during foraging provides useful means to understand how an animal perceives threats and opportunities within its landscape (Brown, Laundré, & Mahesh, 1999). In urban habitats disturbance caused by human activity may have the potential to increase foraging costs in several ways, including increasing the frequency of unnecessary vigilance behaviour that can consequently decrease feeding intake, masking of predator cues and distracting attention that could lead to increased morality risk where risk and monitoring of predator activity cannot be assessed adequately (Luo et al., 2015). As a result, urban wildlife potentially faces different foraging-fear trade-offs compared to their rural counterparts. Studies of urban wildlife suggest that these varying risks could be a key factor in driving many of the reported behavioural differences between urban and rural wildlife, such as bolder, more aggressive and higher levels of risk-taking behaviour exhibited by dwelling urban species and individuals (Garroway & Sheldon, 2013; Lowry et al., 2013).

All habitats vary in risk, and features within these habitats are known to influence an animal's perception of how risky places within its habitat are. The habitat features in urban landscapes that could shape differences in risk perception and risk-taking behaviour remains an area warranting further investigation, particularly at the local microhabitat level where exposure to anthropogenic disturbance may vary. The interaction between risk and habitat use can be conceptualised via the landscape of fear (Laundré et al., 2010). Here, patterns of habitat use by a species can be used to map spatial and temporal variation in risk as it is perceived by the animals, with the underlying assumption that animals will avoid parts of a habitat they fear and perceive to contain risk. This ecology of fear framework has been employed to study the impacts of human activity on habitat use revealing that, for some species, human activity and disturbance can shape habitat use in much the same way as other predator species (Ciuti et al., 2012; Suraci et al., 2019). In other words, disturbance caused by human activity can increase the perception of risk. One of the key methods used for quantifying forager perception of local risk is through the use of giving up density (GUD). This quantifies foraging via the amount of food remaining at standardised artificial food patches placed at different locations within a habitat (Brown, 1988). Based on marginal value theorem (Charnov, 1976), the GUD approach assumes that amount of food remaining at a standardised depletable food patch (the giving up density) reflects the perceived foraging cost at the patch. Lower GUDs (more food consumed/more of the food patch depleted) reflects a lower net cost (low risk feeding opportunity) and high GUD (low proportion of food consumed at a patch) represents a higher net cost (Brown, 1988). GUD studies conducted in urban habitats have found that generally these habitats have lower GUD's compared to rural ones (Abu Baker et al., 2015; Bowers & Breland, 1996b), suggesting that urban habitats might be perceived as safer, although these results could also indicate that urban wildlife are more willing to take greater risks during foraging, perhaps because they face a different balance between food and safety compared to their rural counterparts (Bowers & Breland, 1996). Studies examining behavioural responses to simulated predation risk, such as measuring the flight initiation distance (FID) to an approaching human, have also supported the finding that urban wildlife appear to have reduced vigilance toward human approach. This may be due to reduced sensitivity, or habituation to humans, or a greater willingness to take risks during feeding (Møller, 2010; Uchida et al., 2019). One of the key findings from GUD and FID studies across different habitat types, is the importance of static habitat features on a forager's perception of risk. For example, canopy cover and vegetation can offer protection from some predators, although can impair ability to detect predators for example through blocking sight lines (Embar et al., 2011). Furthermore, due to lower perceived predation risk, these sites could prove more popular with other foragers, thus increasing the risk of competitive encounters (Clermont et al., 2017; Hirsch, 2002). However, unlike static features, competition risk may represent a dynamic for of risk, likely to vary over time and place, yet may correlate with static cues (Leaver et al., 2016; Lima, 1995; Lima et al., 1985).

Risks associated with competition may be different for urban wildlife and could offer a further explanation for the reported increase in aggression and 'boldness' found in urban wildlife for several reasons. Firstly, urban dwelling wildlife may live at higher population densities to their rural counterparts (Rodewald & Shustack, 2008; Shochat et al., 2010), resulting in higher potential for conspecific interaction and conflict. Secondly, resource availability may differ from rural habitats, for example there may be supplementary feeding or refuse sites offering novel and aggregated food patches (Shochat, 2004). It is possible that perceived risk of conspecific competition for food resources could represent a key dimension in the relationships between feeding and risk related behaviours in urban wildlife, and area that current appears understudied. Living at high population density may offer benefits as well as risks. The presence of other foraging conspecifics can provide information about quality feeding opportunities and profitable feeding patches. Conspecifics and heterospecifics can also offer information about predation risk (Magrath, Haff, Fallow, & Radford, 2015). However at feeding locations with low predation risk and high resource quality, foragers may face increased competition as these locations can become popular foraging sites, eventually dominated by more aggressive competitors (Johnson, Grant, & Giraldeau, 2004; Ovadia & Zu Dohna, 2003). Therefore, patch quality (the value of the food at a patch as well as the perceived risk level of the patch) is likely to an important factor influencing the relationships between competition risk and foraging behaviour (Ovadia & Zu Dohna, 2003).

At quality feeding patches, increased risk of aggressive encounters, or increase in competition over resources, will come at an additional cost to feeding through the need for foragers to increase vigilance and increase investment in patch defence behaviours (Partan et al., 2010, 2009). To investigate some of these trade-offs in urban wildlife, the current study uses eastern grey squirrels (*Sciurus carolinensis*) as model species to ask if there are differences in responses to competition risk in foragers feeding at differed levels of habitat urbanisation and proximity to urban habitat features. Although grey squirrels not considered a particularly territorial species, they are known to form dominance hierarchies around feeding sites, with the most dominant individuals tending to be larger adults (Allen & Aspey, 1986; Thompson, 1978). Aggressive encounters between individuals predominantly consist of agonistic chases, as well as social dominance signalling behaviour such as tail flagging and tooth chattering. These interactions can impose a risk of injury through fighting, but are more likely to result in interruptions to foraging through being chased away from a patch by a dominant individual (Thompson, 1978) and cache pilfering(Hopewell & Leaver, 2008). These are likely to represent key foraging costs via the interruption of food acquisition. Jayne et al (2015) found that the presence of conspecifics represents a risk of foraging interruptions to foraging grey squirrels. Following playbacks of conspecific calls, squirrels tended to increase vigilance rather than flee, and tend to return to foraging faster in comparison to responses to predator playbacks, suggesting that conspecifics represent social risk rather than a mortality threat (Jayne et al., 2015).

Following these findings by Jayne *et al* (2015), this study uses conspecific playback calls to simulate a potential competitive intruder and asks whether different static features of the urban built environment impact squirrels' behaviour during foraging and if these could reveal anything about the competitive foraging trade-offs faced under human disturbance. The foraging behaviour of grey squirrels has been well studied making them a good model species for examining foraging responses under varying conditions. However, despite their abundance in urban habitats, how their behaviour is affected by urban factors is less well known, and it remains unclear how particular features of urban habitats might contribute to behavioural differences between urban and rural populations in this species. This may be of interest in areas, such as the UK, where grey squirrels are non-native invaders and have potential to come into conflict with humans (Bonnington et al., 2013, 2014). Whilst urban habitats could provide predation release for grey squirrels, they may form prey for red foxes, domestic dogs and raptors. Furthermore, the non-lethal disturbance from humans could carry foraging costs similar to those of predators for this species (Bateman & Fleming, 2014). In the UK, they are abundant in across urban and woodland habitats, living at higher population densities in urban sites, and are likely to benefit from both direct and indirect supplementary feeding in urban habitats (Bonnington et al., 2013).

Urban environments and anthropogenic disturbance have been found to impact communication and anti-predator behaviour in several other squirrel species. Rural Prairie dogs were found to respond more sensitively to human disturbance compared to urban prairie dogs (*Cynomys ludovicianus)*, although over-time, those living in urban sites showed increased reactivity to human disturbance (Magle, Zhu, & Crooks, 2005). Urban dwelling fox squirrels (*Sciurus niger*) were found to have lower levels of vigilance during foraging compared to those foraging in less urban sites (Mccleery, 2009; Mccleery, Lopez, Silvy, & Gallant, 2008), whilst Rabin *et al* (2006) found that ground squirrels increased vigilance levels in areas with high levels of anthropogenic noise. Similarly, urban grey squirrels were found to have up to 42% increase in vigilance compared to those at less urbanised sites (Sarno, Parsons, & Ferris, 2015) suggesting that human disturbance is a cost to foraging in these species. Explanations for these findings included the possibility that unpredictable noise disturbance and higher population of conspecifics may result in the need for higher vigilance levels, although, to our knowledge, these variables were not tested. Furthermore, these studies did not consider static urban habitat features as predictor variables, rather, habitats were defined as urban or rural on broader habitat scales. The current study attempts to explore these explanations by considering if squirrels at different proximity to urban features varying in foraging and vigilance responses to a cue of conspecific risk.

Building on studies examining anti-predator and vigilance behaviours in urban squirrels, the current study measures a number of habitat features associated with the urban built environment, close to human activity, to consider if these potential static cues of human activity and disturbance risk influence squirrels' responses to a simulated potential conspecific risk event: an auditory conspecific playback. These static habitat features include distance from buildings, roads, and footpaths. Due to the use of an auditory stimulus to represent a cue of social risk, we also measure noise levels as these are likely to influence attention and perception of auditory cues. It is also possible that noise disturbance could represent a dynamic risk cue of human disturbance risk. It is predicted that squirrels foraging close to human built features will show greater levels of vigilance than those foraging further from these features due to the possibility that these sites represent potential cues of human disturbance, however, we may expect them to be less responsive to social risk cues possibly because these 'riskier' locations will represent less risk of social intrusion.

To consider if patch quality impacts the relationships between response to social risk and foraging behaviour, standardised feeding patches are provided and the local patch quality (measured by the amount of seed availability) surrounding each standardised feeding patch is measured. It is predicted that local patch quality will impact responses to conspecific risk with squirrels foraging at feeding patches within higher quality feeding locations likely to show increased vigilance following playbacks due to the increased potential for a competitive encounter (Partan et al., 2010). Squirrels feeding at these locations are also predicted to increase competitive/social signalling behaviours, as we may expect individuals at these higher quality sites to have increased competitive foraging ability (Anderies et al., 2007; Thompson, 1978). The relationships between local food quality and responses to conspecific calls may be further influenced by the forager's exposure to noise disturbance and locality to the urban built features, such as buildings, roads, and footpaths. Squirrels foraging in patches close to these built features and those feeding at patches with high noise variability are predicted to show higher vigilance and longer latency to return to foraging due to the unpredictable nature of noise disturbance impacting risk assessment.

5.2 Methods

Study sites and urban features

Between October- February 2017 and 2018, forty-one artificial feeding locations were established across High Wycombe and Great Missenden, Buckinghamshire UK, where squirrels had been regularly observed foraging at ground level. Locations were selected via walking transects, with an observer noting locations where squirrels were observed foraging. Artificial feeding locations were placed at a minimum of 300 meters apart to minimise the likelihood of repeating observations on the same individuals, with the maximum recorded linear distance of home range size for grey squirrels being 136.7 meters (Doebel & McGinnes, 1974). Each standardised food patch consisted of a circular black tray filled with 5 grams of dry leaf matter and 25 grams of granulated peanuts. Whole peanuts were not used as larger food items may be carried away to be eaten under cover or cashed. Distance from trees are known to impact squirrel risk perception (Lima et al., 1985), therefore all feeding sites were placed at the base of a tree in order to reduce the effects of variation in distances from trees. Squirrels were habituated to these artificial feeding patches prior to behavioural observations for a minimum of seven days, to reduce the likelihood that behaviours observed were responses to the novel food. Each feeding patch was classified as broadly being within either being a park, garden, or within an edge habitat. Edge habitat was defined as a patch that borders a woodland area between either garden or parkland. The GPS location of each feeding patch was then plotted in on an OS map using the ROAM and measure functions in EDINA

DigiMap (EDINA Digimap, Edinburgh, UK) to measure distances from roads, buildings, footpaths, and vegetation at each location.

Local habitat quality at feeding patches

At each of the standardised feeding patches the quality of the surrounding natural feeding resources were quantified using the closest tree to the feeding tray and ground seed counts of the surrounding area. A visual estimate of percentage canopy cover was made using the forestry inventory analysis reference diagrams for plant cover estimation found in Manley *et al*. (2006). Natural food abundance was calculated using mean seed count collected from three 1m^2 quadrant counts thrown from the base of the tree. Seed counts included all fallen seeds and seed cases found within each quadrant. These predominantly included mast from European beech (*Fagus sylvatica*), although many also contained oaks, hazelnut (*Corylus avellane*) and walnut (*Juglans regia)*. A local patch quality index was then calculated for each feeding location using the mean seed count multiplied by the percentage canopy cover (Wauters & Lens, 1995). Seed counts were collected up to three days prior to behavioural observations.

Noise levels

Leading up to behavioural observations noise levels were taken from an observation point, located between 20 – 40 meters from the artificial foraging patch. Noise levels were sampled every 30 seconds using a hand-held Benetech digital sound level meter (A-weighted, range 30 – 130 dB) over a 20-minute period, resulting in 40 sampling points for each patch. If a squirrel arrived at the feeding patch during this time, then sound level sampling was stopped in order to carry out behavioural observations. Noise level recording would then begin again once the squirrel had left the feeding patch if the full 20 minutes of noise sampling had not been completed.

Playback stimuli

Squirrel behaviours at the artificial feeding patches were observed by a single observer from within a camouflaged hide placed at a minimum of 20 meters from the supplementary food patch. Maximum distance was not measured but this was unlikely to exceed 50 meters. Where possible, the hide was placed against vegetation or shrubs to provide additional camouflage. Observations took place between 8:00 and 17:00hrs on dry, still (less than 5 on Beaufort Scale), days between October and February, when squirrels are most likely to actively forage at ground level. Temperatures during observation days ranged between 3 – 17 ° C. Video recordings of behaviour begun as soon as a squirrel arrived within 0.5 meters of the feeding tray. Once squirrels had been observed foraging around the food tray site for a minimum of two minutes the playback begun. Playbacks were played via Bluetooth from a mobile phone to a speaker placed at one meter from the food tray and camouflaged using dry vegetation as cover. Conspecific playbacks were obtained from a recording of a warning ‘kuk’ ‘quaa’ vocalisation from a single, unfamiliar individual (British Library Sounds, W1CDR0001537 BD4). These vocalisations are thought to relate to resource guarding and aggression (Thompson, 1978), although the informative content of grey squirrel calls appears somewhat unknown, the ‘kuk’ ‘quaa’ vocalisations that are expressed when conspecifics are present are thought to offer social warnings (Partan et al., 2010; Thompson, 1978) . Using Audacity 2.2.0 software, audio recordings were cut into ten 15 second segments. Rather than use the same segment for all observations, each squirrel was played only one of these segments. This was done to reduce potential effects of possible referential content in these calls. Calls were played at an amplitude of between 60-70 dB as measured with a sound level meter at 1 meter from the speaker, to reflect the average amplitude found in the wild (Lishak, 1984).

Recording of behavioural responses and observation procedure

Video recording begun when an individual squirrel arrived at the food patch. Squirrels were observed foraging for a minimum of 2 minutes prior to playbacks being initiated, to obtain a measure of baseline foraging. Following playback stimuli, behaviours were continuously video recorded until the squirrel left the patch. Observations were not included for analysis if other squirrels, or heterospecifics such as corvids, interrupted the foraging bout or were seen nearby. All observations were recorded by the same observer from within a pop-up observation hide positioned a minimum distance of 20 meters from the food patch. Video recordings of behaviour were coded using BORIS event logging software (Friard & Gamba, 2016). Pre-playback and playback segments for each video recording were analysed separately. Behavioural analysis focused on continuous sampling of the following behaviours: 1) Vigilance: squirrel stops current activity and looks around with head up. Either in upright bipedal or quadrupedal position. 2) Foraging: searching for food on the ground; sniffing or digging. 3) Food handling: manipulating food items with forepaws and mouth including feeding. This was treated as a separate category from foraging, as this form of feeding may allow squirrels to perform both low level vigilance and feeding (Makowska & Kramer, 2007) 3) social signalling: tail flagging/waving; vocalisations. Behavioural categories were defined based on ethograms described in other sciurid behavioural studies (Boon, Réale, & Boutin, 2007; Lea & Blumstein, 2011; Partan, Fulmer, Gounard, & Redmond, 2010). Latency to return to foraging following the playback was recorded during analysis of post-playback behaviour. Following each foraging trial, the weight of the peanuts remaining after the squirrel had left the patch was used to quantify foraging intake. This was measured using the volume of peanuts consumed divided by the duration (in seconds) at the feeding patch.

Ethics statement

Research was carried out with approval from the University of Exeter Biosciences Ethics Committee (reference 2015/892) and conforms to the Association for the Study of Animal Behaviour (ASAB) guidelines for use of animals in behavioural research (2014). Permissions to conduct research was also obtained from the relevant landowners of each site.

5.3 Analysis

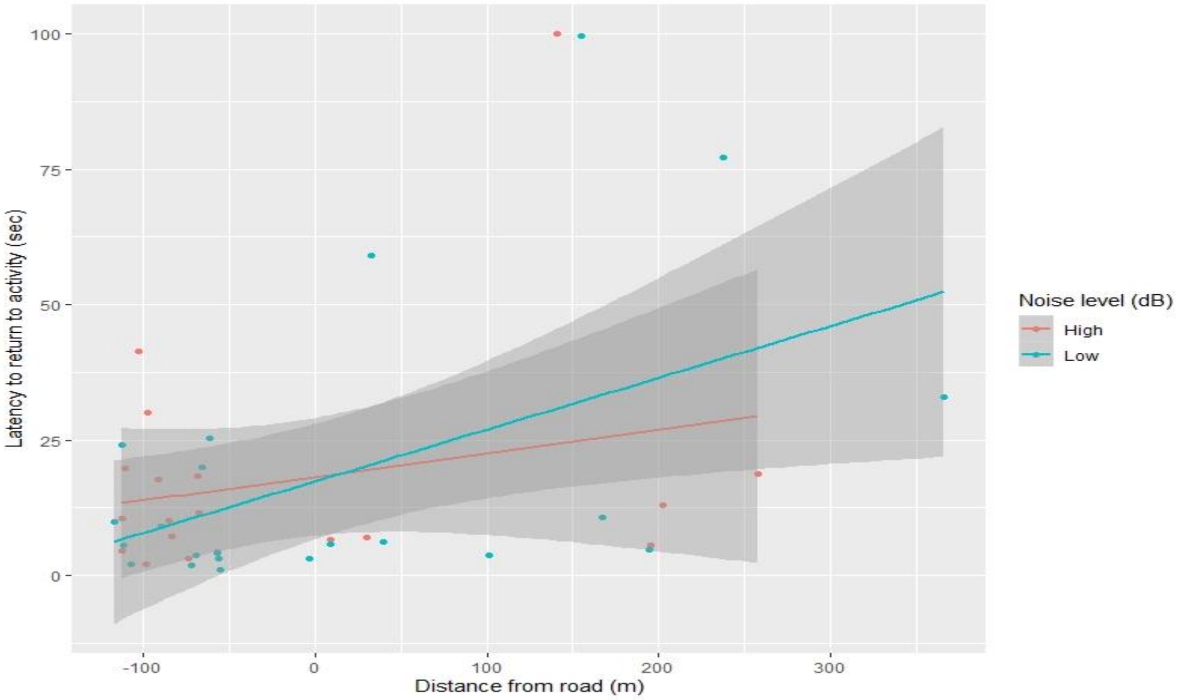
To examine if foraging behaviours, vigilance, feeding rate and social signalling responses to conspecific playbacks were affected by habitat features, data were fitted using generalized linear models with gaussian distribution. Prior to data transformation, habitat features roads and buildings were found to be highly correlated (Appendix E), however both factors were retained in the initial model to examine the possibility that they may represent a different risk cue for foragers, Continuous predictor variables were mean centred prior to analysis. All models were initially fitted with distance to vegetation, buildings, roads, and footpaths, mean and variance sound levels, local patch quality, and habitat type as fixed factors. Two-way interactions between patch quality and each urban feature (distances from road, buildings and footpaths), two-way interactions between each urban feature and noise levels, and two-way interactions between urban features were all fitted in the maximal models. All models were fitted using the *lme4* package (Bates et al., 2015). Final models were selected based on AIC scores. Model reduction was carried out using backwards stepwise regression using the *step* function in the *car* package (Fox & Weisber, 2019). Confidence intervals associated with fixed effects in each of the final models were calculated using the *confint* function. All analyses were carried out in R.

5.4 Results

Latency to return to activity post-playback

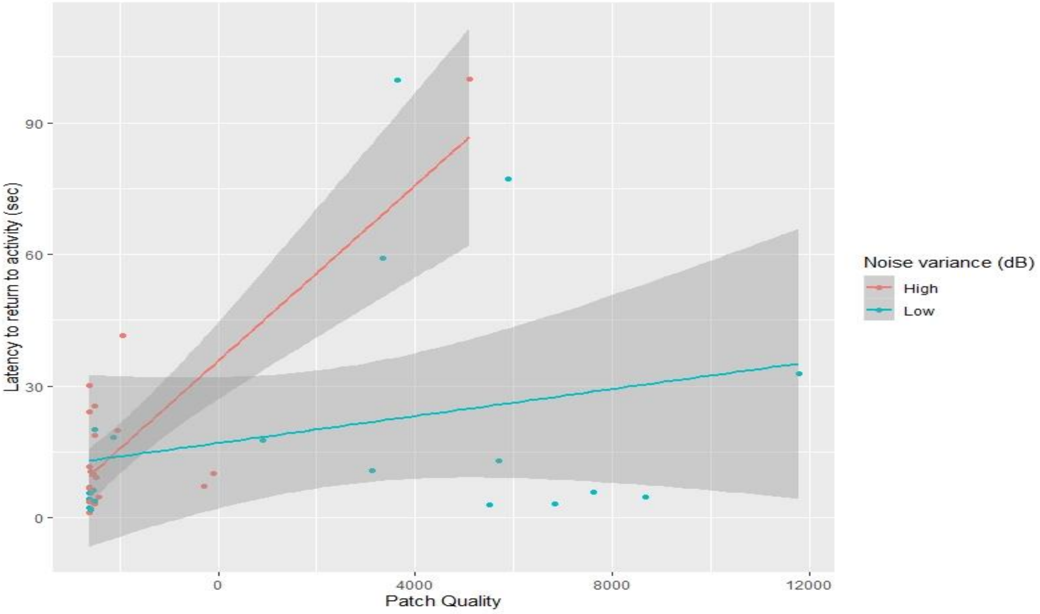
In the final best-fit model (Table 5.1), no significant effects of single habitat features on latency to return to activity were found. However, there was a significant interaction effect between mean noise levels and distance from roads t(40) = -2.964, p = 0.005, with the distance from roads having a more pronounced effect on increasing the latency to return to activity for squirrels feeding at quieter patches (Figure 5.1). There was a significant interaction between habitat quality and variation in noise level on latency to return to activity post-playback t (40) = 2.941, p = 0.005, with squirrels feeding at high quality patches, with high noise variability, showing longer latencies to return to activity following a conspecific playback (Figure 5.2).

Figure 5.1:Interaction between noise level and distance from roads on latency to return to activity post-playback.



**Noise level was split into high and low categories using a median split.*

Figure 5.2: Interaction between noise level and patch quality on latency to return to activity post-playback.



**Noise variance split into high and low categories using a median split.*

Table 5.1: Final generalized linear model of latency to return to activity post-playback.

Fixed Effect	**Estimate**	***SE***	***t***	***p***	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	0.022	3.421	6.472	<0.001	0.0154	28.850
Buildings	0.0146	0.008	1.680	0.102	-0.002	0.3181156902
Roads	-0.0002	0.006	-0.040	0.968	-0.012	0.119
Noise levels	-1.588	1.278	-1.243	0.222	-4.091	0.916
Noise level variance	0.018	0.022	0.842	0.406	-0.025	0.626
Patch Quality	0.0000	0.0001	0.649	0.520	-0.0001	0.003
Roads * Noise levels	-0.0037	0.0012	-2.964	**0.005**	-0.0062	-0.0127
Noise variance * Patch quality	0.00001	0.00000	2.941	**0.005**	0.00005	0.0002

Changes in vigilance

The final model (Table 5.2) suggests that distances from roads, buildings, patch quality and noise variance had significant effects on the change between pre- and post-playback vigilance levels. Squirrels foraging further from roads, t(40) = -3.378, p <0.001, and buildings, t (40) =3.772, p <0.001, showed a greater increase in proportion of time spent vigilant following conspecific playback. Those foraging at higher quality patches showed moderate increases in vigilance, t(40) = -2.40, p<0.001, and foragers at patches with lower variability in noise levels were found to show greater increases in vigilance levels than those feeding in high noise variability patches, t(40) =-3.40, p<0.001 . Significant interaction between patch quality and footpaths suggests that higher quality patches, furthest from footpaths, significantly increased their vigilance levels post-playback, t(40) = 3.172, p = 0.004. Similarly, foragers with greater distance from footpaths at patches of high noise levels were found to respond to playbacks with increased vigilance, t(40) = 2.839, p = 0.009. Significant interactions between road distance and habitat type, and interaction between distance from buildings and habitat type, suggests that differences in vigilance response are further impacted by habitat type with proportion of increase in vigilance at patches further away from buildings, t(40) = 2.443, p = 0.022, or roads, t(40) = 3.289, p = 0.005, varying according to whether foragers were within park, garden or edge habitats (Table 5.2).

Figure 5.3: Interaction between distance from roads and habitat on proportion of vigilance behaviour.

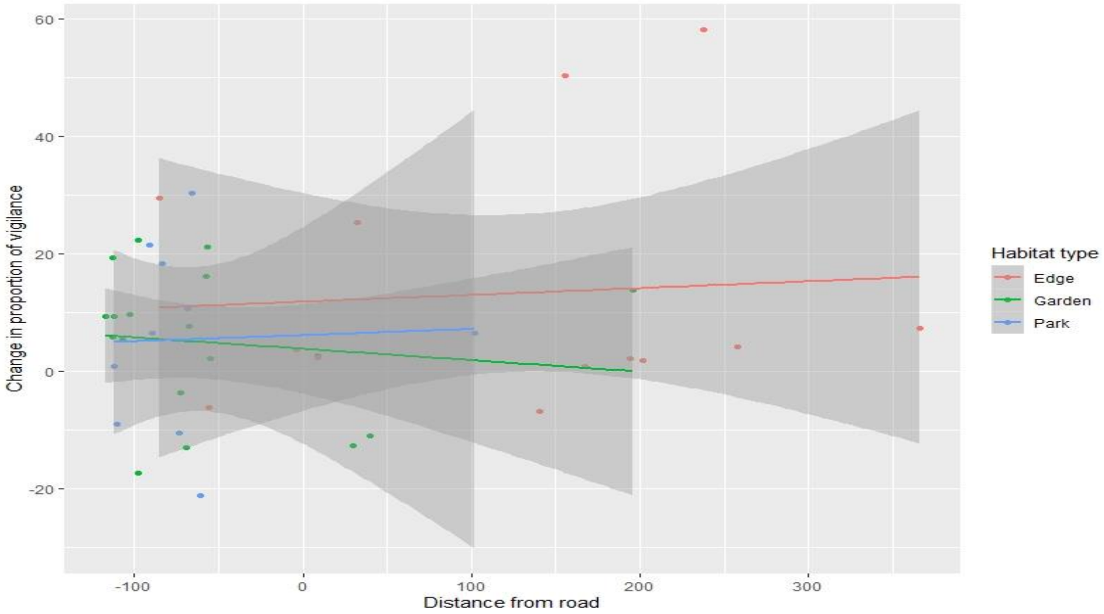


Figure 5.4: Interaction between distance from buildings and habitat on proportion of vigilance behaviour.

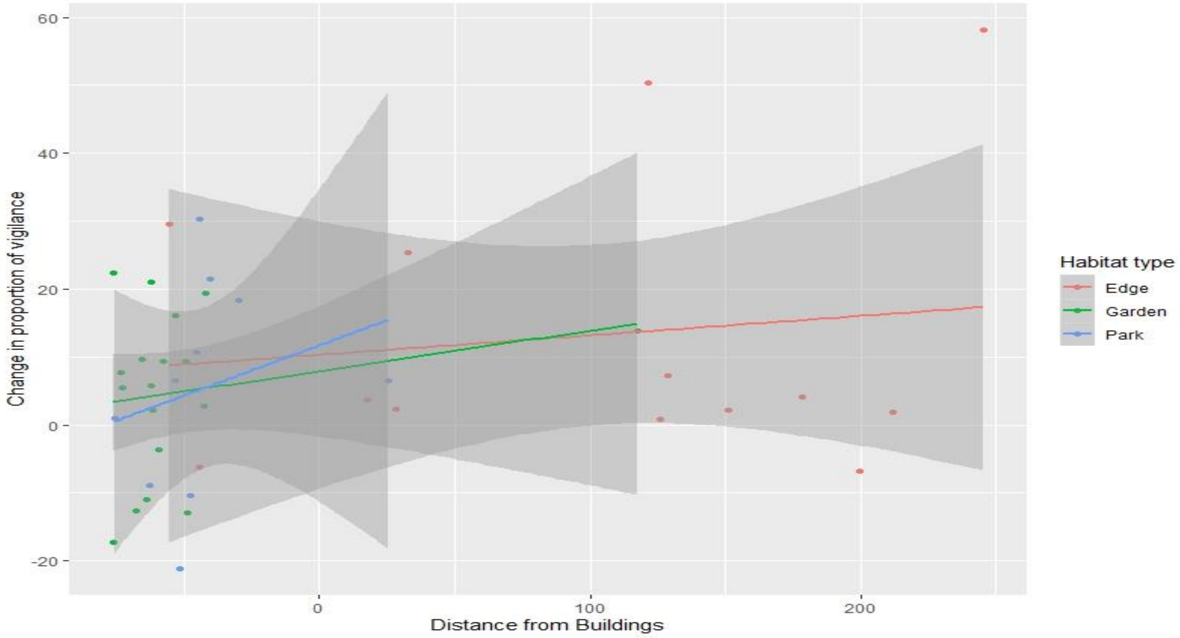


Figure 5.5: Interaction between distance from footpaths and noise level on proportion of vigilance behaviour.

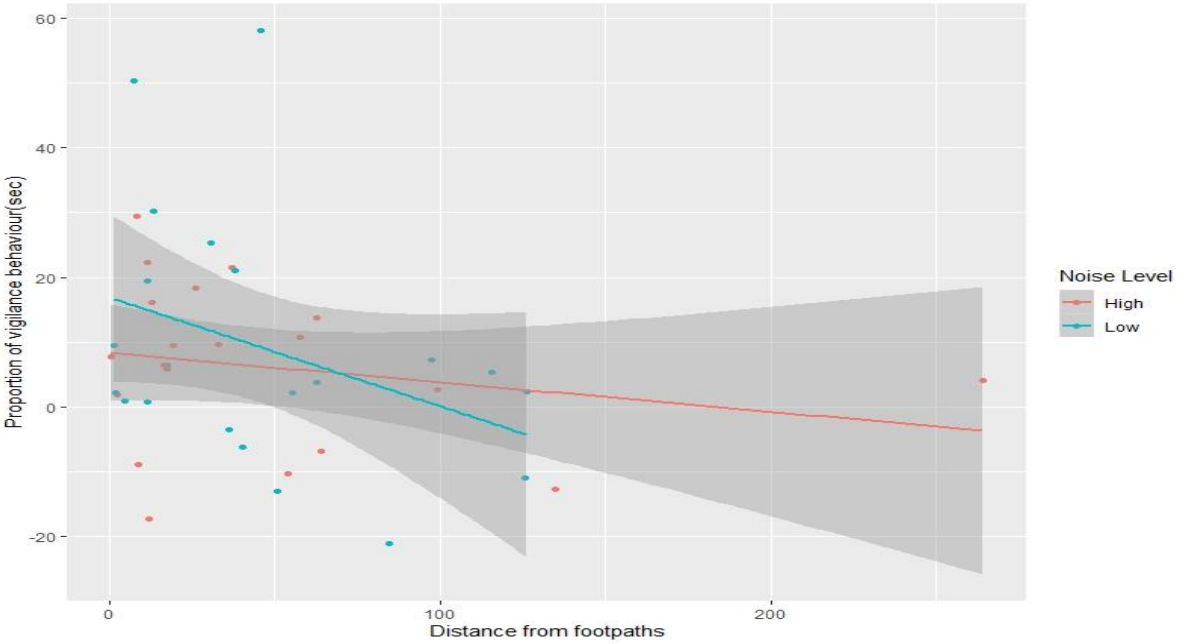


Figure 5.6: Interaction between distance from footpaths and local patch quality on proportion of vigilance behaviour.

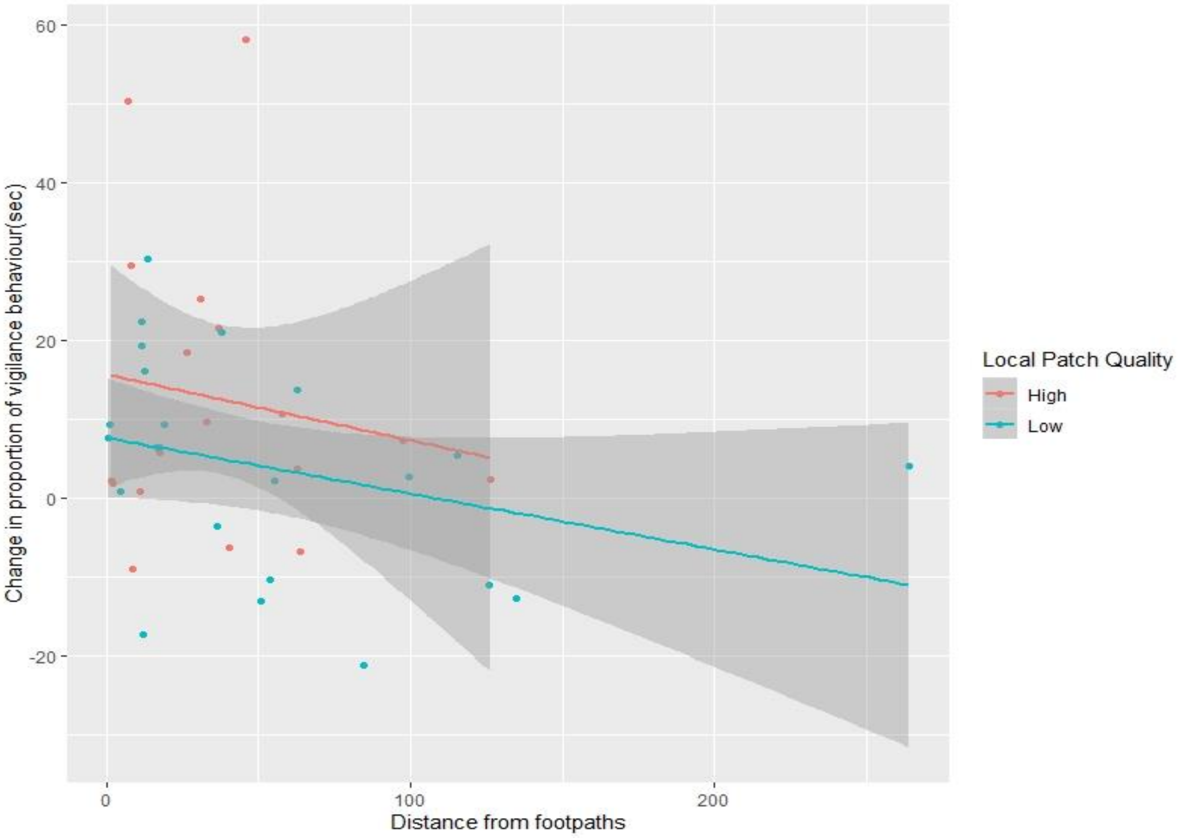


Figure 5.7: Interaction between distance from roads and noise variance on proportion of vigilance behaviour.

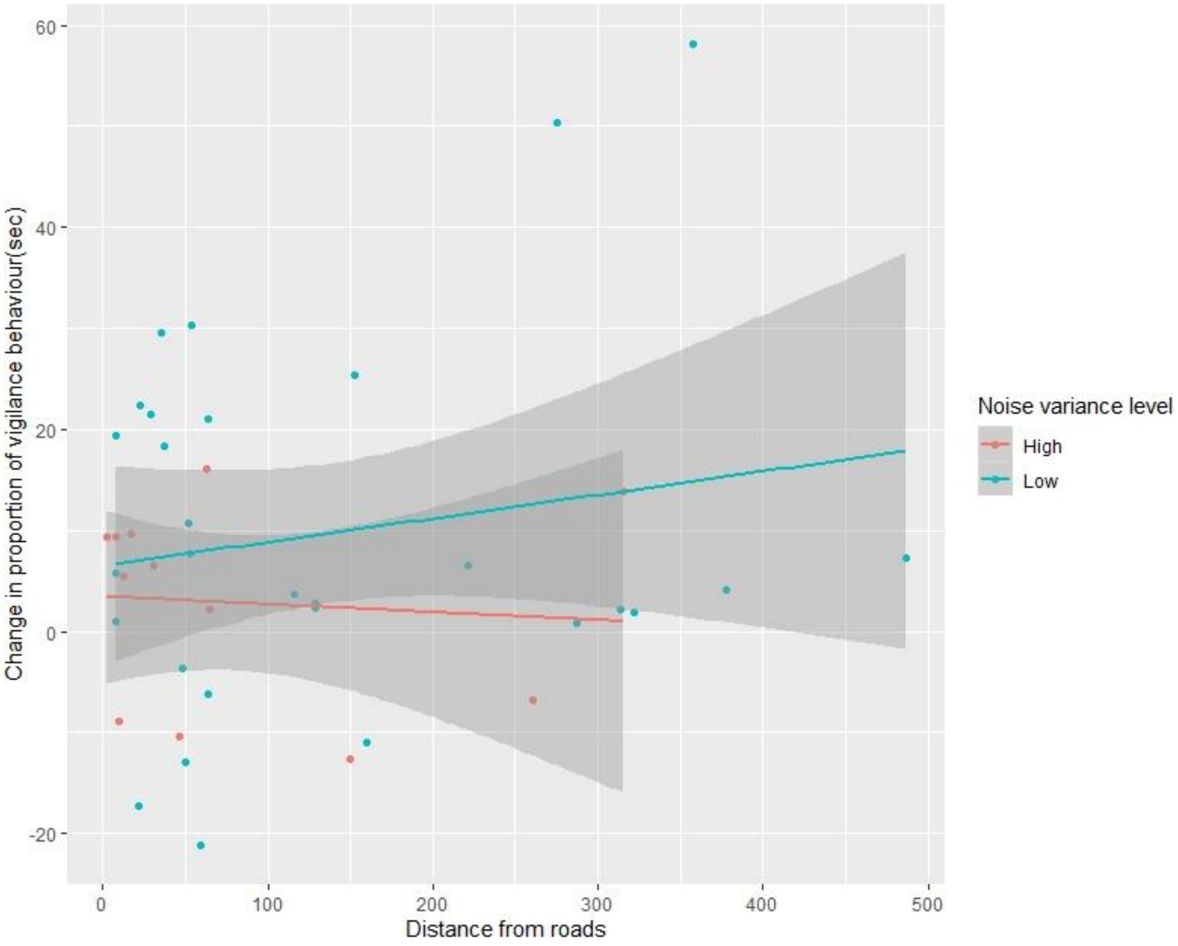


Table 5.2: Final generalized linear model of changes in vigilance levels following play-back.

Fixed Effect	Estimate	SE	*t*	*p*	CI (2.5%)	CI (97.5%)
(intercept)	21.15	8.759	2.414	**0.024**	3.98	38.316
Dist. from vegetation	-2.639	1.444	-1.828	0.08	-5.468	0.189
Dist. From footpaths	0.043	0.0645	0.678	0.504	-0.0827	0.1702404
Dist. Buildings	0.512	0.135	3.772	**< 0.001**	0.245	0.777
Dist. Roads	-0.563	0.166	-3.378	**< 0.001**	-0.89	-0.236
Noise level	2.603	1.310	1.987	0.059	0.034	5.17

Variance in noise level	-0.699	0.205	-3.409	**< 0.001**	-1.102	-2.974
Patch quality	0.00094	0.001	-2.188	**0.039**	0.0007	0.0004
Habitat (Garden)	-3.497	14.58	-0.240	0.812	-32.068	25.074
Habitat (Park)	7.44	14.19	0.524	0.605	-20.377	35.256
Dist. Footpaths * Noise Level	0.122	0.0395	2.839	**0.009**	0.0347	0.189
Footpaths * Patch Quality	<0.0001	<0.0001	3.172	**0.004**	<0.0001	<0.0001
Roads * Variance in Noise	0.006	0.001	-4.052	**<0.001**	0.009	0.003
Roads * Patch Quality	<0.0001	<0.0001	1.917	0.067	<0.0001	<0.0001
Buildings * Habitat (Garden)	-0.216	0.1664	-1.304	0.205	-0.054	0.109
Buildings * Habitat (Park)	1.325	0.0542	2.443	**0.022**	0.0261	2.387
Roads * Habitat (Garden)	0.0656	0.019	3.289	**0.003**	0.265	1.0470
Roads * Habitat (Park)	-0.135	0.249	-0.542	0.593	-0.623	0.353

Changes in foraging duration

Squirrels were found to reduce the proportion of time spent foraging following a conspecific playback. The final model suggested that there were significant effects of urban habitat features on changes in the proportion of foraging behaviours, with small significant decreases in foraging behaviour as distances from footpaths, t(40) = -2.174, p = 0.04, buildings, t(40) = -3.993, p <0.001, and roads, t(40) = 3.166, p = 0.004, increase. Squirrels foraging in garden habitats showed significantly larger decreases in foraging activity following the conspecific call, t (40) = 2.227, p =0.037.

Figure 5.8: Relationships between proportion of time foraging post-playback and habitat features 1) Buildings, 2) Footpaths 3) Roads

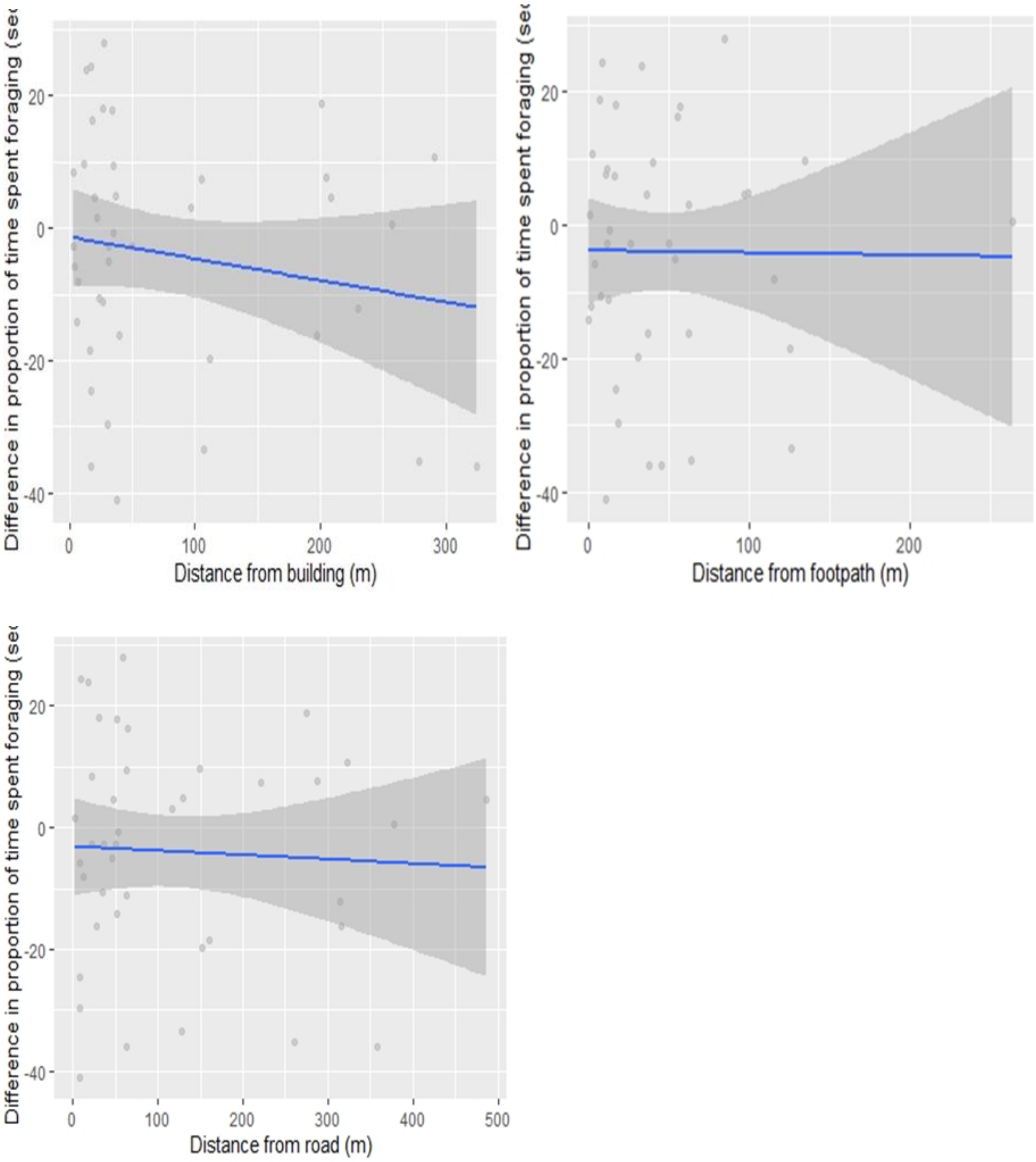


Table 5.3: Final generalized linear model of changes in duration of foraging following play-back.

Fixed Effect	**Estimate**	***SE***	***t***	***p***	**CI (2.5%)**	**CI (97.5%)**
(intercept)	6.395	0.1240	0.516	0.611	-0.179	0.307

Dist. Footpaths	-0.3051	0.1404	-2.174	**0.041**	-0.580	-0.029
Dist. Buildings	-0.5726	0.1434	-3.993	**<0.001**	-0.853	-0.291
Dist. Roads	0.6205	0.1960	3.166	**0.004**	0.236	1.004
Noise Level	-3.061	2.183	-1.402	0.176	-7.340	1.217
Noise level variance	0.5187	0.2774	1.870	0.076	-0.025	1.062
Patch Quality	-0.001739	0.002650	-0.656	0.519	-0.006	0.003
Habitat (Garden)	0.01519	0.06821	2.227	**0.037**	0.181	0.0285
Habitat (Path)	-9.872	0.1890	-0.522	0.607	-0.469	0.271
Dist. Footpaths * Noise Level	0.00951	0.0471	-2.018	0.0571	-0.187	-0.002
Dist. Footpaths * Patch Quality	<0.001	<0.001	-1.144	0.266	<0.001	<0.001
Dist. Roads * Noise Level	0.0315	0.0161	1.949	0.065	<0.001	0.006
Dist. Roads * Patch Quality	<0.001	<0.001	-1.220	0.236	<0.001	<0.001
Patch Quality * Habitat (Garden)	0.072	0.028	2.587	**0.017**	0.001	<0.001
Patch Quality * Habitat (Park)	<0.001	<0.001	-0.949	0.353	-0.002	0.001
Buildings * Habitat (Garden)	0.0181	0.021	0.826	0.418	-0.024	0.061
Buildings * Habitat (Park)	1.461	1.103	1.325	0.20	-0.069	0.003
Roads * Habitat (Garden)	-0.049	0.025	-1.896	0.072	-0.099	0.001

Changes in food handling

Following playback, proportion of time handling food significantly increased as distances from footpaths increased, t (40) = 2.633, p = 0.0164. There was also a small significant reduction in food handling at higher quality patches, t (40) =2.535, p = 0.02, with a significant interaction between distance from footpaths and patch quality, t (40) = -2.206, $p < 0.05$, and significant interactions between distance from buildings, t(40) = -2.457, $p<0.02$, and distance from roads, t(40) = 2.348, $p<0.02$, with habitat types. (Table 5.4).

Figure 5.9: Interaction between distance from footpaths and local patch quality on increase in proportion of food handling.

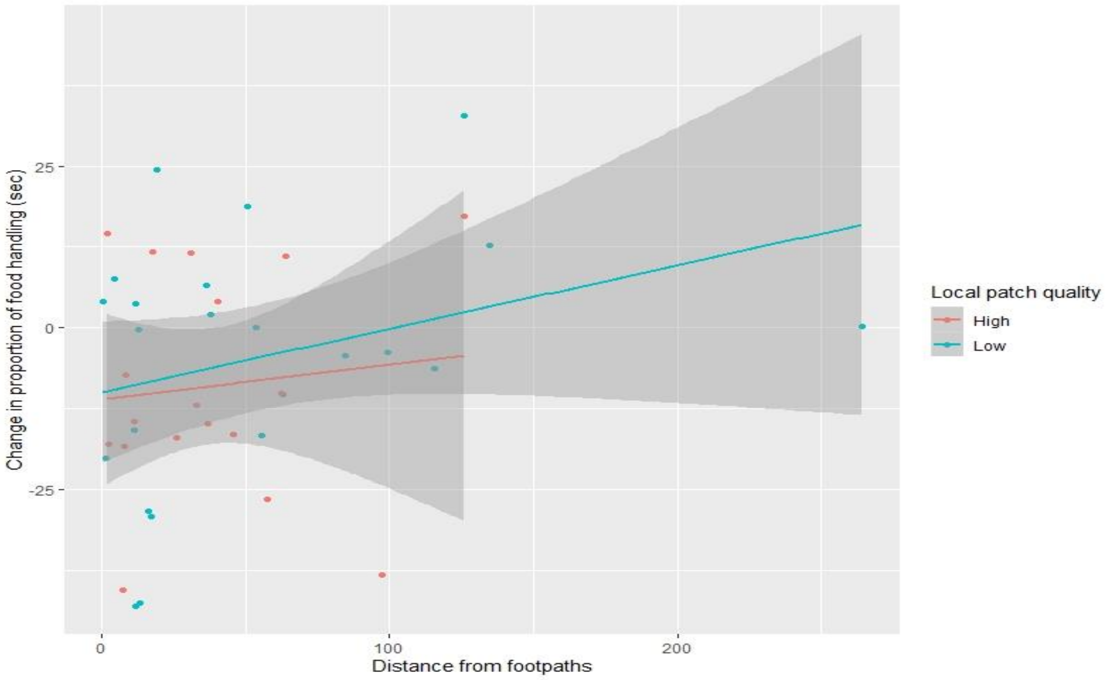


Figure 5.10: Interaction between distance from buildings and habitat type on increase in proportion of food handling.

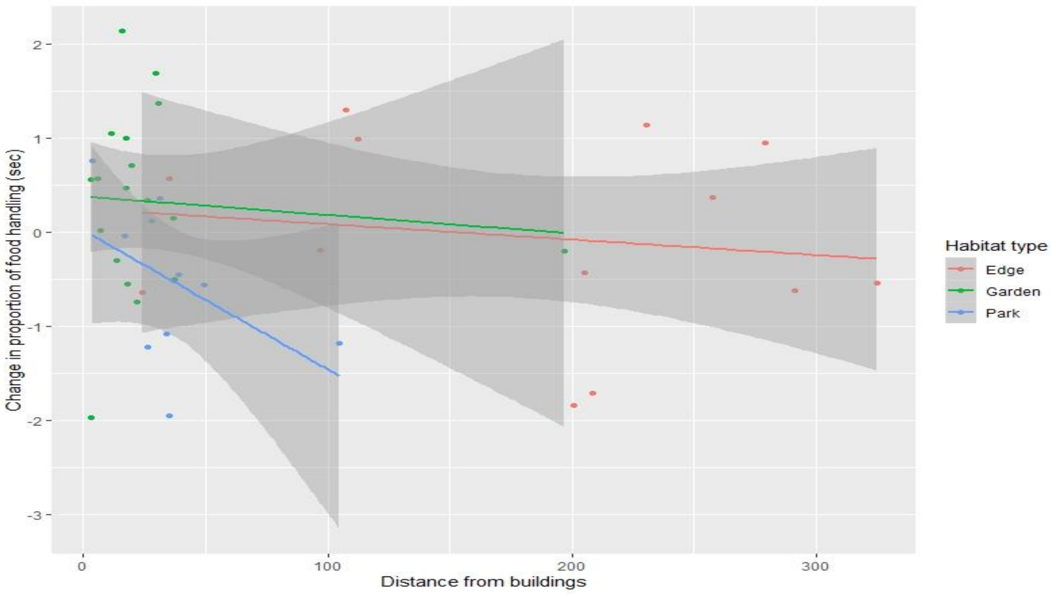


Figure 5.11: Interaction between distance from roads and habitat type on increase in proportion of food handling.

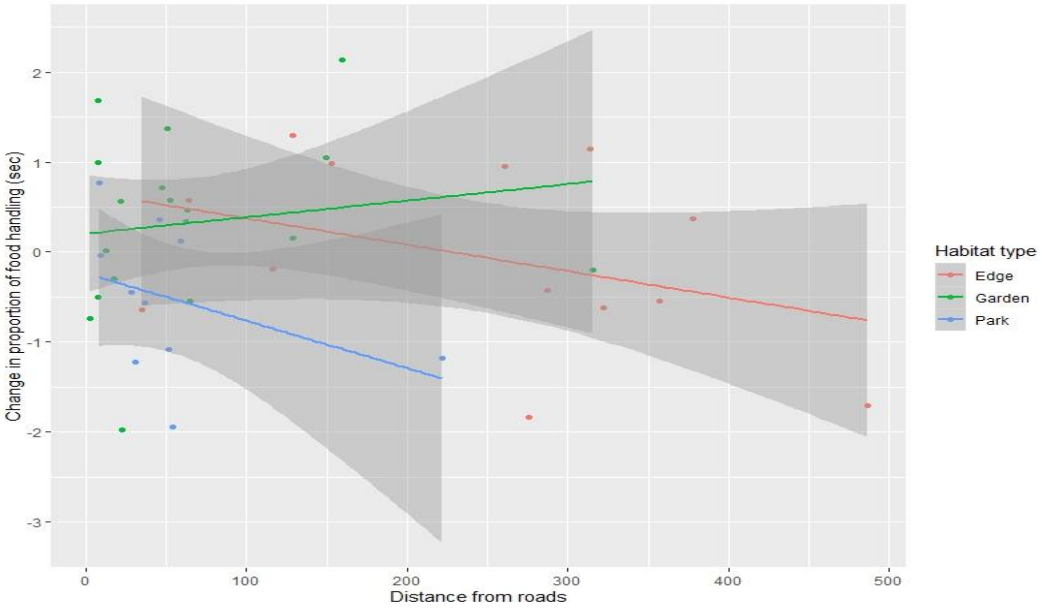


Table 5.4: Final generalized linear model of changes in duration of food handling following play-back.

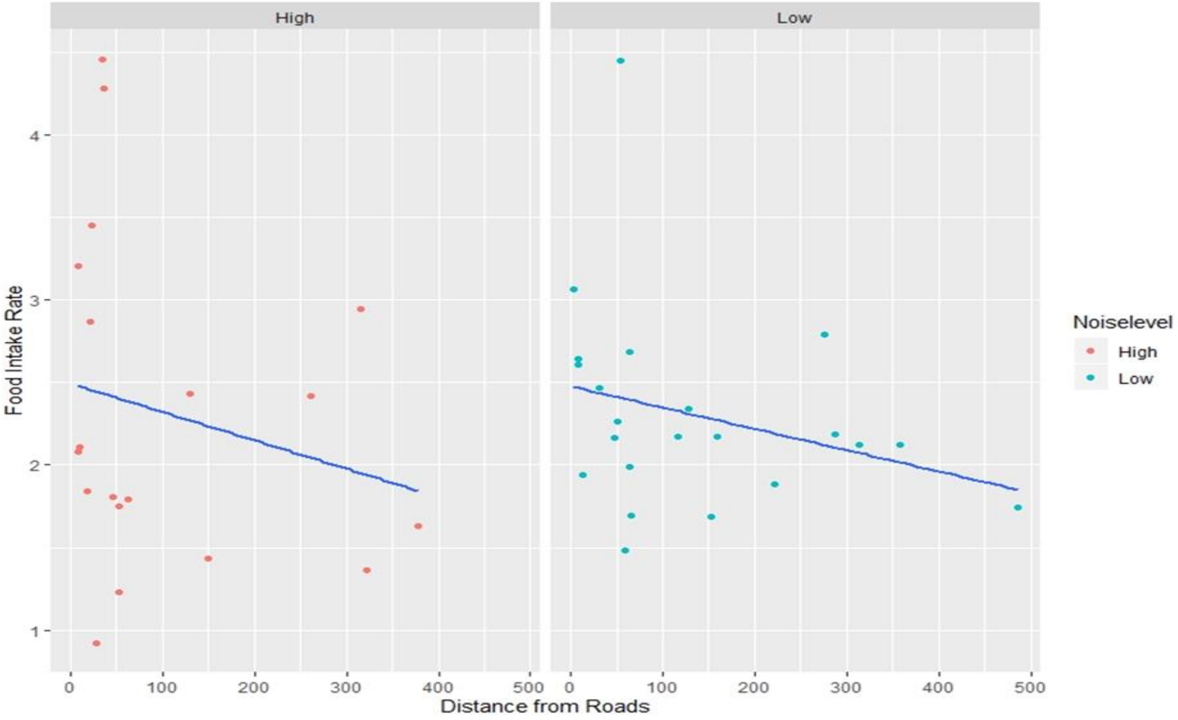
Fixed Effect	Estimate	*SE*	*t*	*p*	CI (2.5%)	CI (97.5%)
(intercept)	-0.024	0.012	-1.959	0.0650	-0.049	0.001
Vegetation	4.103	2.262	1.814	0.0856	-0.033	8.537
Footpath	0.032	0.012	2.633	**0.0164**	0.008	0.057
Building	-0.005	0.017	-0.344	0.7346	-0.039	0.027
Road	-0.006	0.014	-0.452	0.6562	-0.034	0.0216
Noise level	-2.936	2.673	-1.098	0.2857	-8.174	2.302
Noise level variance	0.035	0.033	1.068	0.2989	-0.029	1.006
Patch Quality	0.0007	0.0002	2.535	**0.0202**	0.0001	0.001
Habitat (Garden)	-0.062	0.075	-0.818	0.4237	-0.002	0.086
Habitat (Park)	-0.010	0.022	-0.479	0.6373	-0.054	0.033
Footpaths * Noise level	-0.008	0.006	-1.400	0.1775	-0.020	0.003

Footpaths * Patch Quality	<0.001	<0.001	-2.206	**0.0399**	-0.000	-0.000
Roads * Noise level	-0.003	0.002	-1.509	0.1477	-0.007	0.001
Noise level variance * Patch Quality	<0.001	<0.001	1.706	0.1044	-0.000	0.000
Patch quality * Habitat (Garden)	-0.004	0.003	-1.341	0.1957	-0.010	0.001
Patch Quality * Habitat (Park)	0.001	0.001	1.216	0.2387	-0.000	0.003
Buildings * Habitat (Garden)	0.005	0.028	0.182	0.8574	-0.051	0.061
Buildings * Habitat (Park)	-3.564	1.450	-2.457	**0.0238**	-6.405	-0.072
Roads * Habitat (Garden)	0.0105	0.0184	0.571	0.5747	-0.025	0.046
Roads * Habitat (Park)	1.601	0.068	2.348	**0.0299**	0.026	2.936
Footpaths * Habitat (Garden)	-0.052	0.026	-1.996	0.0605	-1.044	-0.000
Footpaths* Habitat (Park)	-0.068	0.034	-1.982	0.0622	-1.365	-0.000

Feeding intake

Significant interactions between roads and noise levels, t (40) = -2.237, p = 0.036, variance in noise levels and patch quality, t (40) = 2.677, p = 0.014, distance from buildings and habitat type, t (40) = 3.031, p = 0.006, and patch quality and habitat type, t(40) = -3.470, p = 0.002, were found in the final model. Under low noise variance feeding rate was higher at lower quality patches (Figure 5.12). Effects of distance from buildings and roads on feeding rates appeared to differ according to habitat type, with patches at further distances from roads having lower feeding intake rates, whilst this trend appears to be reversed for patches in gardens (Table 5.5, Figure 5.13).

Figure 5.12: Relationships between overall food intake rate and distance from roads under high and low noise levels*



**Noise levels (dB) were divided into categories based in a median split*

Figure 5.13: Relationship between overall food intake rate and distance from buildings under different habitat types

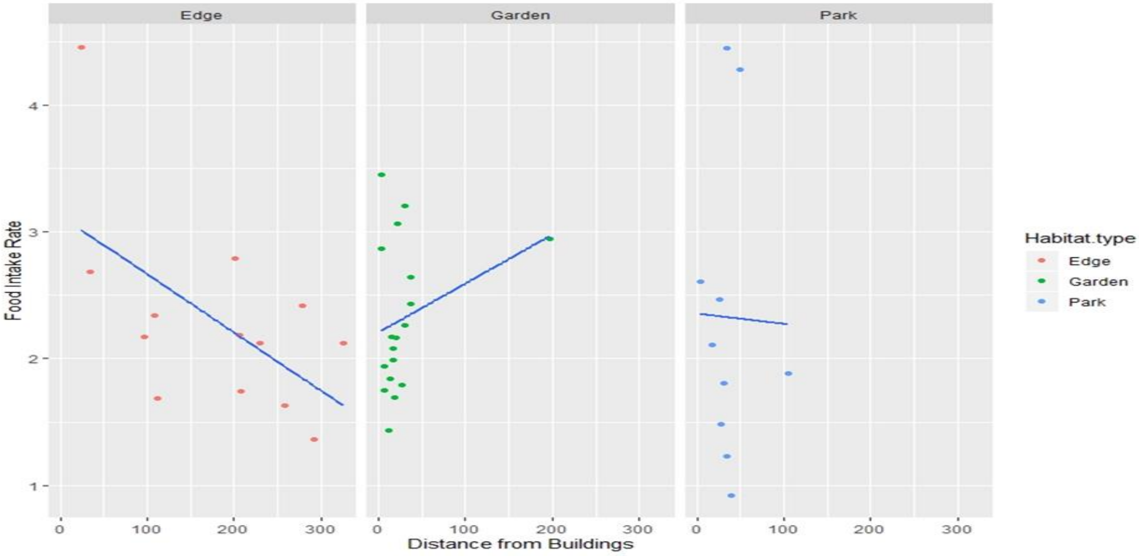
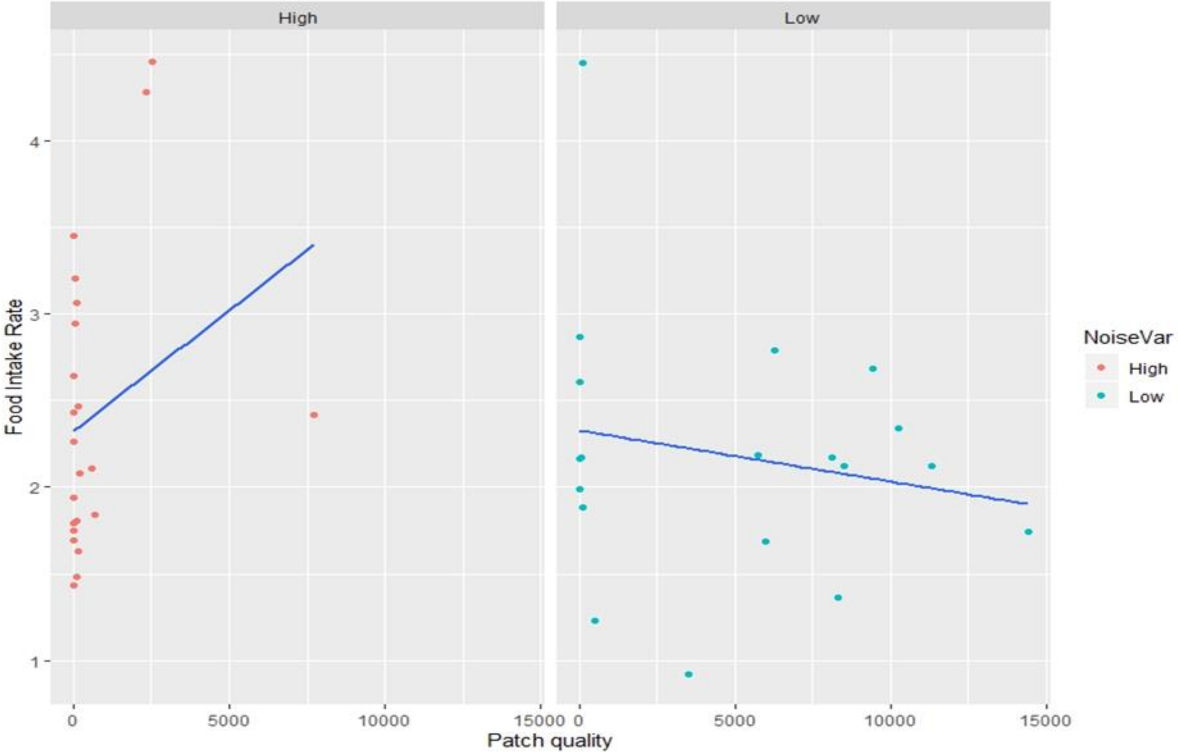


Figure 5.14: Relationship between overall food intake rate and patch quality under different high and low noise variance*



**Noise variance was divided into categories based in a median split.*

Table 5.5: Final generalized linear model of habitat features on overall feeding intake

Fixed Effect	**Estimate**	***SE***	***t***	***p***	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	2.669	0.0406	6.572	<0.001	0.0000	0.0000
Vegetation	-0.0098	0.0079	-1.242	0.2280	-0.0255	0.005
Buildings	0.0002	0.0003	0.834	0.4137	-0.0003	0.0009
Footpath	-0.0003	0.0004	-0.686	0.5002	-0.0011	0.0005
Road	-0.0001	0.0003	-0.459	0.65119	-0.0008	0.0005
Noise level	0.0057	0.0068	0.830	0.415	-0.0077	0.0191
Noise level variance	-0.002	0.0102	-1.949	0.06483	-0.004	0.00001
Patch Quality	0.00002	<0.0001	0.368	0.71668	-0.0000	0.00001
Habitat (Garden)	-0.002	2.679	-0.924	0.36595	-7.725	2.774
Habitat (Park)	-1.036	0.0714	-1.449	0.16208	-2.436	0.0365

Roads * Noise level	-0.0001	0.0006	-2.237	**0.03623**	-0.0002	-0.000
Noise variance * Patch Quality	<0.0001	<0.0001	2.677	**0.01412**	0.00000	0.0000
Patch Quality * Habitat (Garden)	-0.0012	0.0010	-1.161	0.25885	-0.0003	0.00008
Patch Quality * Habitat (Park)	-0.0001	0.0004	-3.470	**0.00229**	-0.0002	-0.00006
Buildings * Habitat (Garden)	0.002	0.00008	3.031	**0.00636**	0.0009	0.0042
Buildings * Habitat (Park)	0.0157	0.005	3.058	**0.00597**	0.0056	0.0257
Roads * Habitat (Garden)	-0.0006	0.0005	-1.168	0.25574	-0.001	0.0004
Roads * Habitat (Park)	-0.006	0.002	-2.802	**0.01067**	-0.0112	-0.0019
Footpaths * Habitat (Garden)	-0.0002	0.0005	-0.040	0.96842	-0.0011	0.0011
Footpaths * Habitat (Park)	-0.001	0.0009	-2.043	0.05381	-0.0038	-0.00007

Social signalling

Social signalling behaviour appears to be affected by distance from roads and the interaction between distance from roads and habitat type, variance in noise levels and patch quality, t(40) = -2.09, $p < 0.05$. Proportion of social signalling behaviour following playback was significantly higher in squirrels foraging at distances further from roads, t(40) =2.252, p = 0.03. There was a significant interaction between distance from roads and habitat type where park was used as the comparison group, t (40) = -2.157, p = 0.04, with the relationship between roads and social signalling behaviour being pronounced in garden habitats (Figure 5.15).

Figure 5.15: Relationships between social signalling behaviour and distance from roads by habitat type

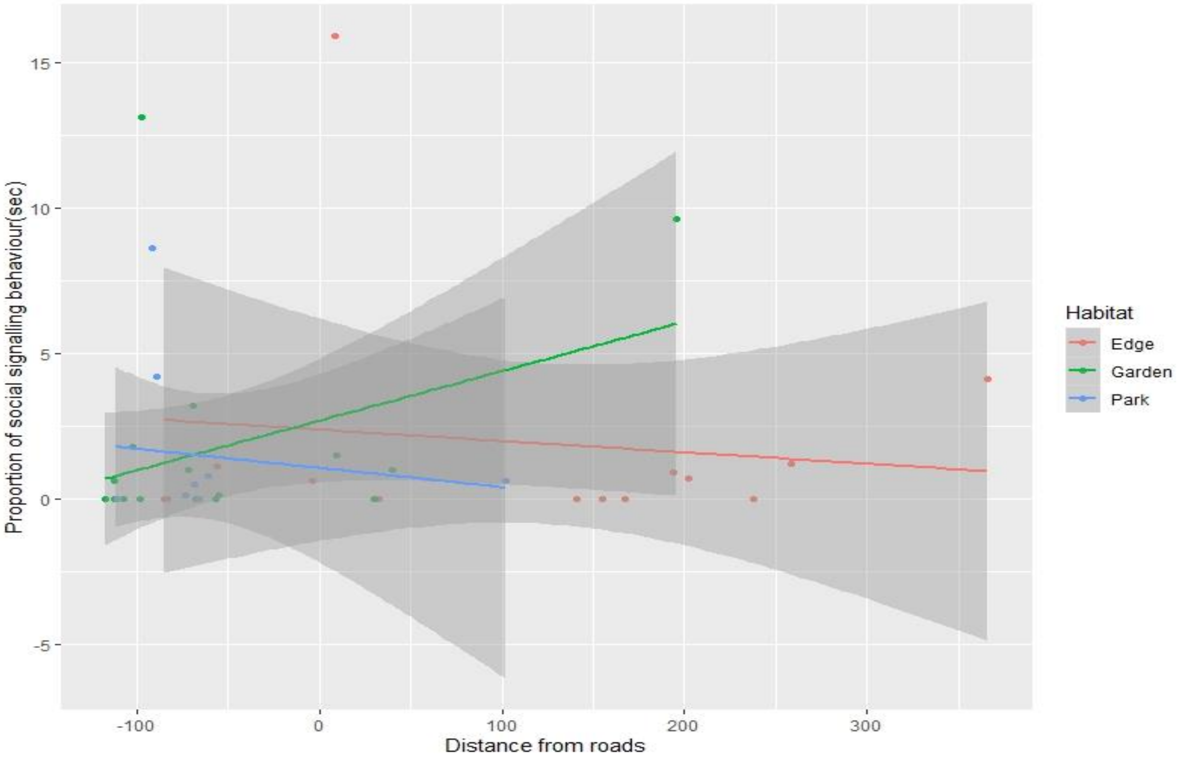
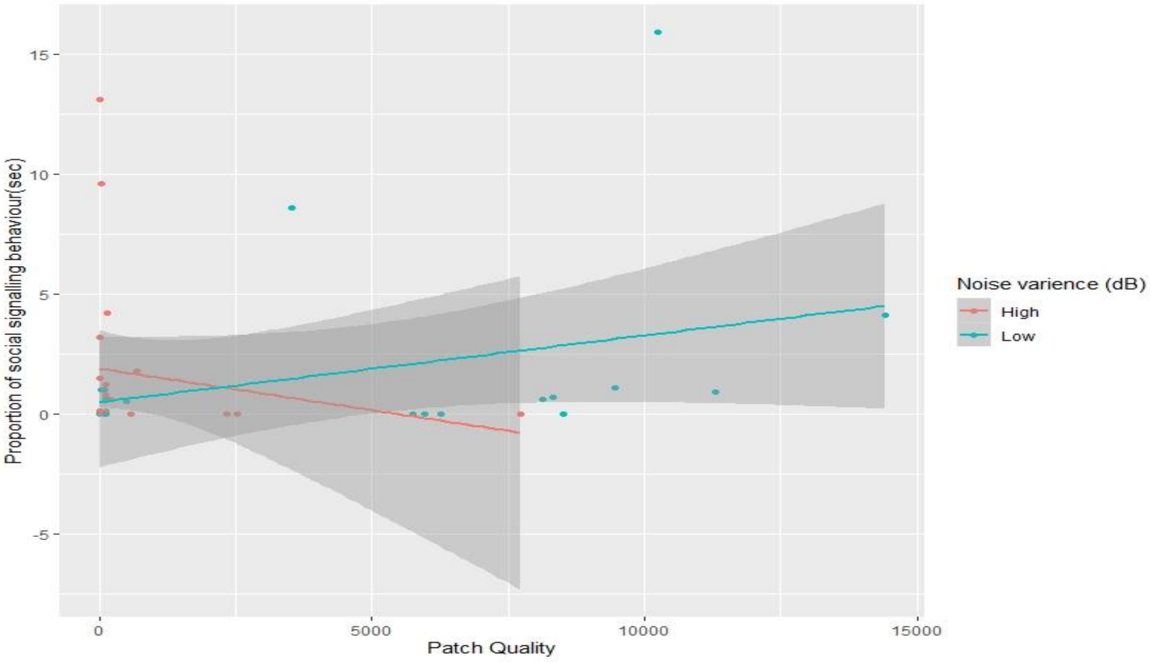


*Figure 5.16: Relationships between social signalling behaviour and patch quality by high and low noise variance**



**Noise variance was divided into categories based in a median split*

Table 5.6: Final generalized linear model for proportion of social signalling behaviours occurring after conspecific playback

Fixed Effect	**Estimate**	***SE***	***t***	***p***	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	-1.664	1.943	-0.856	0.3998	-5.472	2.145
Footpaths	9.121	1.148	0.794	0.4341	-0.001	0.003
Roads	0.003	0.00	2.252	**0.0330**	0.000	0.006
Noise level	0.022	0.0261	0.870	0.3921	-0.028	0.074
Noise level variance	-0.005	0.004	-1.335	0.1934	-0.0135	0.002
Patch Quality	0.0000	0.00004	0.226	0.8227	-0.0000	0.0001
Habitat (Garden)	3.275	3.293	0.994	0.3292	-3.179	9.729
Habitat (Park)	1.735	2.987	0.581	0.5662	-4.118	7.588
Footpaths * Noise level	-0.001	0.0007	-1.391	0.1761	-0.002	0.0004
Footpaths * Patch Quality	0.000	0.000	1.676	0.1058	-0.000	0.00000
Roads * Noise level variance	0.0001	0.00005	2.055	**0.0500**	0.00005	0.0002
Roads * Patch Quality	-0.000	0.0000	-1.796	0.0841	-0.0000	0.0000
Noise level variance * Patch Quality	-0.0000	0.0000	-2.092	**0.0463**	-0.000	-0.0000
Roads * Habitat (Garden)	-0.004	0.002	-1.840	0.0773	-0.009	0.0003
Roads * Habitat (Park)	-0.005	0.002	-2.157	**0.0404**	-0.011	-0.0005

5.5 Discussion

This study suggests that urban grey squirrel responses to an auditory cue of social risk may be modified by urban built structures and noise, with the impact of these effects varying with the quality of the surrounding patch they are foraging in.

Table 5.7: Summary of key findings for the influence of urban habitat features on response to conspecific playback.

Urban feature	***Impact on response to playback***	***Possible explanations***
Noise levels (average)	- Squirrels under high noise levels returned to feeding faster and had decreased vigilance levels.	High noise could mask signal detection(Warren et al., 2006). Foraging under high noise could promote prioritising food intake over vigilance due to potential risk
Variation in noise	- Higher noise variation was linked to increased latency to return to feeding, and higher rates of food intake. - Under higher levels of noise variation, social signalling behaviour reduced as patch quality increased.	Noise variability could reduce reliability of auditory signals and increase perception of risk. Social signalling may be less value where noise is variable. Forgers might invest in maximising food intake where assessing risk is unreliable(Fernández-Juricic & Tellería, 2000).
Roads	- Higher feeding rates, shorter durations of return to foraging, and reduced vigilance levels occurred at proximity to roads. - Lower proportions of social signalling behaviours were recorded close to roads, this was most pronounced in gardens.	Roads may increase risk of disturbance to foraging, therefore forager prioritises food intake due to shorter foraging opportunities.
Buildings	- Foragers closer to buildings showed increased food intake, reduced vigilance, and lower levels of food handling.	Buildings could reduce perceived disturbance costs to foraging, or act as a static cue of risk – with foraging closer to buildings being a cue of reduced risk.

Footpaths	- Decreased food handling further from footpaths.	Food handling may allow for the maintenance of low-level vigilance(Makowska & Kramer, 2007). Closer to footpaths foragers may monitor risks of predation and disturbance by increasing food handling(Parker & Nilon, 2008).
Local habitat quality	- Under low noise variability there was a higher proportion of signalling behaviours at higher quality patches. - Those in higher quality patches took longer latencies to return to foraging and had increased vigilance levels. - Local patch quality was found to interact with urban features, including roads, buildings, and habitat type in proportions of vigilance levels and feeding intake rate.	Local habitat quality may determine the risk-food acquisition trade-off foragers are willing to make. Under low noise variability, foragers at high quality patches seemed to respond to conspecifics with increased signalling behaviour, suggesting patch defence. Foragers at high quality patched also had larger proportions of vigilance and longer latencies to return to forage, suggesting they are more likely to engage in risk monitoring behaviours.

Regardless of foraging location, all squirrels increased vigilance following the playback, supporting the findings from previous studies indicating that conspecific playbacks can pose as a cue of social, or competition risk, to foraging grey squirrels (Jayne et al., 2015). The proportion of vigilance and the time spent foraging were significantly impacted by proximity to urban build features. However, contrary to predictions, squirrels foraging further from roads and buildings showed significantly larger increases in vigilance levels. Similar effects have been shown in studies in urban house finches (*Carpodacus mexicanus*) and blackbirds (*Turdus merula*). In these studies, whilst birds spent less time feeding at more urbanised patches, they showed higher pecking rates and less head up vigilance behaviours. These findings were explained as an attempt to maximise food intake under higher risk of disturbance, where foragers had only a very limited time to acquire resources (Fernández-Juricic & Tellería, 2000; Valcarcel & Fernández-Juricic, 2009). In the current study we found that, although foragers close to buildings and roads showed lower increases in vigilance post-playback, they had significantly higher food intake rates than those foraging further from these urban built features. Grey squirrels have been known to increase feeding rates at patches of higher risk, such as those in open habitat (Newman & Caraco, 1987), so it is likely that in the current study, reduced vigilance represents an attempt to maximise food intake under conditions where there is a risk of disturbance to foraging. Likewise, squirrels feeding closer to footpaths did not show significantly increased vigilance, however they did show increased food handling times. Food handling may allow squirrels to engage in low level vigilance whilst feeding (Makowska & Kramer, 2007). This perhaps indicates that footpaths represent a slightly different level of risk to that of foraging close to buildings and roads, requiring a balance between low level vigilance and food acquisition. Urban grey squirrels foraging in highly urbanised parks, close to pedestrian areas, have been found to modulate responses to pedestrian behaviour on footpaths. Whilst pedestrians can represent a disturbance risk, squirrels seemed to monitor pedestrian behaviour, fleeing only when people moved off footpaths or looked at them (Bateman & Fleming, 2014).This suggests urban squirrels may reduce unnecessary behavioural responses to human disturbance by monitoring behaviour of humans, assessing differing risk levels accordingly (Makowska & Kramer, 2007).

We found that distance from roads impacted proportions of social signalling behaviours, with squirrels feeding at further distances from roads displaying higher proportions of social signalling behaviours. Furthermore, there were interaction effects between roads, noise variance, and patch quality, suggesting the disturbance factors near roads, where there may be increased background noise produced by traffic, reduce the value of social or patch defence communication. It is also possible that roads offer a degree of protection from conspecific competition risk, for example, roads could provide an additional obstacle or barrier for competitors, or perhaps there is less competition at these sites due to reduced patch quality or increased mortality risk at these patches.

Noise disturbance in urban environments has been documented as having wide ranging effects on urban wildlife, including masking communication, diverting attention, and inducing stress responses, which can all come at costs to other fitness enhancing activities (Barber et al., 2010; Kight & Swaddle, 2011). In this study we found that noise levels significantly impacted latencies to return to foraging. It was predicted that high noise levels could increase latency to return to forage following playback, due to the potential effects on masking or disruption of auditory cues, however it was found that squirrels feeding at patches with higher noise levels returned to foraging faster following playbacks compared to those a lower noise level patch. The reason for this may be similar to the effects found in patches close to urban built features – high risk patches may require increased feeding rate where there is a reduced foraging time (Newman & Caraco, 1987). Noise levels had a significant interaction effect with patch quality, with foragers feeding at higher quality, high noise level patches, taking significantly longer to return to forage post-playback. It is possible that local patch quality is associated with likelihood of a competitive interaction, and where higher quality patches are exposed to higher noise levels, it may be more important for squirrels to invest in attention to risk assessment. Squirrels at patches with lower noise variance showed higher increases in vigilance levels following playbacks, suggesting that under lower noise variability squirrels are more attentive to an auditory social risk cue. Further, noise variability interacted with patch quality in its effects on feeding rates and social signalling, with squirrels showing higher feeding rates under low noise, low patch quality conditions, and showing greater proportions of social signalling behaviours under low noise variability at higher quality patches. Whilst background noise can mask alarm calls, noise variability may impact the ability to assess the reliability of these auditory cues (Warren et al., 2006). It is possible that where noise disturbance is highly variable, high levels of attention to social cues may come at a higher cost to foraging, therefore squirrels reduce attention to conspecific cues to maximise food intake under higher disturbance risk conditions.

Using surrounding mast availability as an index of local habitat quality, this study found that squirrels feeding at higher quality patches (higher mast availability) were slower to return to activity following the conspecific call, with this being most apparent in high quality patches under high noise variability. In line with the prediction that foragers at high quality patches may face increased social risk, higher quality patches were also associated with larger increases in vigilance behaviours following conspecific calls. Those foraging at low quality patches under high noise levels had higher overall feeding intake rates than those at higher patch quality, and the proportion of social signalling behaviours were higher in those foraging at high quality patches with low noise variance. These results suggest that, whilst foragers at high quality patches invest more in vigilance and social signalling following a social risk cue, proximity to urban features may reduce some of these social risk monitoring behaviours. This may be due to factors such as noise interference in relation to acoustic cues. Reduced social signalling levels in some patches could also reflect local competition levels. Here, we did not quantify competition levels within each microhabitat. Future work should integrate counts of local squirrel population density, and numbers of squirrels utilising a particular patch in order to understand if patches closer to urban features have reduced competition levels, or if foragers at these locations are more tolerant of feeding close to conspecifics. Further, here, patch quality was assessed in terms of the natural mast availability surrounding the supplementary feeding patch used for observation. Assessment of patch quality at a broader scale may help with interpretations of competition risk level and missed opportunity costs at each feeding patch. For example, garden locations could contain supplementary food from bird feeders. These may represent high quality feeding areas, despite low availability of natural food sources such as mast availability. These sites could provide a high quality, but high competition risk, aggregated food resources (Bonnington et al., 2014). In this study we did not record presence of other supplementary food sources, it could be that the experimental food patches, and the surrounding area, provided in the study did not represent the highest quality food resource available at a site. If other high-quality patches were available locally it could be that squirrels observed in this study were foraging at the experimental patches to avoid high competition at other food resources. Our experimental feeding patch may have offered a ‘safer’ alternative, and therefore represented an area of low competition risk. Further research could benefit from quantifying both natural and supplementary feeding resources at a broader scale to investigate how this could shape squirrel assessment of social risk during foraging.

Conclusions and further research

Urban environments may reduce vigilance and patch defence signalling responses to social risk in grey squirrels. Following a conspecific playback, squirrels foraging under high noise or high noise variability conditions did not show a pronounced increase in risk monitoring related behaviours, such as vigilance, compared to those foraging at low noise disturbance patches. These responses were further modulated by local patch quality and distance to urban built features, with those foraging closer to urban features showing increased feeding intake and reduced vigilance and social signalling. These finding support the suggestion that under higher risk conditions foragers may compensate for reduced time in a patch by increasing feeding intake (Valcarcel & Fernández-Juricic, 2009). These results could also indicate that sites of higher perceived disturbance risk may be less attractive to other foragers, reducing potential for conspecific interactions and competition. When considered separately the urban features roads, buildings, and footpaths had different effects on foraging behaviour and responses to a social risk cue. Squirrels foraging closer to buildings, in general, showed lower levels of vigilance related behavioural responses. It is possible that buildings offer a static cue of risk, in a similar way to trees and vegetation. Buildings, whilst potentially representing an area of human activity, may offer shelter or possible escape routes or represent locations with reduced predation risk. Squirrels were found to increase food handling during feeding near footpaths. This behaviour may allow them to monitor risk under from pedestrian activity (Bateman & Fleming, 2014). This implies that footpaths may represent at different type of risk cue to static cues, such as buildings. For example, footpaths may represent encounters with humans that could vary in disturbance levels across time and space. Therefore, they could be considered a more dynamic cue of risk (Leaver et al., 2016) compared to features such as buildings. Further research could quantify human activity at these locations, for example, by taking measures of pedestrian activity.

Some of these findings may also reflect differences in the way individuals use habitat. Individual habitat use is likely to be non-randomly distributed, and individuals who are more willing to feed under risk may be more likely to forage closer to areas of higher disturbance levels were risk detection might be interrupted or unreliable. Further research could investigate if individuals foraging near these urban features are consistently more risk tolerant (Carter et al., 2013; Dall et al., 2012; Dall & Griffith, 2014), or if they vary in body condition, state, or competitive ability, and to what extent this might drive the distribution of certain behavioural ‘types’ across urban landscape. To date, the influences of microhabitat and nuances of how features of urban landscapes interact with the behaviour of individuals whilst acquiring resources remains an area warranting further work. Whilst this study investigated the behaviour of a successful urban mammal, similar studies involving other species, especially those that are potentially more vulnerable to urbanisation, might offer important insights into the costs of foraging alongside human disturbance in urban habitats. Foraging trade-offs may be helpful to identify possible anthropogenic impacts and understanding the relationships between foraging and habitat features might offer possible mitigation and management interventions.

Chapter 6: General discussion and concluding remarks

The aim of this thesis was to explore habitat use and behavioural variation in urban grey squirrels, with a particular focus on understanding how habitat features of urbanisation could increase perceived risk, and if these can be linked to personality variation. Four research chapters addressed these aims beginning with a systematic review of studies measuring animal personality variation in urban wildlife. Three experimental studies were designed to test to what extent habitat features associated with the urban landscape might alter risk-related behaviours during resource acquisition. This chapter will discuss what was found in relation to the impact of urban features on squirrel behaviour during foraging and reflect on how these could shape personality variation in urban habitats. It will then consider strengths and limitations of the methodology used and discuss some of the problems faced during this research, reflecting on how this can inform and develop future research.

6.1 Risk and habitat use in urban grey squirrels

The ‘landscape of fear’ framework argues that animals usually concentrate foraging activity to areas of their habitat with lowest risks (Laundré et al., 2010). The risks that foragers face can be multiple, and require foragers to make behavioural decisions that balance these multiple risks with safety and food-acquisition (Lima et al., 1985), therefore, these patterns of landscape use also reflect the energetic requirements of foragers as much as they reveal predation risk (Gallagher et al., 2017). To make an assessment of these risks, foragers can use features of their landscape, such as vegetation cover or predator odours (Brown, 1988). Chapters 3 and 5 examined a number of habitat features related to urban environments, to assess if these features might influence risk perception, and if squirrels might differ in how they balance risk, food and safety with differences in exposure to these urban habitat features. Chapter 3 employed giving-up density (GUD) methodology to understand where perception of risk might vary within and between different sites. Whilst this chapter did not examine the behaviour of individuals, understanding factors influencing risk-related behaviours may be important for interpreting relationships between habitat use and personality variation discussed in Chapter 4. Similarly, Chapter 5 addresses questions regarding the impacts of urbanisation levels on resource-acquisition trade-offs in the context of social risk, by investigating if urban landscape features could alter squirrel responses to conspecific playbacks, a potential conspecific competitor cue.

- ***Urban features and GUD***

Chapter 3 found that squirrels living at closer proximity to sites of human activity and disturbance left lower GUDs (consumed more food) than squirrels foraging further from these sites. There was a reduction in the difference between ‘safe’ and ‘risky’ patches at sites closer to buildings and roads, suggesting that these features may lower the perception of risk for grey squirrels, or perhaps reduce the value of cover as ‘safety’ at these locations. In addition, GUD is sensitive to the state of foragers (Olsson & Molokwu, 2008), therefore, these results can indicate that squirrels foraging at these locations place a higher value on obtaining food than safety, or in a state that requires them to take higher risks to obtain food. The results in Chapter 3 provide similar findings to work by Bowers & Breland (1996) who found that urban squirrels feeding close to site of human activity showed lower GUDs. Bowers *et al* (1996) used single GUD patches placed at several points across an urbanisation gradient, which does not allow for the unravelling of differences between the value of safety within local habitat. Using paired ‘safe’ and ‘risky’ patches, the protocol in Chapter 3 allows the same forager to select from alternative options, thus allowing for the assessment of the value of safe patches compared to risky patches. With these modifications, the results supported some of the conclusions drawn by Bowers *et al* .(1996), and provides further evidence that urban grey squirrels are likely to have reduced predation risk, and perhaps increased willingness to take risks to acquire food, in sites close to human activity. However, in this study this effect only occurred at roads and buildings, not in relation to footpaths where we might expect encounters with humans to be high. This could reveal that squirrels use these features differently to assess risk. For example, buildings could provide a static cue, whilst footpaths could provide a dynamic cue of risk. Previous work (for example Leaver et al., 2016) suggests that squirrel may use static cues, rather than dynamic cues, as a ‘rule of thumb’ for assessing risk. Chapter 3 also provides the novel finding that variance in noise levels interacted with proximity to urban features to increase perception of risk, with sites containing higher levels of noise variability having increased differences between safe and risky patches. Mean noise levels did not have this effect, suggesting that it is the variability component of noise, rather than noise levels, that impact risk assessment.

- *Urban features and competition risk*

For some species urban living may involve living at a higher population density than rural populations. Prior work by Bonnington *et al* (2013) found that in urban Sheffield, grey squirrels were living at a higher population density than in rural sites. In the assessment of population density carried out in this thesis, it was found that the urban sites contained higher populations than woodland sites (see Chapter 3). Whilst grey squirrels are not a social species, they may forage in the presence of conspecifics (Hopewell & Leaver, 2008) and where population density is high we might expect a greater amount of social interactions to occur (Parker & Nilon, 2008). Further, higher population density is likely to increase competition for food resources which may provide an explanation for the increased willingness of foragers at more urbanised locations to forage from higher risk patches, as was found in Chapter 3.

For foraging grey squirrels, encounters with conspecifics are likely to contain a risk to foraging activity, including the potential of an aggressive interaction, displacement from foraging area, or increased risk of cache pilfering (Hopewell & Leaver, 2008; Jayne et al., 2015b). Grey squirrels in urban parks have been found to show increased aggression toward conspecifics (Parker & Nilon, 2008), suggesting urban squirrels may experience increased conspecific competition levels compared to rural dwelling squirrels. Behaviours relating to the aggressiveness of individuals can also be linked to individual differences in resource-holding ability, for example the position in a social dominance hierarchy can determine individual access to food, with more aggressive individuals likely to gain more access (Allen & Aspey, 1986; Thompson, 1978). It is possible that grey squirrels may also show individual differences in tolerance to foraging in the presence of conspecifics (Hopewell & Leaver, 2008), and possibly human disturbance, although this remains an area warranting further investigation. Therefore, it might be expected that ability to gain access to resources in urban habitat could interact with an individual differences in tolerance of conspecifics under different levels of urbanisation. To address some of these questions, Chapter 5 attempted to examine if differences in urbanisation levels can influence foragers responses to a cue of a potential conspecific competitor. Previous research has suggested that foraging grey squirrels perceive auditory cue of conspecific calls as a cue of a potential social risk (Jayne et al., 2015), and that urban squirrels might respond with increased aggression towards conspecific cues (Parker & Nilon, 2008; Partan et al., 2010). Chapter 5 builds on these studies and asks if proximity to certain features related to urbanisation impacts responsiveness to cues of potential conspecific intrusion. Previous research relating to antipredator responses to playback stimuli (usually predation cues) during resource-acquisition has produced mixed results in terms of comparisons for urban and rural sciurid species, with some finding that urban dwellers are less responsive to auditory cues of risk (for example, Prairie dogs (Magle et al., 2005); fox squirrels (Mccleery, 2009)) and some studies finding that vigilance levels increase in urban dwellers in response to heterospecific, conspecific and predatory cues (e.g. California ground squirrels (Rabin, Coss, & Owings, 2006); eastern grey squirrels (Partan et al., 2010)).

Where this prior research has, on the most part, classified rural-urban gradients on a broader scale Chapter 5 attempted to look at whether applying a local habitat approach could address these mixed findings by incorporating a microhabitat variables thought to influence risk perception. It asks whether squirrels respond differently to conspecific cues according to certain features that could potentially change the dynamics of risk verses resource-acquisition trade-offs. Results found that all squirrels responded to conspecific playbacks with increased vigilance, but not fleeing, suggesting that this was not perceived as a predation threat, rather, it is likely to represent an interruption to foraging by a conspecific (Jayne et al., 2015). Squirrels at locations further from roads and buildings were found to show larger increases in vigilance, whereas squirrels closer to these features showed increases in food intake rates suggesting that, for squirrels close to these sites, maximising food acquisition is prioritized over vigilance under conditions where there might be an increased disturbance risk to foraging. Squirrels feeding near footpaths significantly increased food handling, rather than vigilance, which perhaps reveals that at sites close to pedestrian activity squirrels adjust to the increased costs of disturbance by maintaining a low level of vigilance (Makowska & Kramer, 2007).

Pervious research has found that grey squirrels are able to assess varying risk levels posed by a pedestrian, and alter behavioural responses according to pedestrian behaviour (Bateman & Fleming, 2014).

Roads were found to impact social signalling behaviours, with high proportions of these found at distances further from roads and buildings. These effects interacted with local patch quality and noise variability, with lower levels of signalling behaviours found at locations with high noise variability. This could indicate that investment in social signalling may be of low value under variable noise conditions, perhaps because noise can mask some forms of signalling (Luo et al., 2015; Morris-Drake et al., 2017). Squirrels feeding under high levels of noise were also faster to return to feeding following the playback. This may be due to reduced sensitivity to noise disturbance(Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2016; Tsurim, Abramsky, & Kotler, 2008), or could reflect foragers attempting to maximise food intake under higher levels of disturbance (Olsson & Molokwu, 2008). Where foragers were feeding at patches with higher quality local food resources, they returned to feeding slower than those at lower quality patches. This may reflect a difference in food-safety trade-offs at locations of varying habitat quality, for example, where food is plentiful foragers may need to take less risks to obtain it. It was found that squirrels at higher quality patches increased vigilance levels and had lower feeding intake rates, compared to those at lower quality patches supporting the hypothesis that those living in higher quality regions of their habitat place a higher value on safety, than those in low quality parts of the habitat.

- ***Are urban habitats safer?***

Results in chapters 3 and 5 suggest that features of the urban built environment (roads and buildings) did not appear to increase perceived predation risk for grey squirrels. Squirrels closer to these sites appear to invest less time in risk monitoring behaviours (such as vigilance in response to conspecific calls back) and showed more wiliness to forage at ‘risky’ patches. This may indicate that grey squirrel behaviour moves from being predator-constrained to being food-limited in more urban locations, where foragers prioritise food acquisition over safety. This was apparent in Chapter 5 where it was found that at locations containing higher local abundance of food resources, squirrels responded with increased vigilance and social signalling behaviours compared to those foraging at low resource locations, where they responded to risk by increasing feeding intake.

From previous research on urban squirrel populations, the grey squirrel appears to be successful at living alongside humans, and this thesis suggests that this is likely to be due to their ability to adjust foraging behaviour to the appropriate levels of fear in order to mitigate the costs to foraging caused by disturbance, as found in other studies of squirrel foraging behaviour (Jayne et al., 2015). By incorporating local microhabitat variables, these chapters reveal that when monitoring animal behaviour in urban landscapes, studies could benefit from considering multivariate environmental factors influencing differences in food-acquisition trade-offs being made in urban environments.

6.2 Personality variation in the grey squirrel

Theoretical models of personality variation suggest that resource acquisition trade-offs under risk are likely to play a major role in the structure and maintenance of personality variation (Dall et al., 2012; Dall & Griffith, 2014) and the value of food and safety may differ for individuals over time and context. Many of the behavioural traits described in empirical studies of animal ‘personality’, for example exploration, and aggression, may all represent ‘boldness’: the reaction of an individual to a potentially ‘risky’ situation. In relation to this, many theoretical explanations for ‘personality’ variation also emphasise the role of individual differences in state. This includes age, sex, size, body condition, such as fat reserves (Sol et al., 2017) as a cause of individual behavioural differences. These differences in state can also include the environmental conditions faced by the individual, such as the weather conditions (Wolf & Weissing, 2010). Both individual state and the environmental context are important to consider together because they represent the various constraints to behavioural decisions an individual can make in a given situation (Montiglio et al., 2015). Chapter 4 considered personality variation in grey squirrels at sites varying in urban levels. The ‘state’ variables, sex and body condition, were included as factors likely to affect behavioural decisions of individuals. Several environmental urban ‘context’ variables were also included: distance from roads, buildings, and footpaths, as well as noise factors. These factors reflected the same landscape features explored in Chapter 3.

Chapter 4 used behavioural responses to handling, and behaviour within an open field arena to quantify differences in behavioural repeatability. Using principle component analysis to detect underlying behavioural ‘traits’, it was found individual behaviour could be measured along a continuum of slow-fast escape during handling and human presence, and slow-fast exploration of the arena. These behaviours showed repeatability, suggesting these behaviours relate to personality variation in grey squirrels, something that had not been recorded in the literature before. Urban squirrels had lower repeatability for responses within arena and higher repeatability for handling responses. However, these differences were not significant between sites. On average there was a difference between sites in terms of average levels of exploration and escape behaviour, with urban squirrels being faster explorers and woodland dwelling squirrels being slower, however, from the results, differences in the structure of personality variation could not be inferred due to high overlapping confidence intervals. This study did not find a significant effect of urban microhabitat features on individual responses, although there was a trend between faster escape responses and distance from roads and buildings. Although not found to be significant, these could offer a possible factor driving faster escape response times in squirrels at the urban sites, as squirrels living closer to roads may need to have faster ‘escape’ responses to cross these sites.

It was predicted that squirrels living close to human disturbance would distribute themselves according to individual differences in escape and exploration behaviours. Unfortunately, in Chapters 3 and 5 it was not possible to identify all individual foragers, however the findings from these chapters may form future avenues for investigation of personality variation if individuals can be repeatedly measured over time. Given that GUDs and responses to conspecific cues did vary according to microhabitat, these may be more relevant behaviours for this level of investigation, whereas escape behaviour and exploration may be relevant for squirrels on a broader site level. Competition over resources is likely to be one of the common mechanisms for driving distribution of individuals across their habitat, and the benefits of particular individual behavioural strategies are likely to depend on the distribution of the other behavioural strategies expressed in the population (Dall &

Griffith, 2014). Therefore individual differences in state are likely to interact with the social context, or the distribution of local conspecifics (Wolf & McNamara, 2012). Therefore, future work incorporating a more detailed exploration of competition levels and competition dynamics could provide an important contribution to understanding risk-related behaviours in urban squirrels.

6.3 Personality variation in urban wildlife

Chapter 2 revealed that differences in the structure of personality variation in urban wildlife is not yet widely studied, despite the growing trend in animal personality research. In a search of the literature, few of the studies looking at urban wildlife personality variation were found to measure repeatability, an essential component of 'personality' (Dall & Griffith, 2014; David & Dall, 2016). Chapter 2 found that many of these studies have been carried out on avian species, with mammals seemingly underrepresented. Currently, predictions about the possible structure of this level of variation in urban populations can be difficult to make due to limited studies across taxa, with different species likely face different problems under urbanisation. Whilst it may be difficult to make generalisations in terms of how personality variation will be structed by urbanisation, the 'landscape of fear' framework can provide useful means to consider how individual behaviour might be structured according to the perceived and actual risks encountered within their habitat. Although Chapters 3 and 5, did not identify individuals in the analysis, they have demonstrated that local habitat matters for resource -acquisition trade-offs in grey squirrels, revealing that the balance between safety and feeding can change according to urban features. With individual differences in risk taking being impacted by state, social context and perceived risk, methodology from these can be used to investigate individual behaviour and personality variation in future work on urban wildlife.

6.4 Methodological considerations

- ***Use of open-field tests***

Open field tests (OFT) were originally used to quantify activity and exploration behaviours in laboratory rats, although they are now becoming an established method of measuring behaviour in studies of animal personality variation (Perals et al., 2017). Although widely used and standard practice, the use of OFT in studies of personality variation has been criticised for a number of reasons, particularly due to concerns about the labelling of behaviours and behavioural ‘traits’. Greggor *et al* (2015) noted that although OFTs are thought to measure activity and exploration, they may be measuring fear and neophobia in some species (Greggor et al., 2015). Carter *et al* (2013) raised concerns that behaviours expressed in OFTs can be difficult to label, with the possibility that many researchers could be committing ‘jingle-jangle’ fallacy whereby the behaviours may be labelled as the same trait, but represent different behaviours, or by labelling two different behaviours as the same. Examples are likely to include behaviours such as exploration and activity as ‘boldness’, or the labelling of neophilia and neophobia as ‘exploration’ . Therefore labelling behaviour in OFTs should be treated with caution (Carter et al., 2013). There may also be some question as to whether behaviours expressed in OFTs represent biologically relevant behaviours in wild animals, although studies have been able to link behaviour in OFTs to ecologically relevant behaviour including dispersal (Dingemanse et al., 2012), and maternal provision (Boon et al., 2007).

In the field OFTs can be difficult to use, especially on larger or highly active animals. They also require the need for repeated recapture, which could be problematic for some species, for example if trapping and handling requires potentially invasive or stressful processes. However, they do provide advantages in that they can offer a controlled and standardized arena in which to measure behaviour and can be adapted for different species and research questions. For example, they can be modified by adding novel objects or holes to separate exploration from activity behaviour (Boon, Reale, & Boutin, 2008). In Chapter 4 the OFT was modified so that it included holes in the floor to separate exploration behaviours for activity, it also included an exit so that squirrels were not trapped in the arena and could escape once they had located the exit, this was done in order to reduce fear related activity. In the early trials a solid cover was added, because prior to this, squirrels had tried to jump up at a clear Perspex lid. Grey squirrels are known to perceive cover as safer than open habitat, therefore the addition of this helped to standardise perception of cover in the field.

This thesis found that the OFT measured a form of exploration during escape in a novel environment, with individuals found to be repeatable in this behaviour. While escape responses under novel conditions, or threat of predation (potentially caused by the presence of a human observer), are likely to represent an ecologically relevant behaviour for squirrels, this was not examined in Chapter 4. Where it is possible to mark and observe free-ranging animals over time, future work should design and incorporate additional *in situ* field tests to provide validation for the findings in an OFT (for examples see: Perals et al., 2017; Uchida, 2020), and explore what these mean for resource- acquisition trade-offs in urban wildlife perhaps by relating these to the protocols used in Chapters 3 and 5.

- ***Tracking of individuals***

Studies requiring the repeated measures of the same individual overtime are most often done under laboratory conditions, perhaps for good reasons. Several papers reviewed in Chapter 2 brought wild animals temporarily into the lab to assay behaviour under controlled conditions, and to allow behaviours to be measured over time. This thesis attempted to measure repeatability in wild free-ranging individuals, which required repeated trapping across seasons. For some species this could potentially affect some of the characteristics of the sample where certain individuals may be harder to re-trap than others. For example, young male grey squirrels disperse from natal habitat whereas females remain (Koprowski, 1996), this could mean that males are easier to trap during dispersal but may not be re-trapped again. This is one of the key reasons for the use of only adult squirrels in Chapter 4. The sample also contained predominantly males, possible reasons for this could be due to sex ratio at these sites, or that males were more trappable. The labour intensity of re-trapping individuals in the wild also places constraints on the ability to collect large sample sizes, or perhaps more importantly for personality variation research, constraining the number of repeated samples taken from individuals (Dingemanse & Dochtermann, 2013). In chapter 3 trapping effort data was not deliberately recorded at the time, however, obtaining sufficient sample sizes in the field can be labour intensive and although not quantified, gaining an adequate sample size in woodland squirrels seemed to require increased trapping effort compared to squirrels in gardens.

One of the key issues for animal personality research is transferring laboratory findings to the field and to address what these behaviours mean for individuals in the wild. Recent use of technology, such as RFID, geolocators and GPS tracking, has made it possible to track individuals using their habitat. These have revealed individual differences in movement and space use (Spiegel et al., 2017), exploration (Ferrer et al., 2019; Morand-Ferron, Hermer, Jones, & Thompson, 2019), territorial responses (Sprau, de Goede, & Naguib, 2010), as examples. Camera trapping could be used where individuals can be visually marked for identification. Employing this into the protocol for Chapter 3 and 5 could provide useful data for future work, however, this was not possible for data collected in this thesis due to financial and logistical constraints.

Chapter 5 adopted direct field observations. Attempts were made to utilise PIT tags at some of the sites where squirrels had been marked for Chapter 4. A Radio-frequency identification reader was trialled, but due to constraints in field seasons, it was not possible to record enough tagged individuals, perhaps due to the time that had passed since they had been tagged in Chapter 4. Direct field observations are time intensive, and for grey squirrels they may have to be limited to Autumn and Winter when squirrels forage more readily at ground level, making then easier to observe. Use of additional technology, such as camera traps could help future research to address if these behaviours are relatively consistent over seasons as we may expect risk-resource acquisition trade-offs to vary for grey squirrels across seasons, for example, differences between breeding and non-breeding.

6.5 Conclusions and Further Research

This thesis attempted to view behavioural variation in a common urban mammal through some of the conceptual elements of the landscape of fear and animal personality variation. It was identified that, whilst investigation of differences in animal behavioural variation in urban wildlife is a growing area of research, few studies are considering differences in the structure of personality variation between urban and rural populations in terms of what this reveals about any possible differences in ecological pressures experienced. It attempted to incorporate local habitat features associated with urbanisation into the understanding behavioural variation in grey squirrels, including behavioural consistency in behaviours during escape, exploration of novel arena, and the behavioural responses to a risk. It was found that grey squirrels show between-individual variance in escape and exploration behaviours, although it did not find that this was significantly impacted by urbanisation. However, mean levels in these behaviours did vary according to site with urban squirrels showing faster response times. Microhabitat features were found to impact responses to conspecifics and the trade-offs between food and safety, with squirrels foraging closer to urban features seeming to prioritise food acquisition over safety. This is likely to suggest that grey squirrels move from predator constrained behaviours, to food constrained behaviour in urban landscapes.

- ***Should we be concerned about behavioural variation in urban wildlife?***

In a meta-analysis of rates of phenotypic changes associated with human altered environmental contexts, Hendry *et al* (2008) found that behavioural plasticity plays a pivotal role in a species ability to live alongside human disturbance. Effects of human disturbance are likely to be fast-paced, and abrupt, leading to faster rates of phenotypic changes compared to populations in ‘natural’ contexts (Hendry, Farrugia, & Kinnison, 2008). Investigations of behavioural variance within and between populations have demonstrated that not all species and populations show the same amount of behavioural plasticity (Hendry, 2016; Hendry et al., 2008), a phenomena that is often discussed in the context of personality variation under urbanisation (Miranda et al., 2013). More broadly, authors have argued that ‘animal personality’ doesn’t offer anything new for behavioural ecology in that it is a ‘re-branding’ of ideas and frameworks already integrated into the study of individual variation and behavioural plasticity (Beekman & Jordan, 2017). Part of these criticisms may arise because ‘personality’ variation is a relatively new term in behavioural ecology, and as such there are sometimes disparities between studies using terms relating to ‘personality’ and the definitions of the behaviours observed (David & Dall, 2016).

The literature reviewed in Chapter 2 found that there were only a limited number of studies of personality variation in urban wildlife that measured repeatability (between individual variance), one of the core elements of ‘personality’. Behaviours did not appear to be defined the same way, which can make it difficult to compare between these studies (David & Dall, 2016). From the studies included in Chapter 2 it did not appear that there was a notable trend across studies in terms of differences between urban and rural populations in the level of personality variation expressed. Overall, studies found that it was the average levels of risk-related behaviours, such as aggression and activity/exploration, that may be higher in urban wildlife, but this does not currently appear to impact levels of repeatability levels across urbanisation gradients, although broadly, behavioural repeatability in urban wildlife appears slightly lower suggesting greater behavioural flexibility in these populations. Chapter 2 argues that these studies could benefit from incorporating a microhabitat and ‘landscape of fear’ approach to defining the environment individuals experience, rather than using broad definitions such as urban verses rural sites, in an attempt to reveal if there are factors in urban environments that could impact personality variation. Chapter 4 found that grey squirrels exhibited differences in mean levels of behaviour according to site. Further, it found that behaviour in the OFT had lower levels of repeatability in urban sites than woodland site (garden = 0.382, park – 0.287, woodland = 0.533), and higher levels of repeatability in handling responses at the least and most urban sites (Garden = 0.7, woodland 0.6). However, overlapping confidence intervals suggested that it could not be concluded that there were clear differences in behavioural variation levels across these sites. Furthermore, individual microhabitat did not appear to have a significant effect on the behaviours measured. Therefore, findings from Chapters 2 and 4 could suggest that perhaps urbanisation is not having major impacts on levels of behavioural variation, although it does appear to impact average levels of behaviour.

The investigation of personality variation under urbanisation is relatively new. Therefore, results so far are unlikely to be generalisable across species and populations. Despite this thesis finding no significant impact of urbanisation on personality variation, monitoring levels of behavioural variation across in populations under urbanisation is likely to become a useful means to monitor potential impacts on different species. From the broader field of animal personality variation, it has been found that variability in behaviour is linked to generic diversity and fluctuating environmental pressures (Dingemanse et al., 2004), is shaped by social context (Bergmüller & Taborsky, 2010)and predation levels (Biro et al., 2003), and that the structure of personality variation can provide clues about the selective pressures faced by a population (Boon et al., 2007a, 2007b; Dingemanse et al., 2004). This thesis investigated a species that currently appears abundant in urban habitats, and in this regard, we can conclude that grey squirrels can successfully adjust to living in human dominated habitats. Choosing a study system that is abundant across urbanisation levels provides advantages, especially in terms of gaining adequate samples, as well as understanding a successful urban species. However, future work on species impacted more heavily by urbanisation may reveal more about how urbanisation influences behavioural variation.

Some authors have suggested that understanding individual variation in behaviour could be useful in the management of human-wildlife conflict. For example, certain behavioural 'types' may become more vulnerable to conflict with humans (Swan, Redpath, Bearhop, & McDonald, 2017). This may be useful for managing 'problem' populations, for example, Honda *et al* (2018) discuss the role of manipulating personality variation via selective harvesting in urban populations. Using urban deer as an example of a species popular with the general public, yet requires management due to increased population densities in cities where they become associated with vehicle collisions, they argue that individuals could be selectively managed to reduce 'boldness' in populations, to avoid roads where collisions are likely (Honda, Iijima, Tsuboi, & Uchida, 2018). Human attitudes towards wildlife may also shape structure of personality variation, without conscious attempts to do so. For example, certain species may be more vulnerable to certain control methods such as trapping or poisoning. This could affect the distribution of behavioural strategies, in similar ways to the effects of trophy hunting and overharvesting has had on behaviour, physiology and morphology in many wild populations (Allendorf & Hard, 2009). For vulnerable species living in urban environments, understanding behavioural variation could help inform ways to increase population diversity, for example, by designing urban landscapes with behavioural heterogeneity in mind. Species with low population numbers may have higher risk of losing behavioural diversity, in part because frequency dependant effects may be less in small populations (Anthony & Blumstein, 2000; Bergmüller & Taborsky, 2010). For example, in the UK populations of hedgehog (*Erinaceus europaeus)* are low, yet occupy areas of urbanisation (Dowding, Harris, Poulton, & Baker, 2010). As an example, future work in supporting this species could involve understanding personality variation in this species, and how behavioural diversity could be maintained.

Conclusion

This thesis examined the possible links between urban landscape features and behavioural responses to risk, to explore how these factors might influence the structure of behavioural variation under urbanisation. Urban squirrels appeared more tolerant of predation risk by increasing use of ‘riskier’ patches in locations close to urban features. Squirrels feeding at more urbanised patches were found to increase feeding intake, reduce vigilance, and reduce social signalling behaviours in response to a conspecific playback than squirrels further from urban habitat features. Together these results suggest the behaviour of foraging urban grey squirrels appear to move from being constrained by predation-risk to being food-resource limited, meaning that urban squirrels will prioritise food acquisition over safely when foraging near roads and buildings. Variation in noise levels, rather than mean noise levels, close to features of anthropogenic disturbance, appear to increase costs of foraging at urban sites, suggesting that this is a costly feature of urban habitats for grey squirrels. Grey squirrels were found to show repeatability in escape and exploration responses, suggesting that this is an aspect of personality variation in grey squirrel populations. Significant differences in levels of variation were not found across urban-rural sites, however average levels of these behaviours did vary significantly across sites, with urban squirrels showing faster escape responses and faster exploration times. Whilst the work may not generalise beyond the populations studied in this thesis, overall, these results help to clarify how features of urban habitats can change risk-related behaviours in grey squirrels. These findings can present some new avenues for research into behavioural variation under urbanisation, including further work integrating microhabitat with risk-related trade-offs and personality variation in grey squirrels. It also highlights where research into personality variation in urban wildlife could be developed further by standardising descriptions of urbanisation levels, and the features of urban landscape.

Appendix

Appendix A

Appendix Table A.1: Summary of studies reviewed in Chapter 2

Behaviour	**Habitat**	**Index of urbanisation/human disturbance**	**Species**	**Other measures**	**Method**	**Duration between assays**	**N (M,F)**	**R (repeatability)**	**Outcome**	**Source**
Risk taking/Boldness	Agricultural land	Nesting distance from roads	Burrowing owl (*Athene cunicularia*)	N/A	FID to approaching human (field)	Repeatability over 4 + trials conducted over one month.	N= 103; N= 36 for reaction norm trials	0.88 - 0.92	Individual FID is repeatable. Owls breeding close to roads have consistently shorter FID	(Martina; Carrete & Tella, 2010)
Boldness toward humans; aggression towards predator; exploration	Urban Vs rural	Human presence	Burrowing owl (*Athene cunicularia*)	N/A	FID; predator model; exploration of novel food.		FID N= 375; Exploration N= 253; Predator response N = 165	Urban: 0.83 Rural: 0.96	Individual FID is consistent over life-span. Urban show shorted FID.	(Martina Carrete & Tella, 2013)
Activity & aggression	Urban V Rural	Site of capture (artificial structure or trees/hedgerow)	3 species of orb spider (*Larinioides sclopetarius; Zygiella x-notata, Nucteneaumbratical)*	N/A	Novel environment test; contest test using same-sex conspecific.	Each test conducted twice. 1 – 3 weeks between assays.	61 *L. sclopetarius, 61 Z. x-notata,* 85 *N. umbratica*.	Activity L. sclopetarius (mean r = 0.493); Z. x-notata (mean r = 0.426), and N. umbratica (mean r = 0.481) Aggression 0.832, 0.838, 0.781	Urban dwelling species had higher activity and lower aggression.	(Kralj-Fišer & Schneider, 2012)
Exploration & boldness	8 sites – urbanisation index used based on habitat variables.	(Method by Czúni, Lipovits, & Seress, 2012) Aerial images split into squares of 100m, covering an area of 1km – defined by predominant landscape features (buildings,	4 species Ground beetle	Population density; temperature	Open-field test; thanatosis behaviour	2 and 7 days after first test.	N. brevicollis (N = 295 individuals) and P. oblongopunctatus (N=472 individuals),	Activity in open field (0.249–0.321)	Beetles from highly urbanised were more active. Exploration linked to increased boldness	(Wiebke Schuett et al., 2018)

		paved roads, vegetation).								
Activity, boldness & anti-predator behaviour	4 sites – rural – urban, based on landscape characteristics	Human build/landscape characteristics	Speckled wood butterfly (Pararge aegeria)	NA	Open field test for larvae stage; response to stick 'predator' during pupae stage; struggle rate and activity in novel arena at adult phase.			0.23 for larvae tests; 0.98 for pupal anti-predator.	Effect off urbanisation on activity was found in males.	(Kaiser et al., 2018)
Exploration	14 sites across a gradient	Satellite imagery used to quantify landscape cover. Urban index created using PCA.	black-capped chickadees (Poecile atricapillus)	NA	Wild caught – exploration of novel room, and exploration of altered novel room.	5 trials per assay.	N = 157	Urban (R = 0.53) forest (R = 0.29)	Urban were faster explorers, and higher repeatability for exploration	(M. J. Thompson et al., 2018)
Boldness and aggression (males)	9 urban; 8 rural	Defined by human population density and proximity to city centre.	Great tit (Parus major)	NA	Response to playbacks of territorial intrusion. Five behavioural responses measured	24 hours.	27 Urban, 27 Rural.	*Latency to fly:* Urban: 0.57 Rural: 0.61 *Latency to sing:* Urban: 0.68 Rural: 0.56 *Approach:* Urban: 0.21 Rural 0.60 *Time with 5m of speaker*: Urban: 0.15 Rural 0.32 *No. flights*:	Urban showed greater response to playbacks	(Hardman & Dalesman, 2018)

								Urban: 0.12 Rural: 0.40		
Boldness, exploration.	Six populations: 2 rural, 2 urban, 2 urban with introduced predator.	City and forested areas selected.	brown anoles (A. sagrei),	Predator density	Escape distance; response to capture; Captive tests of exploration and response to simulated predator attack.	Lab assay 2 days after field assay.	N = 120 males	Boldness: 0.350 Exploration: 0.470	Urban habitat with more predators were less active.	(Lapiedra et al., 2017)
Boldness/wariness	2 sites: urban and rural	City and rural	black swans (Cygnus atratus).	Individuals (N= 80) genotyped at DRD4 and SERT genes	FID toward human approach.	Varies (min. 1 day)		R = 0.61 for FID	Urban had larger FID than rural, genetic differences found between these populations on DRD4.	(Van Dongen et al., 2015)
Boldness & aggression	3 sites: 2 urban and a rural (game reserve)	Proximity to town	Song sparrows (Melospiza melodia).	NA	Aggressive response to playbacks; boldness tested by FID	1 day	N = 26 rural, N = 38 Urban	FID response: 0.762	Aggression and boldness higher in urban; correlation between aggression and boldness found in rural, not urban.	(Scales et al., 2011)
Dominance; Exploration; Neophobia/ Consumer innovation	14 sites, urbanisation category given based on PCA.	Satellite imagery used to quantify landscape cover. Urban index created using PCA.	Black capped chickadees	CORT	Response to novel food during 3 trials. Dominance displacement at feeder. Exploration in novel environment	1 day	N = 170	R = 0.47 for exploration (N = 70); R = 0.20 for food neophobia; R = 0.027 for consumer innovation;	Urbanisation did not predict neophobia responses or exploration.	(Prasher et al., 2019)
Boldness, problem solving, neophobia	8 sites of varying levels of human	Percentage of anthropogenic structures 1km2	Barbados Bullfinch (Loxigilla	Immunocompetence via amount of inflammation	Problem solving measured with draw-	3 days	Urban = 26 Rural = 27	boldness was 0.427; neophobia was	Urbanised birds faster problem-solving and bolder, however	(Audet et al., 2015)

	disterbance	around capture site.	barbadensis)	(swelling) induced by phytohemaggluti-nin (PHA) injection.	lid task. Neophobia assayed via novel object placed next to food. Boldness assay latency to approach food in an open arena.			0.350	were more neophobic. Urban had enhanced immunocompetence.	
Activity; boldness	3 urban polds, 3 rural	Percentage of build up area around site. Sites < 3% build classed as rural; sites > 15% build classed as urban.	damselfly (Coenagrion puella)	Experimental exposure to pesticide	Boldness – latency to move after being probed on lamellae. Activity in familiar environment over 10 mins.	Three tests prior to pesticide exposure. Tested again 4 days following – another 3 trials. Total of six trials per individual.	Urban = 30 Rural = 30	Activity (range 0.277 - 0.542) Boldness(range 0.252 - 0.447)	Mean levels of behaviours effected by pesticide exposure. However this did not impact repeatability. Behavioural syndromes between activity and boldness after pesticide exposure was strongest in rural.	(Tüzün et al., 2017)
Activity, exploration & boldness	2 urban, 2 non-urban sites	Approximate distance from city.	Delicate skink Lampropholis delicata	Food preferences (natural compared to commonly found food in urban).	Boldness assessed by basking preferences (open vs cover site). Activity and exploration of novel arena.	3 days		Activity, r = 0.210; Exploration r = 0. 232; Food preference r = 0.50; boldness (r =−0.11)	No difference in activity, exploration, or food preferences between populations although these all show individual repeatability. Boldness was not repeatable and did not differ between sites.	(Moule et al., 2015)

Activity	Urban vs Desert	City centre	Western black widow (Latrodectus Hesperus)	NA	activity across 3 contexts: startle; startle + prey; startle + mate.	48 hours	10 urban 10 Desert	Startle: 0.5 – 0.9 Startle + prey: 0.08 – 0.142 Startle + Mate: 0.698 – 0.710	Found evidence of individual repeatability across context, but this did not differ between urban and desert spiders.	(Halpin & Johnson, 2014)

Appendix B

Image A.1 Overview of sites used in Chapter 3 – 5. All images via Google Earth

Image: gardens

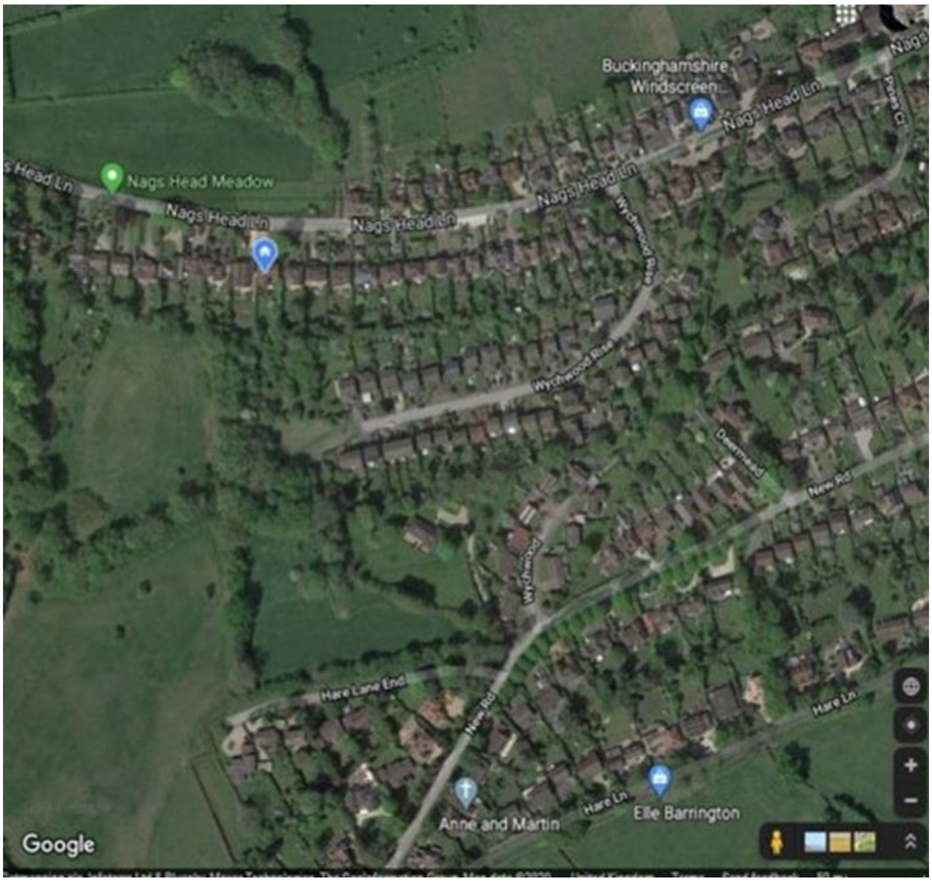


Image: Wycombe Museum

Image: Parks High Wycombe

Image: pepperboxes woodland

Image: Priestfield Arboretum

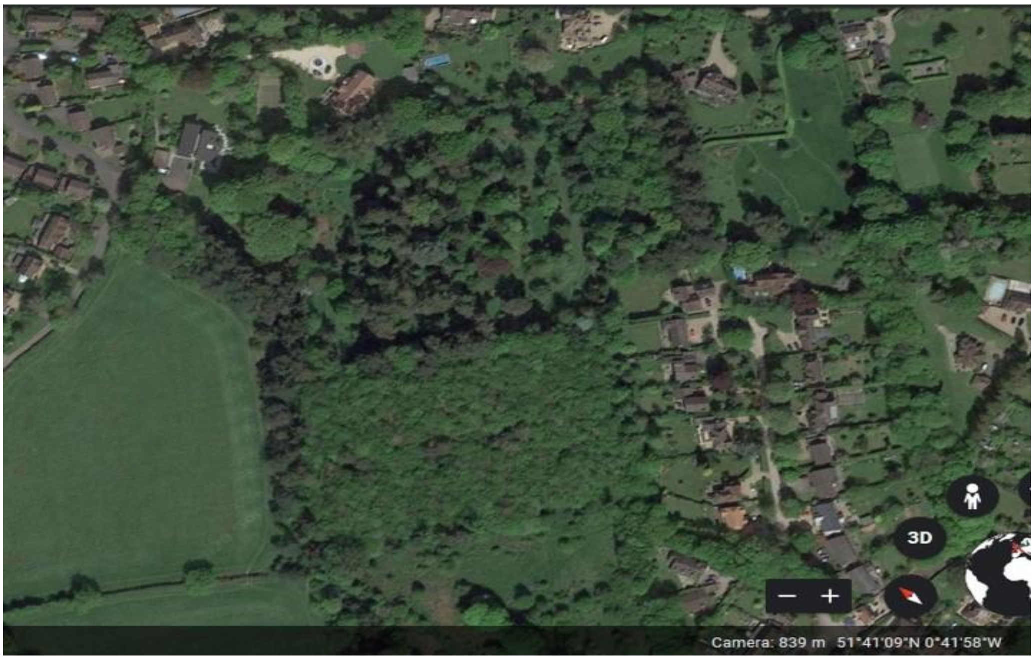
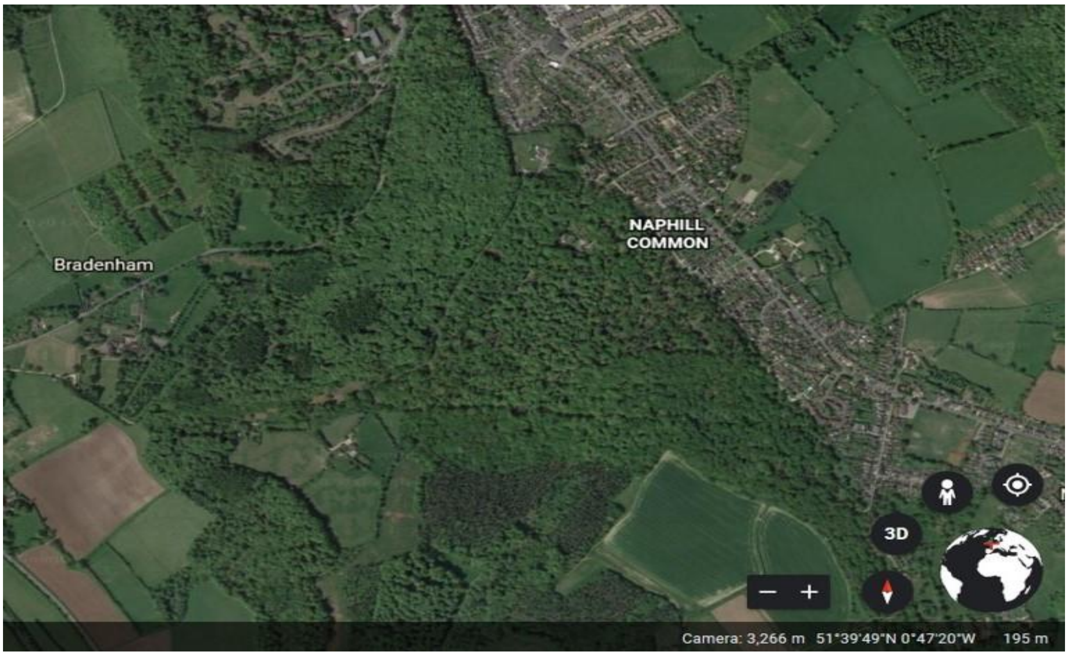


Image: Naphill Forest



Appendix C:

Image A.2: Grid layout and positions of GUD trays.

Image: Wycombe museum site

Image: Park site

Image: Gardens site

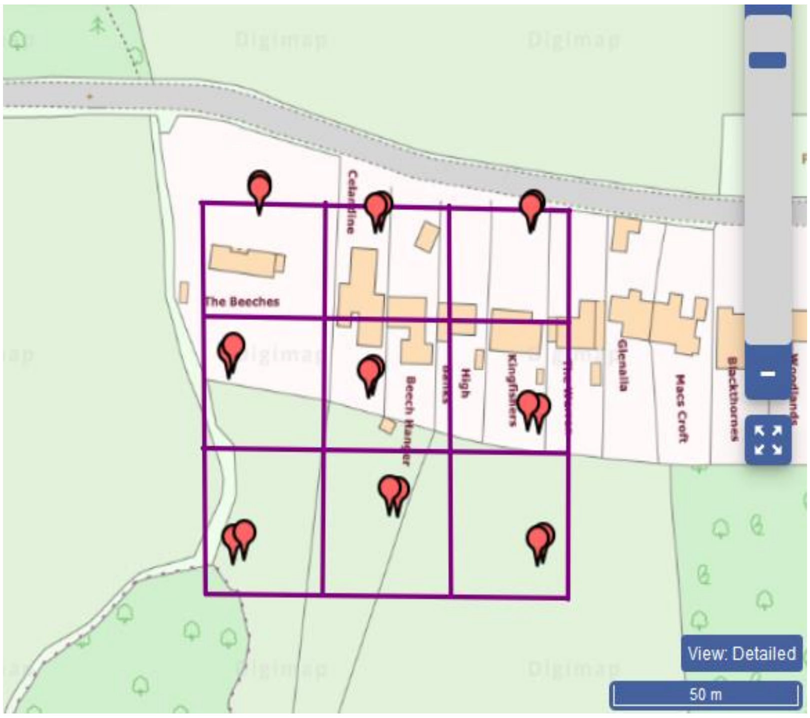


Image: Arboretum site

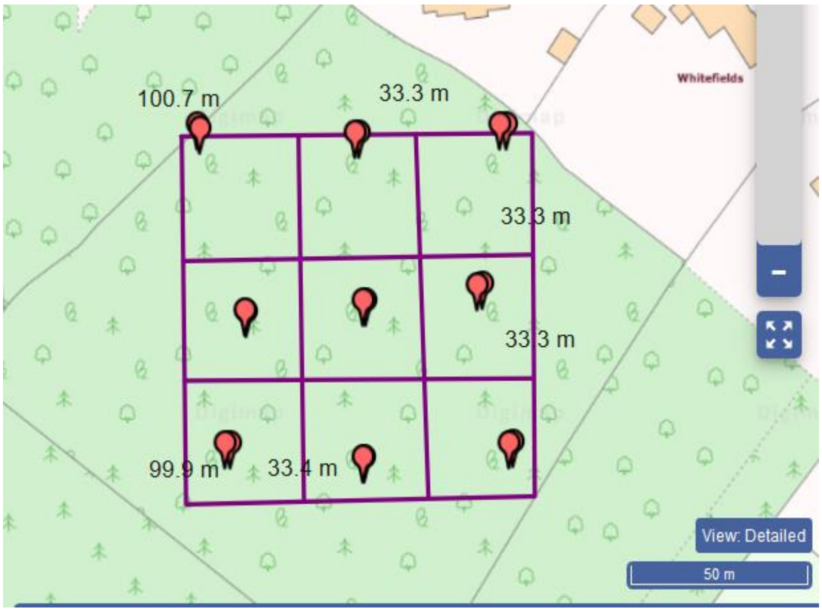


Image: Pepperboxes wood site

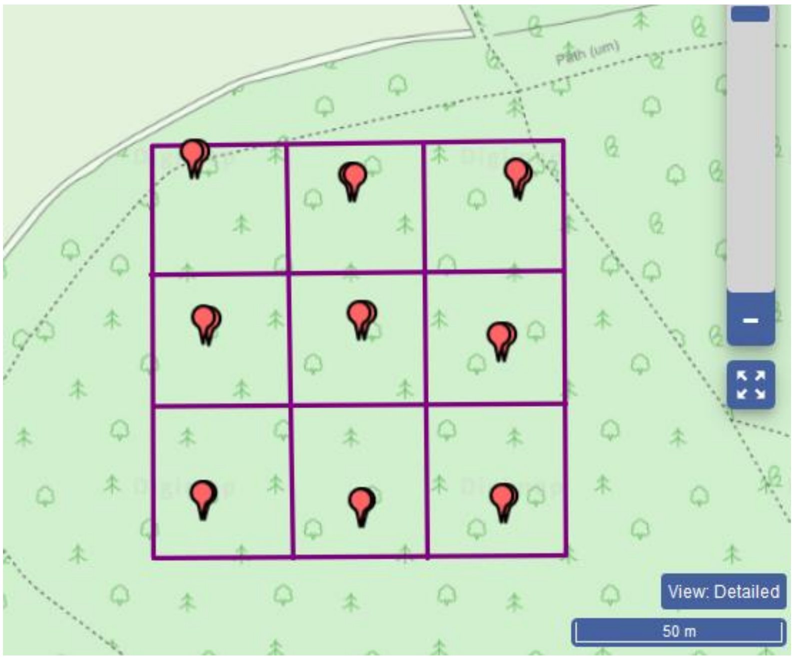
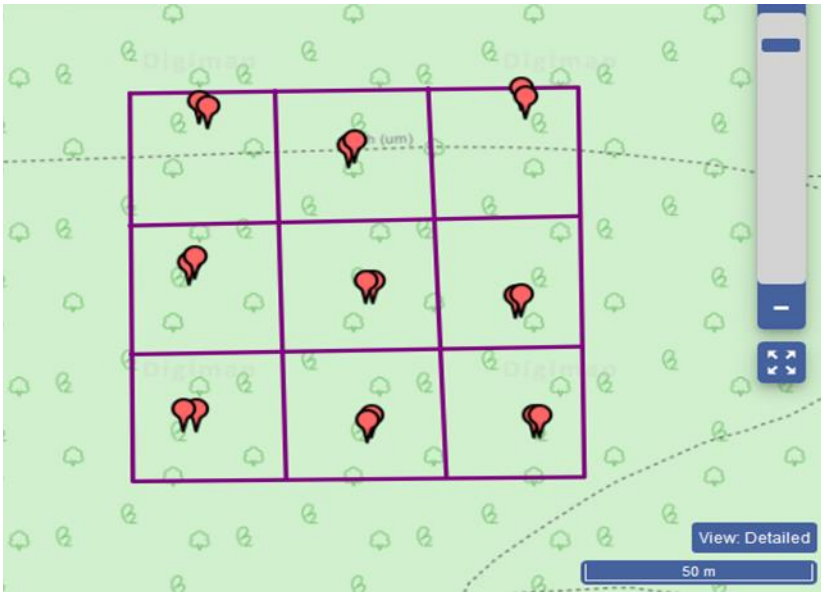
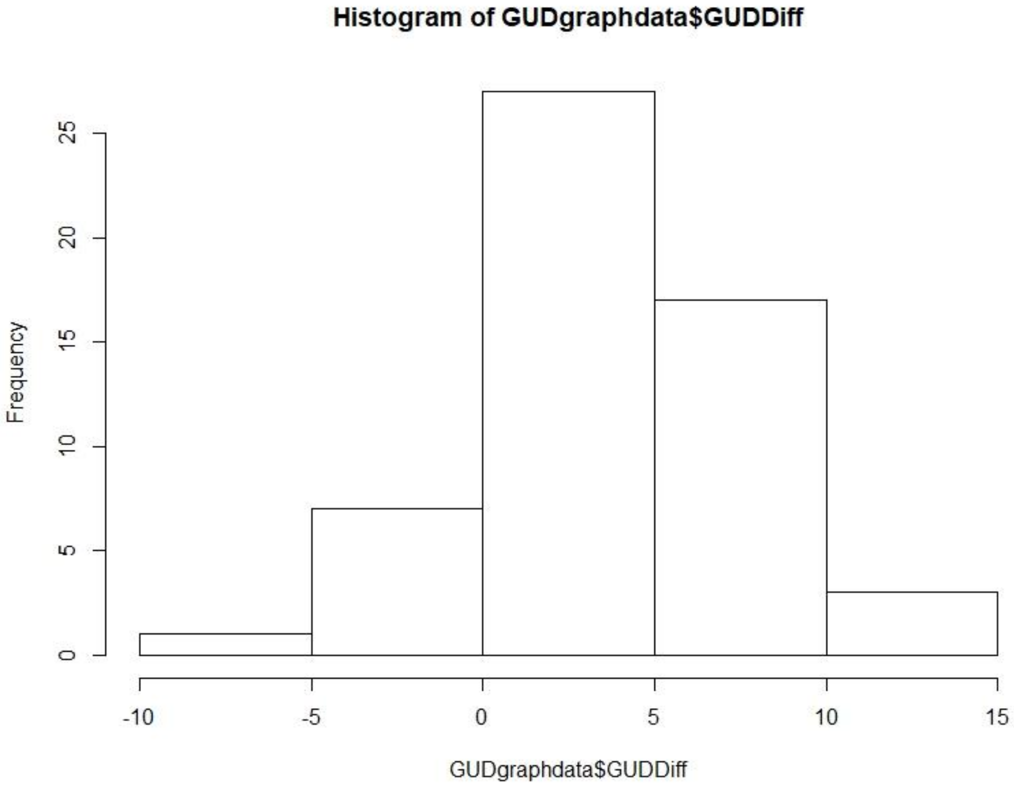


Image: Pepperboxes wood site



Frequency distribution histograms and q-q plots for outcome variables: difference in GUD between safe and risky patches (GUDDiff).



Quantile-quantile plot for outcome variable: difference in GUD between safe and risky patches (GUDDiff).

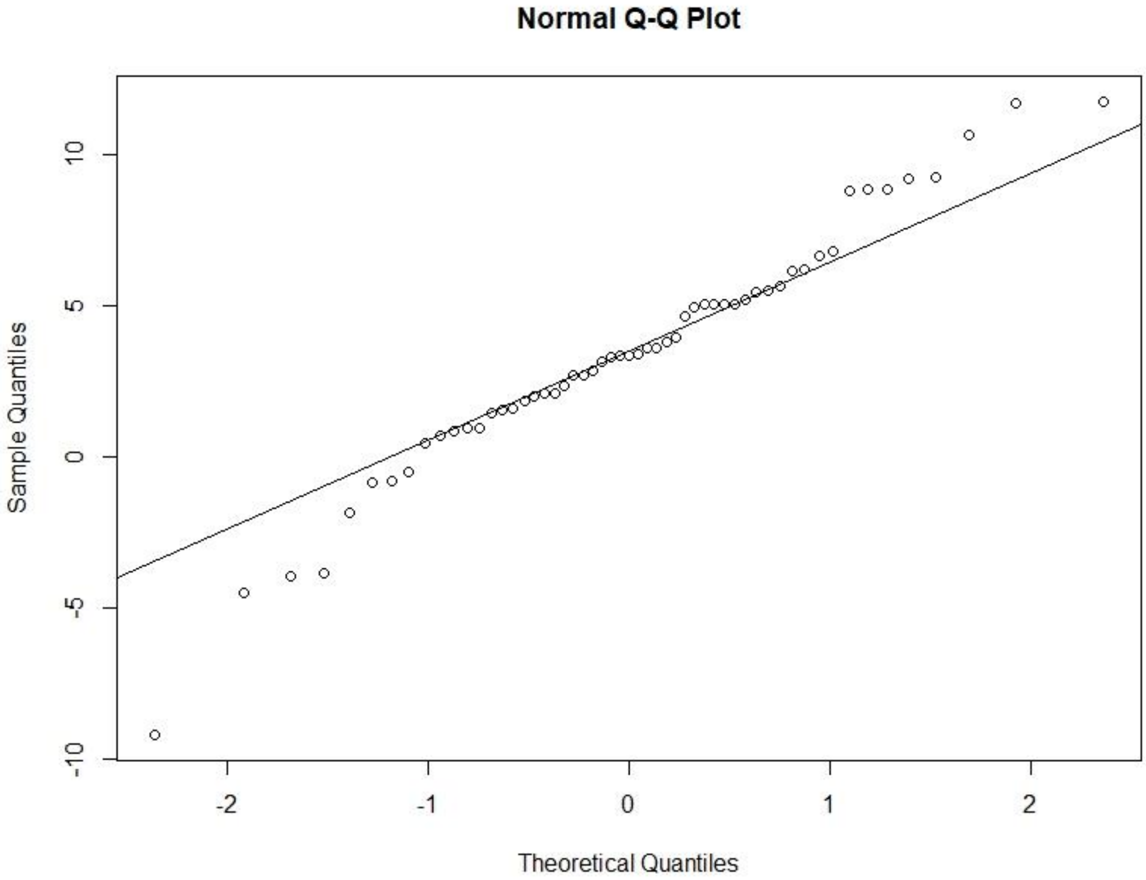


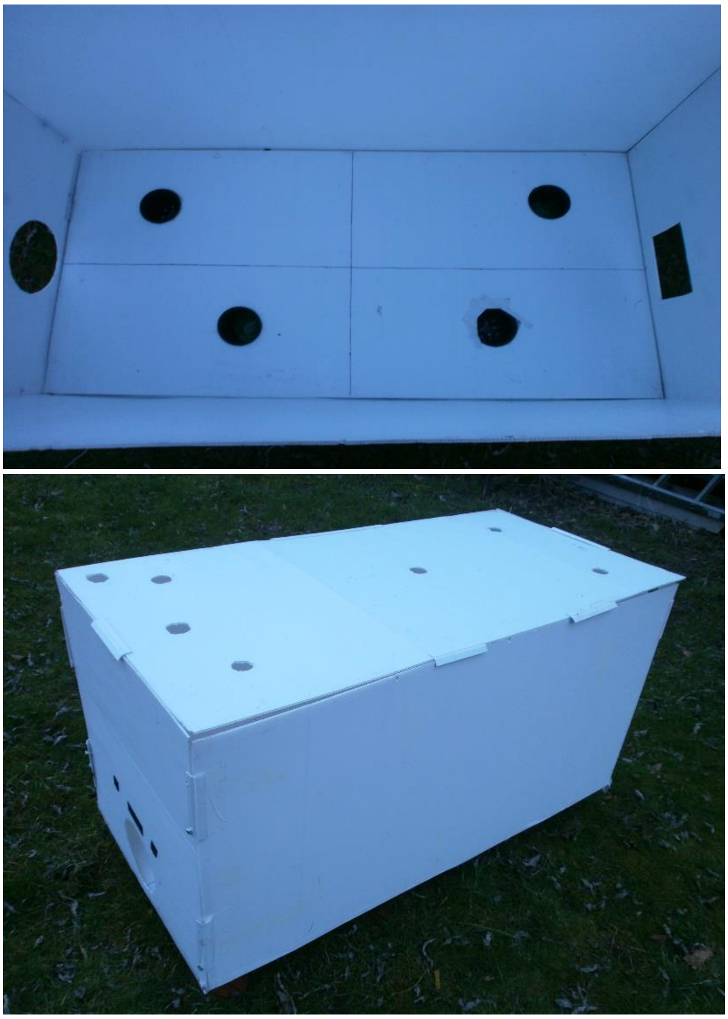
Table A.2 Correlation matrix (Pearson) showing strength of correlations between independent variables (prior data transformations) used in GUD study.

	Dist. To Road	Dist. To Building	Dist. To Footpath	Population	Noise variability	Mean noise levels
Dist. To Road	1.0000000	0.95011824	0.14717742	-0.2028731	-0.2546843	-0.4670569
Dist. To Building	0.9501182	1.00000000	0.07457393	-0.3046109	-0.3109541	-0.4623357
Dist. To Footpath	0.1471774	0.07457393	1.00000000	0.2475632	-0.0219677	-0.2852124
Population	-0.2028731	-0.30461089	0.24756319	1.0000000	0.3591281	0.0530284
Noise variability	-0.2546843	-0.31095414	-0.02196770	0.3591281	1.0000000	0.4187785

Mean noise levels	-0.4670569	-0.46233573	-0.28521239	0.0530284	0.4187785	1.0000000

Appendix D:

Image A.3: Open-field arena used in chapter 3



Images A.4: Handling cone and trap used in Chapter 3.

Table: A.3 Descriptions of behaviour in open-field test (Chapter 3).

Behaviour	***Description***
Vocal	Vocalisation scored as Yes/No
Enter arena	Latency to enter the arena from moment the trap door is opened.
Walk	Locomotion/walking
Motionless	Stationary/still
Head in hole	Places head into flowerpot
Rear Scan	Standing on black legs, upright posture, looking around
Scan	Still but with head moving/looking around
Groom	Grooming face or body, includes scratching.
Squares	Number of squares crossed in arena

Table A.4: Full PCA of all behaviours and their factor loadings. Behavioural categories with weak factor loadings were removed.

```
Eigenvalues
                       Dim.1   Dim.2   Dim.3   Dim.4   Dim.5   Dim.6   Dim.7   Dim.8   Dim.9
Dim.10
Variance               3.291   1.486   1.452   1.123   0.793   0.655   0.574   0.378   0.197
0.051
% of var.             32.906  14.862  14.524  11.231   7.926   6.548   5.740   3.783   1.972
0.507
Cumulative % of var.  32.906  47.768  62.293  73.524  81.450  87.997  93.738  97.521  99.493
100.000

Variables
                     Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
breaths            | -0.005  0.001  0.000 |  0.703 33.271  0.494 | -0.181  2.248  0.033 |
time.to.cone       |  0.194  1.140  0.038 | -0.158  1.678  0.025 |  0.705 34.256  0.498 |
time.to.arena..s.  |  0.438  5.817  0.191 | -0.599 24.171  0.359 | -0.032  0.071  0.001 |
```

```
walk             |  0.826 20.755  0.683 |  0.123  1.013  0.015 |  0.174  2.092  0.030 |
still            |  0.061  0.112  0.004 | -0.383  9.855  0.146 |  0.583 23.422  0.340 |
head.in.hole     |  0.660 13.222  0.435 |  0.393 10.415  0.155 |  0.260  4.644  0.067 |
rear.scan        |  0.795 19.185  0.631 | -0.191  2.453  0.036 | -0.414 11.824  0.172 |
scan             |  0.812 20.038  0.659 | -0.259  4.507  0.067 | -0.378  9.861  0.143 |
groom            |  0.604 11.094  0.365 |  0.184  2.275  0.034 | -0.085  0.501  0.007 |
squares          |  0.533  8.637  0.284 |  0.392 10.362  0.154 |  0.401 11.083  0.161 |
> dimdesc(res)
$Dim.1
$Dim.1$quanti
                  correlation      p.value
walk                0.8264158 3.420257e-27
scan                0.8120137 1.353807e-25
rear.scan           0.7945502 7.830313e-24
head.in.hole        0.6596079 2.650067e-14
groom               0.6042118 1.115192e-11
squares             0.5331037 5.678037e-09
time.to.arena..s.   0.4375046 3.416452e-06
time.to.cone        0.1936903 4.882847e-02


$Dim.2
$Dim.2$quanti
                  correlation      p.value
breaths             0.7031916 8.630916e-17
head.in.hole        0.3934280 3.602455e-05
squares             0.3924357 3.784510e-05
scan               -0.2588117 7.981929e-03
still              -0.3826996 6.088416e-05
time.to.arena..s.  -0.5993580 1.792841e-11


$Dim.3
$Dim.3$quanti
             correlation      p.value
time.to.cone   0.7053642 6.313580e-17
still          0.5832552 8.192817e-11
squares        0.4012101 2.433810e-05
head.in.hole   0.2597108 7.759074e-03
scan          -0.3784467 7.459071e-05
rear.scan     -0.4144081 1.223384e-05
```

Table A.5: Summary of GLMMs full and final models for OFT and handling behaviour.

	Random term	**Var.**	**Fixed effect**	**estimate**	**SE**	**df**	**t**	**p**
Arena Behaviour	***Full model***							
	ID	0.0203	Assay Time	-0.0479	0.0636	41.72	-0.754	0.4549
	Assay Time	0.0007	Body condition	-0.1152	0.0505	41.7795	-2.279	**0.0278**
	Residual	0.0076	Site (park)	-0.1109	0.214638	28.3906	-0.517	0.6092
			Site (woods)	0.1698	0.198873	29.6452	0.854	0.3998
			Sex (male)	-0.1009	0.064235	30.1106	-1.571	0.1266

			Urban distance score	-0.6124	0.6685	28.6752	-0.916	0.3673
			Road	0.4745	0.5522	29.2765	0.859	0.3971
			Footpath	-0.0446	0.0666	22.284	-0.670	0.5099
			Assay time * body condition	-0.0397	0.0206	41.5674	-1.930	0.0604 .
			Assay time * site (park)	0.022	0.0558	41.8568	0.395	0.6950
			Assay Time * site (woods)	-0.0958	0.0734	41.4552	-1.305	0.1992
			Assay time * sex (male)	0.0384	0.0412	41.4544	0.933	0.3561
			Assay time * urban distance score	0.0289	0.0831	41.365	0.348	0.7298
			Body condition * site (park)	0.1288	0.0696	30.5577	1.850	0.0740
			Body condition * site (woods)	0.1534	0.1214	25.6948	1.264	0.2177
	Final model							
	ID	0.0162081	Body Condition	-0.1743	0.0346	40.0444	-5.028	**<0.0001**
	Assay Time	0.0006005	Site (park)	-0.3466	0.0621	32.5274	-5.576	**< 0.0001**
	Residual	0.0084934	Site (woods)	-0.1278	0.0659	32.7996	-1.937	0.06135
			Sex (male)	-0.0856	0.0503	31.9484	-1.702	0.09852
			Body condition * Site (park)	0.1493	0.0497	36.4385	3.005	**0.0047**
			Body condition * site (woods)	0.1597	0.0786	34.5188	2.032	**0.0498**
Handling response	***Full model***							
	ID	0.1736615	Assay Time	-0.24960	0.1299	42.9488	-1.921	0.0614
	Assay Time	0.0002587	Body condition	0.0134	0.0785	49.7797	0.172	0.8644
	Residual	0.0504086	Site (park)	-0.3028	0.2205	42.9258	-1.373	0.1768

			Site (woods)	0.4388	0.2845	42.0488	1.542	0.1306
			Sex (male)	0.15582	0.1644	41.7040	0.948	0.3487
			Urban distance score	0.02181	0.3208	42.0264	-0.068	0.9461
			Road	-0.1505	0.3214	42.0731	-0.468	0.6420
			Assay time * body condition	0.02872	0.0528	42.5806	0.544	0.5894
			Assay time * site (park)	0.13198	0.1428	42.7341	0.924	0.3607
			Assay Time * site (woods)	0.33090	0.1882	42.5608	1.758	0.0860
			Assay time * sex (male)	0.09872	0.1055	42.6158	0.935	0.3549
			Assay Time * urban distance score	-0.23155	0.2131	42.4078	-1.086	0.2835
	Final model							
	ID	0.17040	Site (park)	-0.2516	0.1740	36.1696	-1.446	0.15666
	Assay time	0.00000	Site (woods)	0.5187	0.2469	36.6900	2.101	0.04255
	Residual	0.04846	Distance from road	-0.1809	0.1083	36.2316	-1.671	0.10326

Table A.6: Comparison of random effects structures for null models including intercepts for individuals, separate intercepts for individuals and assay, and interaction between individual and assay. (Chapter 3)

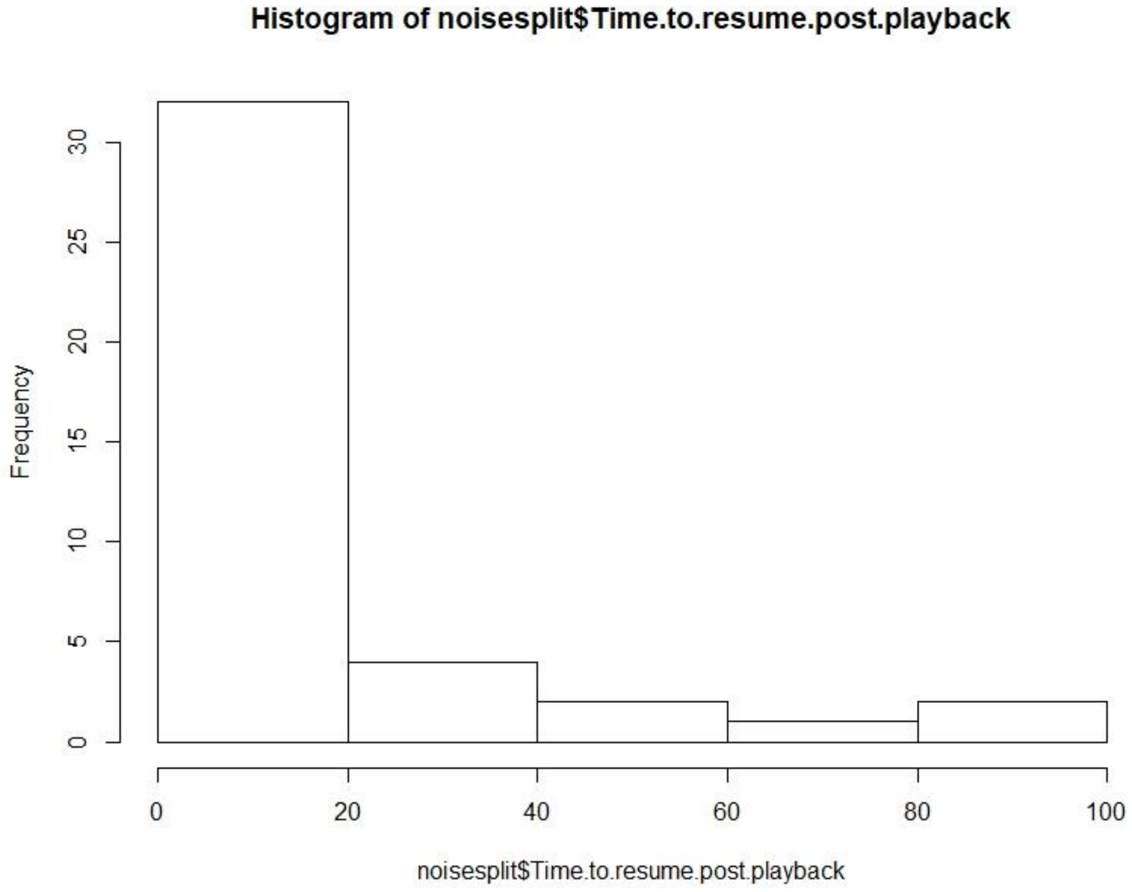
	Null model structure	*df*	*AIC*	*Log Likelihood*	χ^2	*P*
Arena behaviour	M1: Y ~ 1 + (1 | ID)	3	-66.886	36.443		
	M2: Y ~ 1 + (1 | Assay) + (1 | ID)	4	-67.207	37.604	62.018	< 0.001
	M3: Y ~ 1 + (0 + Assay | ID)	3	-7.189	6.595		
Handling response	M1: Y ~ 1 + (1 | ID)	3	82.532	-38.266		

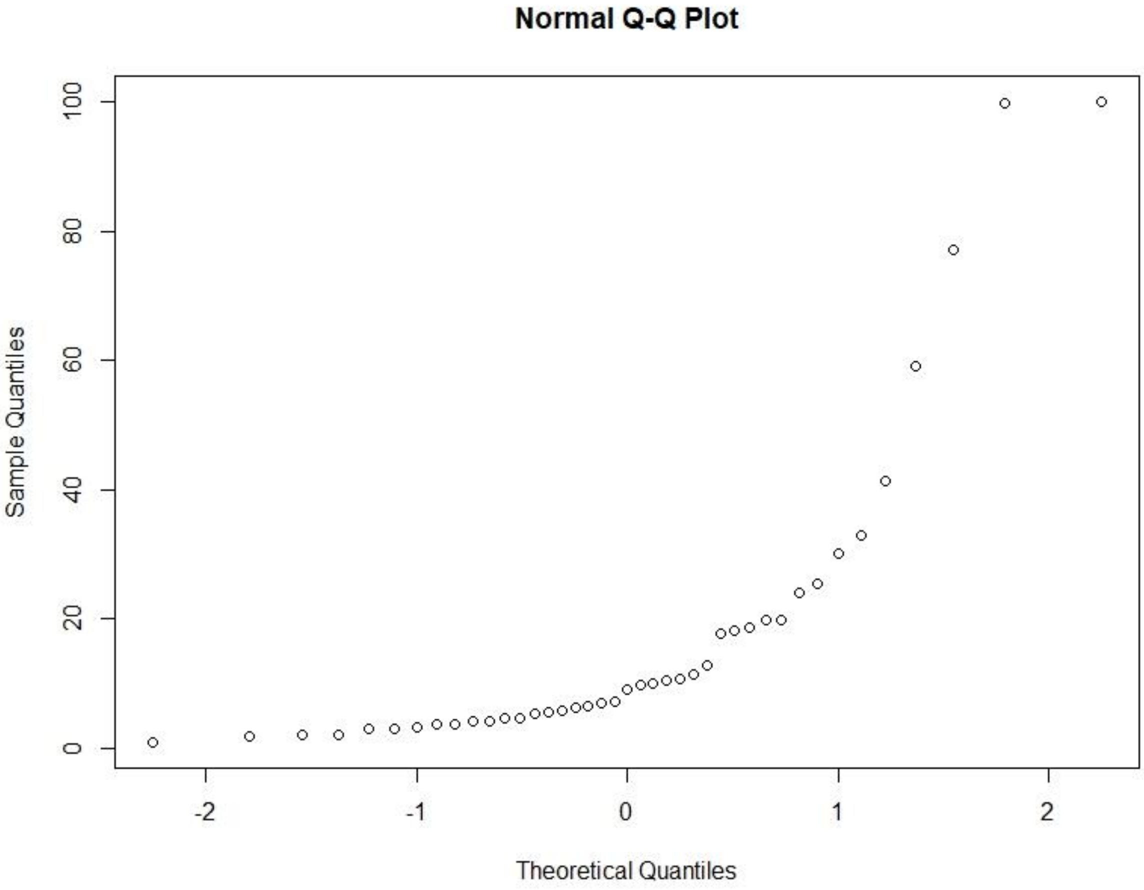
	M2: Y ~ 1 + (1 | Assay) + (1 | ID)	4	84.532	-38.266	52.545	< 0.001
	M3: Y ~ 1 + (0 + Assay | ID)	3	135.077	-64.538		

Appendix E:

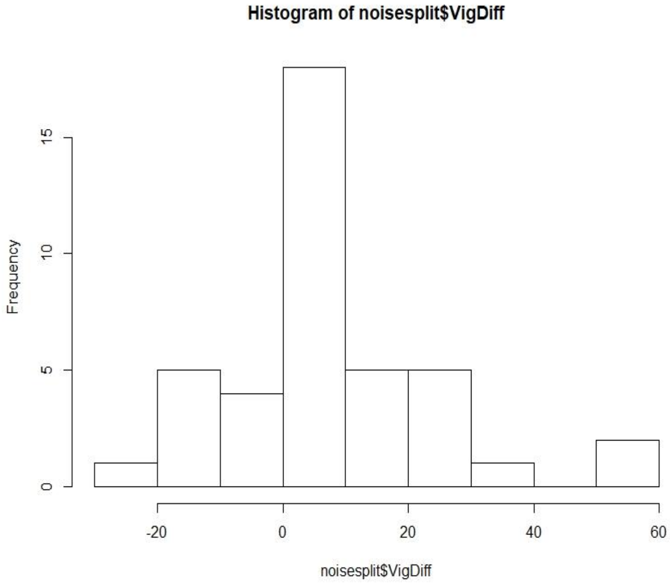
Frequency distribution histograms and q-q plots for outcome variables prior to transformation:

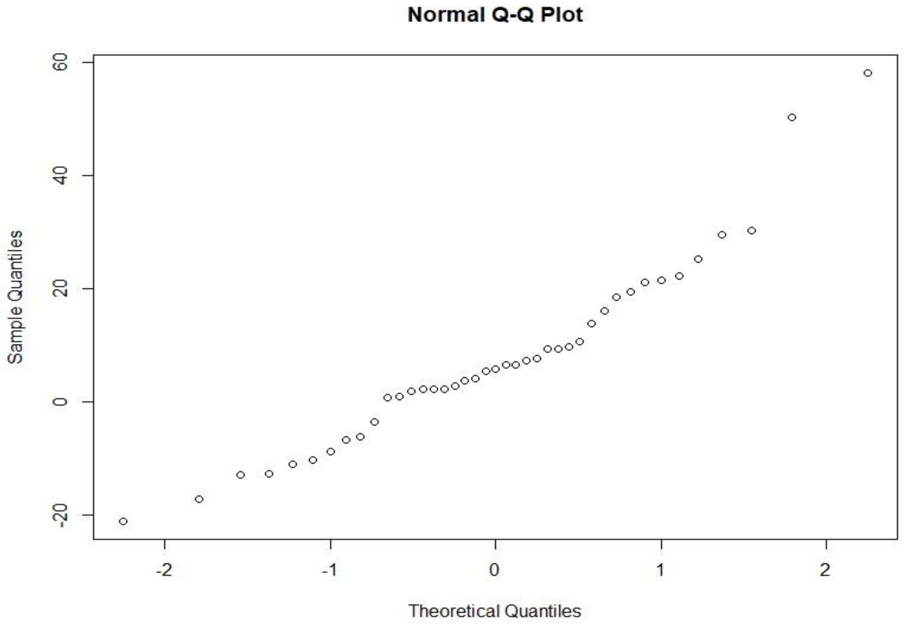
Outcome variable: latency to return to activity



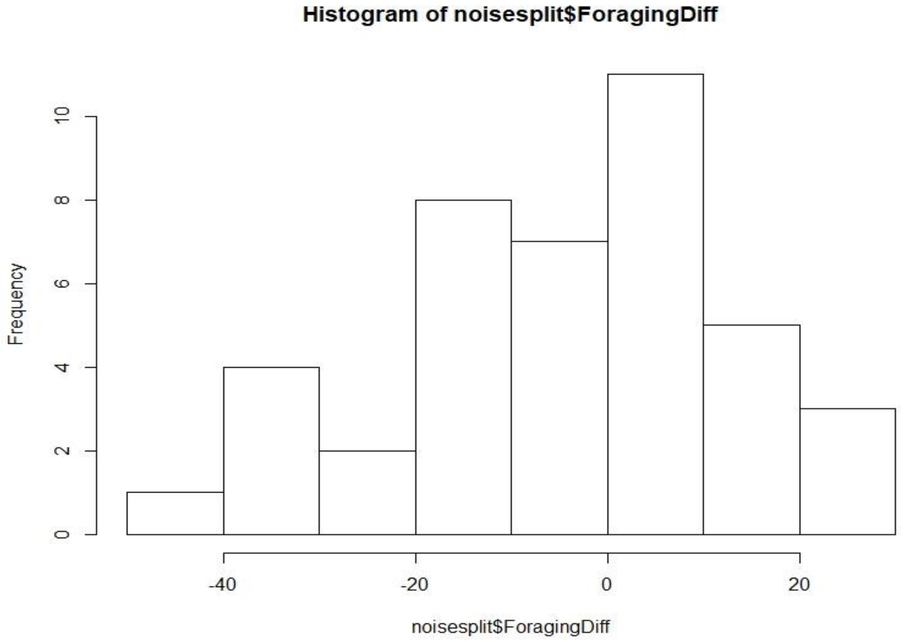


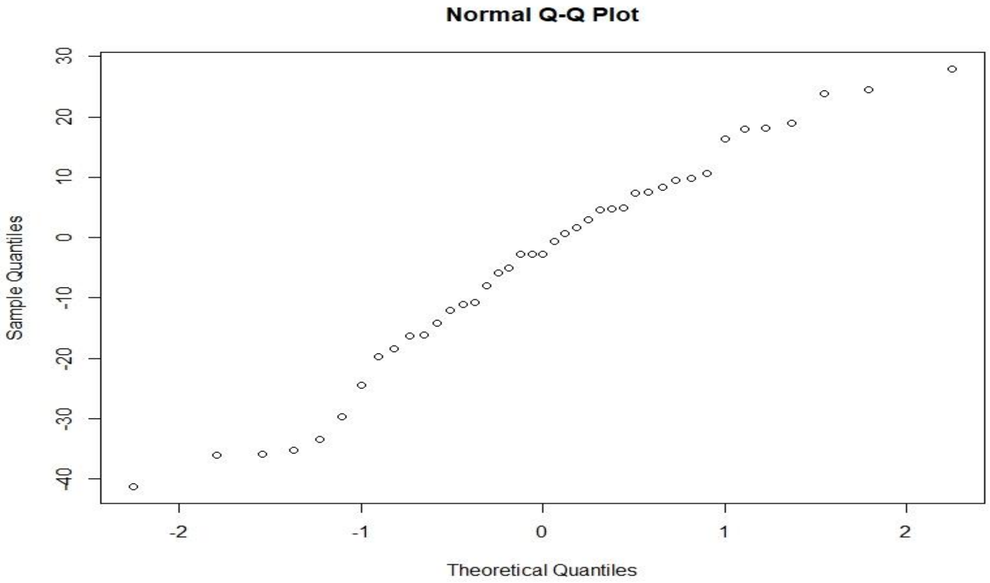
Outcome variable: Change in proportion of vigilance



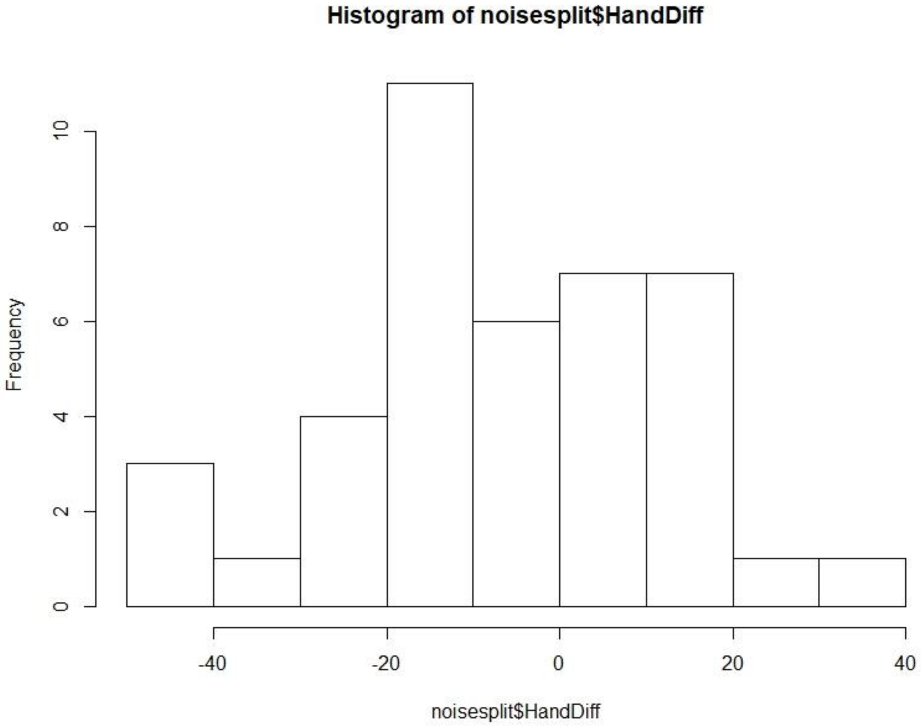


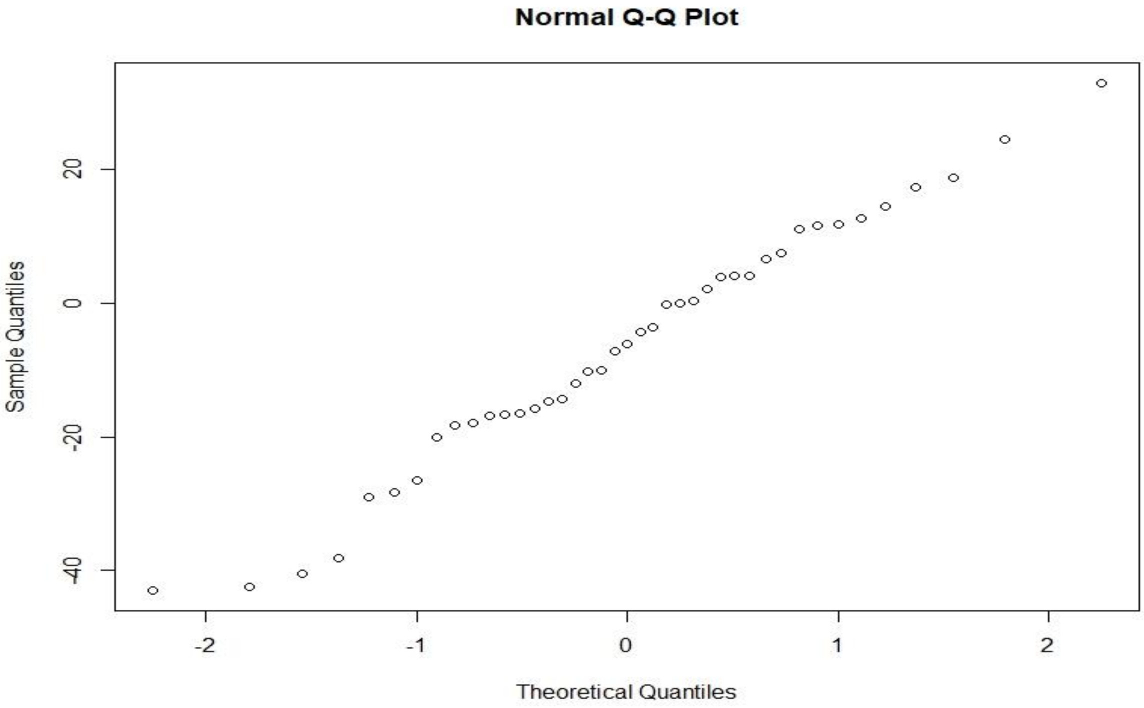
Outcome variable: Change in proportion of foraging



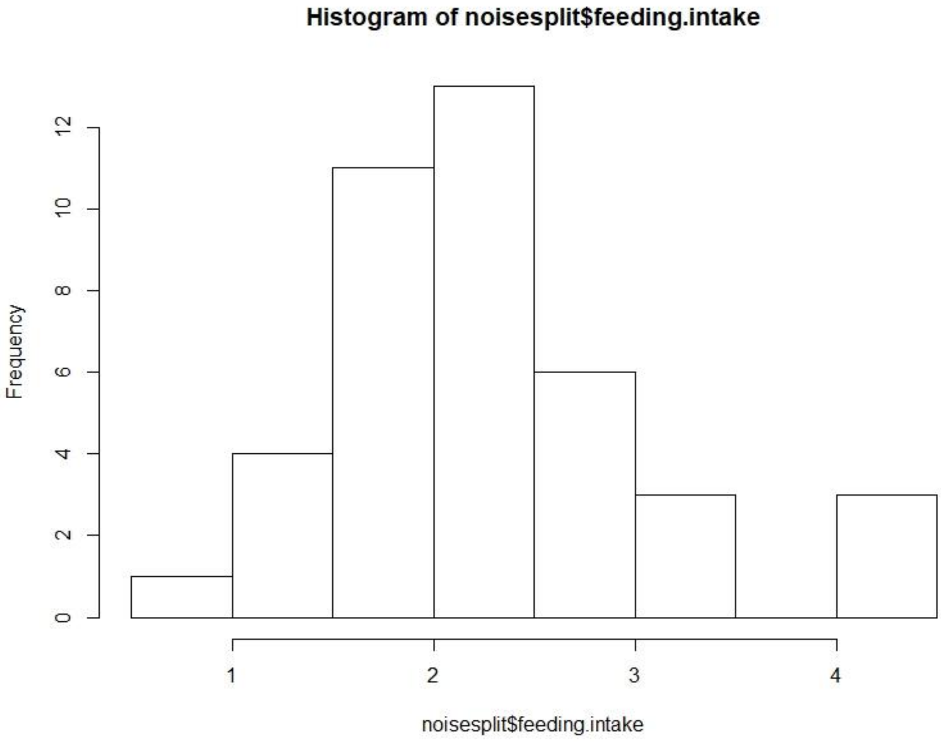


Outcome variable: Change in proportion of food handling





Outcome variable: food intake



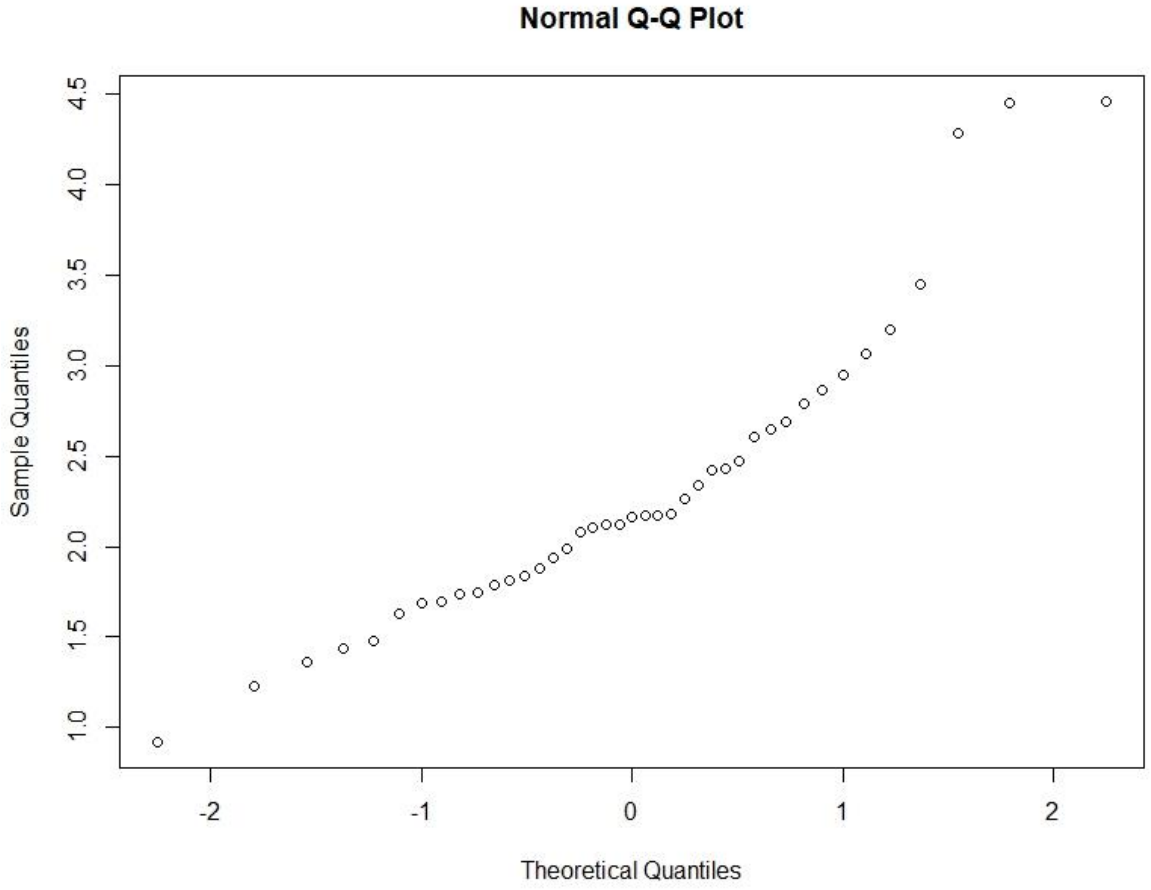


Table A.7 Correlation between habitat features prior to transformation (Chapter 5)

```
             Vegetation    Footpath        Build                  Road      dBMean       dBVar
Vegetation  1.000000000  0.14163763 -0.01777089  0.007583299  0.49098933  0.22820049
Footpath    0.141637630  1.00000000  0.18617261  0.348933000 -0.09734868 -0.02105548
Build      -0.017770892  0.18617261  1.00000000  0.902041023 -0.09904664 -0.21790871
Road        0.007583299  0.34893300  0.90204102  1.000000000 -0.11166454 -0.28628740
dBMean      0.490989334 -0.09734868 -0.09904664 -0.111664539  1.00000000  0.61598471
dBVar       0.228200490 -0.02105548 -0.21790871 -0.286287402  0.61598471  1.00000000
```

Chapter 5 figures

Figure A.1: Relationships between urban features and change in proportion of vigilance behaviours

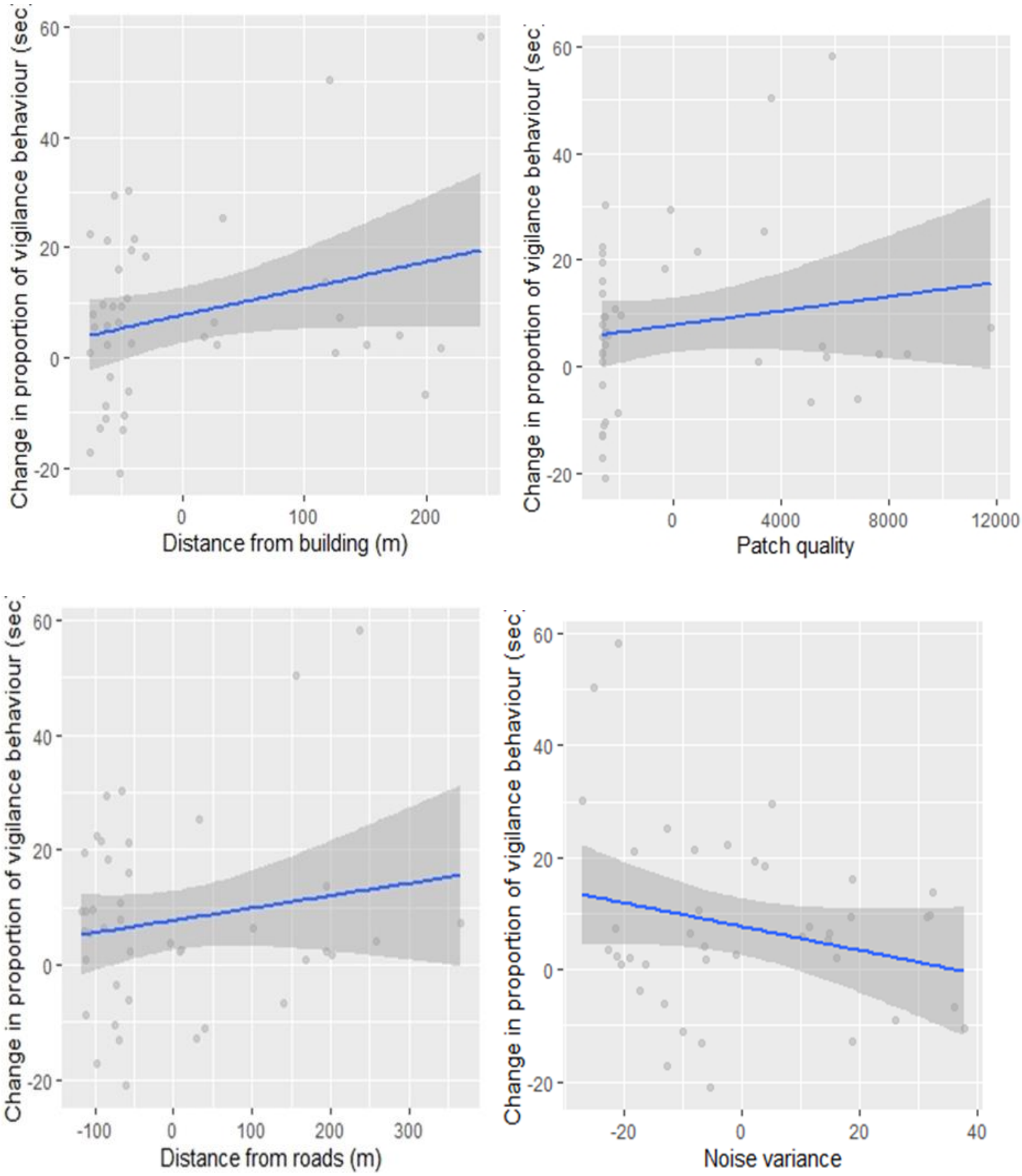
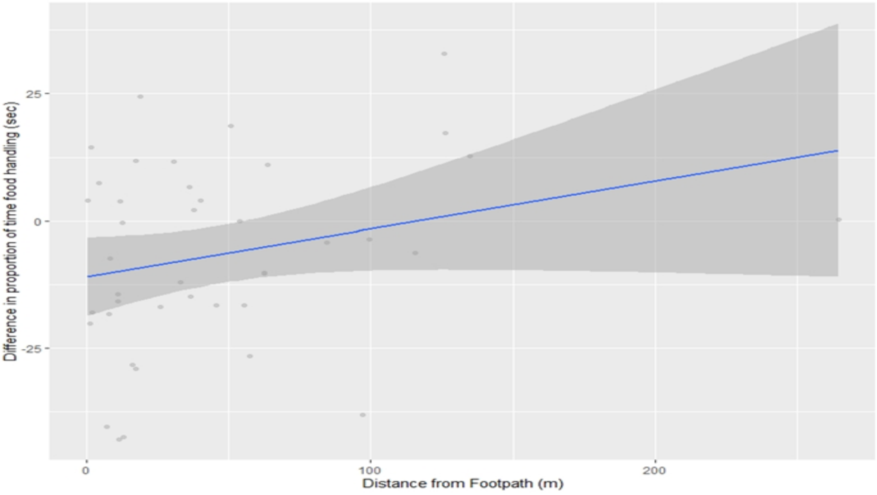


Figure: A.2: Relationship between distance from footpaths and change in proportion of food handling behaviours



References:

Abu Baker, M. A., & Brown, J. S. (2010). Islands of fear: Effects of wooded patches on habitat suitability of the striped mouse in a South African grassland. *Functional Ecology*, *24*(6), 1313–1322. https://doi.org/10.1111/j.1365-2435.2010.01757.x

Abu Baker, M. A., Emerson, S. E., & Brown, J. S. (2015). Foraging and habitat use of eastern cottontails (*Sylvilagus floridanus*) in an urban landscape. *Urban Ecosystems*. https://doi.org/10.1007/s11252-015-0463-7

Adriaenssens, B., & Johnsson, J. I. (2013). Natural selection, plasticity and the emergence of a behavioural syndrome in the wild. *Ecology Letters*, *16*(1), 47–55. https://doi.org/10.1111/ele.12011

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology & Evolution*, *30*(2), 114–126. https://doi.org/10.1016/j.tree.2014.11.007

Allen, D. S., & Aspey, W. P. (1986). Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): a quantitative assessment. *Animal Behaviour*, *34*, 81–89. https://doi.org/10.1016/0003-3472(86)90009-6

Allendorf, F. W., & Hard, J. J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. *In the Light of Evolution*, *3*, 129–147. https://doi.org/10.17226/12692

Amy, M., Sprau, P., de Goede, P., & Naguib, M. (2010). Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits. *Proceedings. Biological Sciences / The Royal Society*, *277*(1700), 3685–3692. https://doi.org/10.1098/rspb.2010.0598

Anderies, J. M., Katti, M., & Shochat, E. (2007). Living in the city: resource availability, predation, and bird population dynamics in urban areas. *Journal of Theoretical Biology*, *247*(1), 36–49. https://doi.org/10.1016/j.jtbi.2007.01.030

Anthony, L. L., & Blumstein, D. T. (2000). Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N(e). *Biological Conservation*, *95*(3), 303–315. https://doi.org/10.1016/S0006-3207(00)00037-9

Arvidsson, L. K., & Matthysen, E. (2016). Individual differences in foraging decisions: information-gathering strategies or flexibility? *Behavioral Ecology*, *00*, arw054. https://doi.org/10.1093/beheco/arw054

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., & Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology : Official Journal of the International Society for Behavioral Ecology*, *23*(5), 960–969. https://doi.org/10.1093/beheco/ars059

Audet, J.-N., Ducatez, S., & Lefebvre, L. (2015). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, *00*, arv201. https://doi.org/10.1093/beheco/arv201

Baker, P. J., Ansell, R. J., Dodds, P. A. A., Webber, C. E., & Harris, S. (2003). Factors affecting the distribution of small mammals in an urban area. *Mammal Review*, *33*(1), 95–100. https://doi.org/10.1046/j.1365-2907.2003.00003.x

Baker, P. J., Bentley, A. J., Ansell, R. J., & Harris, S. (2005). Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, *35*(3–4), 302–312. https://doi.org/10.1111/j.1365-2907.2005.00071.x

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010a). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, *25*(3), 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Bateman, P. W., & Fleming, P. a. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Journal of Zoology*, n/a-n/a. https://doi.org/10.1111/jzo.12156

Bateman, P. W., & Fleming, P. A. (2012). Big city life: Carnivores in urban environments. *Journal of Zoology*, *287*(1), 1–23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Beale, C. M., & Monaghan, P. (2004a). Behavioural responses to human disturbance: a matter of choice? *Animal Behaviour*, *68*(5), 1065–1069. https://doi.org/10.1016/j.anbehav.2004.07.002

Beale, C. M., & Monaghan, P. (2004b). Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, *41*(2), 335–343. https://doi.org/10.1111/j.0021-8901.2004.00900.x

Bedoya-Perez, M. A., Carthey, A. J. R., Mella, V. S., McArthur, C., & Banks, P. B. (2013). A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology*, *67*(10), 1541–1553. https://doi.org/10.1007/s00265-013-1609-3

Beekman, M., & Jordan, L. A. (2017). Does the field of animal personality provide any new insights for behavioral ecology? *Behavioral Ecology*, *28*(3), 617–623. https://doi.org/10.1093/beheco/arx022

Bell, A. M, Hankison, S.J & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022.Bell

Bell, A. M. (2005). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, *18*(2), 464–473. https://doi.org/10.1111/j.1420-9101.2004.00817.x

Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, *10*(9), 828–834. https://doi.org/10.1111/j.1461-0248.2007.01081.x

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*(6), 620–623. https://doi.org/10.1098/rsbl.2007.0415

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation.

Trends in Ecology and Evolution, *25*(9), 504–511. https://doi.org/10.1016/j.tree.2010.06.012

Bergvall, U. A., Schäpers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging decisions in fallow deer, Dama dama. *Animal Behaviour*, *81*(1), 101–112. https://doi.org/10.1016/j.anbehav.2010.09.018

Biro, P. A., Post, J. R., & Parkinson, E. a. (2003). From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. *Ecology*, *84*(9), 2419–2431. https://doi.org/10.1890/02-0416

Bleicher, S. S. (2017). The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bókony, V., Kulcsár, A., Tóth, Z., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PloS One*, *7*(5), e36639. https://doi.org/10.1371/journal.pone.0036639

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., … Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*(4), 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bolnick, D. I., Svanbäck, R., Fordyce, J. a, Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, *161*(1), 1–28. https://doi.org/10.1086/343878

Bolnick, Svanbäck, Fordyce, Yang, Davis, Hulsey, & Forister. (2017). The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist*, *161*(1), 1. https://doi.org/10.2307/3078879

Bonier, F. (2012). Hormones in the city: endocrine ecology of urban birds. *Hormones and Behavior*, *61*(5), 763–772. https://doi.org/10.1016/j.yhbeh.2012.03.016

Bonier, F., Martin, P. R., Sheldon, K. S., Jensen, J. P., Foltz, S. L., & Wingfield, J. C. (2007). Sex-specific consequences of life in the city. *Behavioral Ecology*, *18*(1), 121–129. https://doi.org/10.1093/beheco/arl050

Bonier, F., Martin, P. R., & Wingfield, J. C. (2007a). Urban birds have broader environmental tolerance. *Biology Letters*, *3*(6), 670–673. https://doi.org/10.1098/rsbl.2007.0349

Bonnington, C., Gaston, K. J., & Evans, K. L. (2013). Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. *Urban Ecosystems*, *17*(2), 533–546. https://doi.org/10.1007/s11252-013-0331-2

Bonnington, C., Gaston, K. J., & Evans, K. L. (2014). Assessing the potential for Grey Squirrels *Sciurus carolinensis* to compete with birds at supplementary feeding stations. *Ibis*, *156*(1), 220–226. https://doi.org/10.1111/ibi.12107

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., … Morellet, N. (2014). Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, *00*, 1–10. https://doi.org/10.1093/beheco/aru169

Bonnot, Nadège, Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., & Hewison, A. J. M. (2013). Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife*

Research, *59*(2), 185–193. https://doi.org/10.1007/s10344-012-0665-8

Boon, A. K., Re, D., & Boutin, S. (2008). Personality , habitat use , and their consequences for survival in North American red squirrels Tamiasciurus hudsonicus, (April). https://doi.org/10.1111/j.2008.0030-1299.16567.x

Boon, A. K., Réale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, *10*(11), 1094–1104. https://doi.org/10.1111/j.1461-0248.2007.01106.x

Boutin, S., Wauters, L. a, McAdam, A. G., Humphries, M. M., Tosi, G., & Dhondt, A. a. (2006). Anticipatory reproduction and population growth in seed predators. *Science (New York, N.Y.)*, *314*(5807), 1928–1930. https://doi.org/10.1126/science.1135520

Bowers, M. A., Jefferson, J. L., & Kuebler, M. G. (1993). Variation in Giving-Up Densities of Foraging Chipmunks (*Tamias striatus*) and Squirrels (*Sciurus carolinensis*). *Oikos*, *66*(2), 229. https://doi.org/10.2307/3544809

Bowers, Michael A, & Breland, B. (1996b). Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. *Ecological Applications*, *6*, 1135–1142. Retrieved from http://www.jstor.org/stable/10.2307/2269597

Brown, J. S. D.(1988). Patch use as an indication of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*, 37-47 ST-Patch use as an indication of habitat.

Brown, J. S., Laundre, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Brown, J., Kotler, B., & Mitchell, W. (1997). Competition between birds and mammals: A comparison of giving-up densities between crested larks and gerbils. *Evolutionary Ecology*, *11*(6), 757–771. https://doi.org/10.1023/A:1018442503955

Brown, J. S., Laundré, J. W., & Mahesh, G. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. Journal of Mammalogy.

Brown, J.S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, (1), 49–71. Retrieved from http://www.uic.edu/labs/squirrel/brown/pdfs/070.pdf

Candler, S., & Bernal, X. E. (2014). Differences in neophobia between cane toads from introduced and native populations. *Behavioral Ecology*, *00*, 1–8. https://doi.org/10.1093/beheco/aru162

Canestrelli, D., Bisconti, R., & Carere, C. (2015). Bolder Takes All? The Behavioral Dimension of Biogeography. *Trends in Ecology and Evolution*, *31*(1), 35–43. https://doi.org/10.1016/j.tree.2015.11.004

Careau, V., Montiglio, P.-O., Garant, D., Pelletier, F., Speakman, J. R., Humphries, M. M., & Réale, D. (2015). Energy expenditure and personality in wild chipmunks. *Behavioral ecology and sociobiology*, *69*(4), 653-661. https://doi.org/10.1007/s00265-015-1876-2

Carere, C., & Van Oers, K. (2004). Shy and bold great tits (*Parus major*): Body temperature and breath rate in response to handling stress. *Physiology and Behavior*, *82*(5), 905–912. https://doi.org/10.1016/j.physbeh.2004.07.009

Carrete, M., & Tella, J. (2010). Individual consistency in flight initiation distances in burrowing owls : a new hypothesis on disturbance- induced habitat selection. *Biology Letters*, *6*(October 2009), 167–170.

Carrete, M., & Tella, J. L. (2013). High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Scientific Reports*, *3*, 3524. https://doi.org/10.1038/srep03524

Carrete, Martina, & Tella, J. L. (2017). Behavioral Correlations Associated with Fear of Humans Differ between Rural and Urban Burrowing Owls. *Frontiers in Ecology and Evolution*, *5*(May), 1–9. https://doi.org/10.3389/fevo.2017.00054

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, *88*(2), 465–475. https://doi.org/10.1111/brv.12007

Carthey, A. J. R., & Banks, P. B. (2015). Foraging in groups affects giving - up densities : solo foragers quit sooner. *Oecologia*, *178*, 707–713. https://doi.org/10.1007/s00442-015-3274-x

Chamberlain, D. E., Cannon, A. R., & Toms, M. P. (2004). Associations of garden birds with gradients in garden habitat and local habitat. *Ecography*, *27*(5), 589–600. https://doi.org/10.1111/j.0906-7590.2004.03984.x

Chan, A. A. Y.-H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, *6*(4), 458–461. https://doi.org/10.1098/rsbl.2009.1081

Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., & Grégoire, A. (2017). Urbanization Is Associated with Divergence in Pace-of-Life in Great Tits. *Frontiers in Ecology and Evolution*, *5*(May), 1–13. https://doi.org/10.3389/fevo.2017.00053

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*. https://doi.org/10.1016/0040-5809(76)90040-X

Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., & Boyce, M. S. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1746), 4407–4416. https://doi.org/10.1098/rspb.2012.1483

Ciuti, Simone, Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. a, & Boyce, M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS One*, *7*(11), e50611. https://doi.org/10.1371/journal.pone.0050611

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159–170. https://doi.org/10.1093/beheco/5.2.159

Clermont, J., Couchoux, C., Garant, D., & Réale, D. (2017). Assessing anti-predator decisions of foraging eastern chipmunks under varying perceived risks: The effects of physical and social environments on vigilance. *Behaviour*, *154*(2), 131–148. https://doi.org/10.1163/1568539X-00003414

Clinchy, M., Zanette, L. Y., Roberts, D., Suraci, J. P., Buesching, C. D., Newman, C., & Macdonald, D. W. (2016). Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology*, *27*, arw117. https://doi.org/10.1093/beheco/arw117

Cohen, J. E. (2003). Human population: the next half century. *Science (New York, N.Y.)*, *302*(5648), 1172–1175. https://doi.org/10.1126/science.1088665

Czúni, L., Lipovits, Á., & Seress, G. (2012). Estimation of Urbanization Using Visual Features of Satellite Images. *International Conference on Geographic Information Science*, 24–27.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, *15*(10), 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S. R. X., & Griffith, S. C. (2014). An empiricist guide to animal personality variation in ecology and evolution. *Frontiers in Ecology and Evolution*, *2*(February), 1–7. https://doi.org/10.3389/fevo.2014.00003

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

David, M., & Dall, S. R. X. (2016). Unravelling the philosophies underlying ‘Animal Personality’ studies: a brief re-appraisal of the field. *Ethology*, *122*, 1–9. https://doi.org/10.1111/eth.12445

Delarue, E. M. P., Kerr, S. E., & Rymer, T. L. (2015). Habitat complexity, environmental change and personality: A tropical perspective. *Behavioural Processes*, *120*, 101–110. https://doi.org/10.1016/j.beproc.2015.09.006

Dill, M. (1989). The influence of distance to refuge on flight initiation distance in the gray squirrel *(Sciurus carolinensis)*. *Canadian Journal of Zoology, 67*(1)*,* 233-235

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings. Biological Sciences / The Royal Society*, *271*(1541), 847–852. https://doi.org/10.1098/rspb.2004.2680

Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *Journal of Animal Ecology*, *81*(1), 116–126. https://doi.org/10.1111/j.1365-2656.2011.01877.x

Dingemanse, N. J., & Dochtermann, N. a. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *The Journal of Animal Ecology*, *82*(1), 39–54. https://doi.org/10.1111/1365-2656.12013

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, *76*(6), 1128–1138. https://doi.org/10.1111/j.1365-2656.2007.01284.x

Dingemanse, N., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*(9), 1159–1184. https://doi.org/10.1163/156853905774539445

Diquelou, M. C., Griffin, A. S., & Sol, D. (2015). The role of motor diversity in foraging innovations : a cross-species comparison in urban birds. *Behavioral Ecology*, *00*, 1–8. https://doi.org/10.1093/beheco/arv190

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, *9*(1), 5–12. https://doi.org/10.1007/s11252-006-3262-3

Doebel, J. H., & McGinnes, B. S. (1974). Home range and activity of a gray squirrel population. *Journal of Wildlife Management*, *38*(4), 860–867. https://doi.org/10.2307/3800057

Donovan, T. M., Jones, P. W., Annand, E. M., & Thompson, F. R. (1997). Variation in local-scale edge effects Mechanisms and landscape context. *Ecology*, *78*(7), 2064–2075.

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour*, *80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Doyle, G., & Yule, E. P. (1959). Grooming activities and freezing behaviour in relation to emotionality in albino rats. *Animal Behaviour*, *7*(1–2), 18–22. https://doi.org/10.1016/0003-3472(59)90025-9

Ducatez, S., Clavel, J., & Lefebvre, L. (2015). Ecological generalism and behavioural innovation in birds: technical intelligence or the simple incorporation of new foods? *Journal of Animal Ecology*, *84*(1), 79–89. https://doi.org/10.1111/1365-2656.12255

Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, *17*(6), 1011–1019. https://doi.org/10.1093/beheco/arl035

Dunn, M., Marzano, M., Forster, J., & Gill, R. M. A. (2018). Public attitudes towards “pest” management: Perceptions on squirrel management strategies in the UK. *Biological Conservation*, *222*(July 2017), 52–63. https://doi.org/10.1016/j.biocon.2018.03.020

Embar, K., Kotler, B. P., & Mukherjee, S. (2011). Risk management in optimal foragers: The effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos*, *120*(11), 1657–1666. https://doi.org/10.1111/j.1600-0706.2011.19278.x

Engelhardt, S. C., & Weladji, R. B. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (Sciurus carolinensis), *830*(May), 823–830. https://doi.org/10.1139/Z11-054

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural Syndromes in Urban and Rural Populations of Song Sparrows. *Ethology*, *116*, 588–595. https://doi.org/10.1111/j.1439-0310.2010.01771.x

Fernández-Juricic, E. (2002). Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia*, *131*(2), 269–278. https://doi.org/10.1007/s00442-002-0883-y

Fernández-Juricic, E., & Tellería, J. L. (2000). Effects of human disturbance on spatial and temporal feeding patterns of blackbird turdus merula in urban parks in madrid, spain. *Bird Study*, *47*(1), 13–21. https://doi.org/10.1080/00063650009461156

Ferrer, I. R., Thompson, M. J., & Morand-Ferron, J. (2019). Is exploration a metric for information gathering ? Attraction to novelty and plasticity in black - capped chickadees. *Ethology*, *00*(October), 1–10. https://doi.org/10.1111/eth.12982

Ferryman, M., Mayle, B. a., & Morgan, G. W. (2006). Visual method for evaluating the state of sexual development in male grey squirrels (*Sciurus carolinensis*). *Reproduction, Fertility and Development*, *18*(3), 383–393. https://doi.org/10.1071/RD05129

Fischer, J. D., Cleeton, S. H., & Timothy, P. (2012). Urbanization and the Predation Paradox: The Role of Trophic Dynamics in Structuring Vertebrate Communities. *BioScience*, *62*(9), 809–818. https://doi.org/10.1525/bio.2012.62.9.6

Flamand, A., Rebout, N., Bordes, C., Guinnefollau, L., Bergès, M., Ajak, F., … Petit, O. (2019). Hamsters in the city: A study on the behaviour of a population of common hamsters (Cricetus cricetus) in urban environment. *PLoS ONE*, *14*(11), 1–15. https://doi.org/10.1371/journal.pone.0225347

Fletcher, R. J., Orrock, J. L., & Robertson, B. A. (2012). How the type of anthropogenic change alters the consequences of ecological traps. *Proceedings. Biological Sciences / The Royal Society*, *279*(1738), 2546–2552. https://doi.org/10.1098/rspb.2012.0139

Flyger, V. F. (1959). A Comparison of Methods for Estimating Squirrel Populations. *The Journal of Wildlife Management*, *23*(2), 220–223.

Foltz, S. L., Ross, A. E., Laing, B. T., Rock, R. P., Battle, K. E., & Moore, I. T. (2015). Behavioral Get off my lawn : increased aggression in urban song sparrows is related to resource availability. *Behavioral Ecology*, *00*, 1–10. https://doi.org/10.1093/beheco/arv111

Fox, J. F. (1982). Adaptation of Gray Squirrel Behavior to Autumn Germination by White Oak Acorns. *Evolution*, *36*(4), 800–809.

Fox, J., & Weisber, S. (2019). An R Companion to Applied Regression. *Third Edition. Sage, Thousand Oaks CA*. Retrieved from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Francis, R. a., & Chadwick, M. a. (2012). What makes a species synurbic? *Applied Geography*, *32*(2), 514–521. https://doi.org/10.1016/j.apgeog.2011.06.013

French, S. S., González-Suárez, M., Young, J. K., Durham, S., & Gerber, L. R. (2011). Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PloS One*, *6*(3), e17686. https://doi.org/10.1371/journal.pone.0017686

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1).

Fuller, R. a, Warren, P. H., & Gaston, K. J. (2007). Daytime noise predicts nocturnal singing in urban robins. *Biology Letters*, *3*(4), 368–370. https://doi.org/10.1098/rsbl.2007.0134

Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy Landscapes and the Landscape of Fear. *Trends in Ecology & Evolution*, *32*(2), 88–96. https://doi.org/10.1016/j.tree.2016.10.010

Garroway, C. J., & Sheldon, B. C. (2013). Urban behavioural adaptation. *Molecular Ecology*, *22*(13), 3430–3432. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/23967452

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear : Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Getschow, C. M., Rivers, P., Sterman, S., Lumpkin, D. C., & Tarvin, K. a. (2013). Does Gray

Squirrel (*Sciurus carolinensis*) Response to Heterospecific Alarm Calls Depend on Familiarity or Acoustic Similarity? *Ethology*, *119*(11), 983–992. https://doi.org/10.1111/eth.12145

Gil, D., Klett-mingo, J. I., & Pav, I. (2016). Great tits , *Parus major* , increase vigilance time and reduce feeding effort during peaks of aircraft noise. *Animal Behaviour*, *115*, 29–34. https://doi.org/10.1016/j.anbehav.2016.02.021

Gill, S. A., Job, J. R., Myers, K., Naghshineh, K., & Vonhof, M. J. (2015). Toward a broader characterization of anthropogenic noise and its effects on wildlife. *Behavioral Ecology*, *26*(2), 328–333. https://doi.org/10.1093/beheco/aru219

Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, *25*(2), 90–98. https://doi.org/10.1016/j.tree.2009.07.016

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*. https://doi.org/10.1037/0033-2909.127.1.45

Greggor, A. L., Clayton, N. S., Fulford, A. J. C., & Thornton, A. (2016). Street smart: faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds. *Animal Behaviour*, *In press*, 123–133. https://doi.org/10.1016/j.anbehav.2016.03.029

Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance: Improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, *6*, 82–89. https://doi.org/10.1016/j.cobeha.2015.10.007

Griffin, A. S., Netto, K., & Peneaux, C. (2017). Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings. *Current Opinion in Behavioral Sciences*, *16*, 15–22. https://doi.org/10.1016/j.cobeha.2017.01.004

Gurnell, J. (1996). The Effects of Food Availability and Winter Weather on the Dynamics of a Grey Squirrel Population in Southern England. *Journal of Applied Ecology*, *33*(2), 325–338.

Haigh, A., Butler, F., O'Riordan, R., & Palme, R. (2017). Managed parks as a refuge for the threatened red squirrel (*Sciurus vulgaris*) in light of human disturbance. *Biological Conservation*, *211*, 29–36. https://doi.org/10.1016/j.biocon.2017.05.008

Haigh, A., O'Riordan, R., & Butler, F. (2017). Variations in aggression and activity levels amongst squirrels inhabiting low and high density areas. *Ecological Research*, *32*(6), 931–941. https://doi.org/10.1007/s11284-017-1506-8

Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L., & Mulder, R. a. (2015). Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young? *Frontiers in Ecology and Evolution*, *3*(March), 1–14. https://doi.org/10.3389/fevo.2015.00028

Halpin, R. N., & Johnson, J. C. (2014). A Continuum of Behavioral Plasticity in Urban and Desert Black Widows. *Ethology*, *120*(12), 1237–1247. https://doi.org/10.1111/eth.12297

Hanmer, H. J., Thomas, R. L., & Fellowes, M. D. E. (2017). Provision of supplementary food for wild birds may increase the risk of local nest predation. *Ibis*, *159*(1), 158–167. https://doi.org/10.1111/ibi.12432

Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs among urban and rural great tits (*Parus major*). *Scientific Reports*, *8*(1), 1–12.

https://doi.org/10.1038/s41598-018-23463-7

Hasegawa, M., Ligon, R. a., Giraudeau, M., Watanabe, M., & McGraw, K. J. (2014). Urban and colorful male house finches are less aggressive. *Behavioral Ecology*, *25*(3), 641–649. https://doi.org/10.1093/beheco/aru034

Hendry, A. P. (2016). Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics. *Journal of Heredity*, 25–41. https://doi.org/10.1093/jhered/esv060

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x

Herborn, K. a, Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Behavioral Personality predicts behavioral flexibility in a fluctuating , natural environment, *00*, 1–6. https://doi.org/10.1093/beheco/aru131

Hernández, M., Navarro-Castilla, Á., Piñeiro, A., & Barja, I. (2018). Wood mice aggressiveness and flight response to human handling: Effect of individual and environmental factors. *Ethology*, *124*(8), 559–569. https://doi.org/10.1111/eth.12760

Hilton, G. M., & Packham, J. R. (2003). Variation in the masting of common beech (*Fagus sylvatica L.*) in northern Europe over two centuries (1800-2001). *Forestry*, *76*(3), 319–328. https://doi.org/10.1093/forestry/76.3.319

Hinsley, S. A., Bellamy, P. E., Harrison. N. M., Speakman, J. R., Wilson, . A. K., & Ferns, P. N. (2008). Effects of structural and functional habitat gaps on breeding woodland birds : working harder for less. *Landscape Ecology*, *23*, 615–626. https://doi.org/10.1007/s10980-008-9225-8

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *52*(6), 458–464. https://doi.org/10.1007/s00265-002-0536-5

Honda, T., Iijima, H., Tsuboi, J., & Uchida, K. (2018). A review of urban wildlife management from the animal personality perspective: The case of urban deer. *Science of the Total Environment*, *644*, 576–582. https://doi.org/10.1016/j.scitotenv.2018.06.335

Hopewell, L. J., & Leaver, L. A. (2008). Evidence of social influences on cache-making by grey squirrels (*Sciurus carolinensis*). *Ethology*, *114*(11), 1061–1068. https://doi.org/10.1111/j.1439-0310.2008.01554.x

Houston, A. I., Prosser, E., & Sans, E. (2012). The cost of disturbance: a waste of time and energy? *Oikos*, *121*(4), 597–604. https://doi.org/10.1111/j.1600-0706.2011.19594.x

Hume, G., Brunton, E., & Burnett, S. (2019). Eastern Grey Kangaroo (*Macropus giganteus*) Vigilance Behaviour Varies between Human-Modified and Natural Environments. *Animals*, *9*, 494.

Jayne, K., Lea, S. E. G., & Leaver, L. A. (2015a). Behavioural responses of Eastern grey squirrels, *Sciurus carolinensis*, to cues of risk while foraging. *Behavioural Processes*, *116*, 53–61. https://doi.org/10.1016/j.beproc.2015.05.002

Johnson, C. A., Grant, J. W. A., & Giraldeau, L. A. (2004). The effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology*, *15*(3), 412–418. https://doi.org/10.1093/beheco/arh026

Johnson, M. T. J., & Munshi-South, J. (2017). Evolution of life in urban environments.

Science, *358*(6363). https://doi.org/10.1126/science.aam8327

Jones, K. A., & Godin, J. G. J. (2010). Are fast explorers slow reactors? Linking personal type and anti-predator behavior. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1681), 625–632. https://doi.org/10.1098/rspb.2009.1607

Kaiser, A., Merckx, T., & Dyck, H. Van. (2018). Urbanisation and sex affect the consistency of butterfly personality across metamorphosis. *Behavioral Ecology and Sociobiology*, *72*(12), 188 https://doi.org/10.1007/s00265-018-2616-1

Kays, R., & Parsons, A. W. (2014). Mammals in and around suburban yards, and the attraction of chicken coops. *Urban Ecosystems*, 1–15. https://doi.org/10.1007/s11252-014-0347-2

Kight, C. R., & Swaddle, J. P. (2011). How and why environmental noise impacts animals: An integrative, mechanistic review. *Ecology Letters*, *14*(10), 1052–1061. https://doi.org/10.1111/j.1461-0248.2011.01664.x

Kilpatrick, A. M. (2003). The impact of thermoregulatory costs on foraging behaviour: A test with American Crows (*Corvus brachyrhynchos*) and eastern grey squirrels (*Sciurus carolinensis)*. *Evolutionary Ecology Research*, *5*(5), 781–786.

Kimmig, S. E., Brandt, M., Schleimer, A., Beninde, J., Hofer, H., Börner, K., … Frantz, A. C. (2019). Beyond the landscape : resistance modelling infers physical and behavioural gene flow barriers to a mobile carnivore across a metropolitan area ., *2020*(00), 1–19. https://doi.org/10.1111/mec.15345

Klett-Mingo, J. I., Pavón, I., & Gil, D. (2016). Great tits, Parus major, increase vigilance time and reduce feeding effort during peaks of aircraft noise. *Animal Behaviour*, *115*, 29–34. https://doi.org/10.1016/j.anbehav.2016.02.021

Koolhaas, J. M. (2008). Coping style and immunity in animals: making sense of individual variation. *Brain, Behavior, and Immunity*, *22*(5), 662–667. https://doi.org/10.1016/j.bbi.2007.11.006

Koprowski, J. L. (1996). Natal Philopatry, Communal Nesting, and Kinship in Fox Squirrels and Gray squirrels. *Journal of Mammalogy*, *77*(4), 1006–1016.

Kovacs, E. K., Crowther, M. S., Webb, J. K., & Dickman, C. R. (2012). Population and behavioural responses of native prey to alien predation. *Oecologia*, *168*(4), 947–957. https://doi.org/10.1007/s00442-011-2168-9

Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. (2012). Habitat complexity : approaches and future directions. *Hydrobiologia*, *685*(1), 1–17. https://doi.org/10.1007/s10750-011-0974-z

Kralj-Fišer, S., Hebets, E. A., & Kuntner, M. (2017). Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. *Behavioral Ecology and Sociobiology*, *71*(8). https://doi.org/10.1007/s00265-017-2353-x

Kralj-Fišer, S., & Schneider, J. M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behaviour*, *84*(1), 197–204. https://doi.org/10.1016/j.anbehav.2012.04.032

Lamanna, J. A., & Martin, T. E. (2016). Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, *19*(4), 403–413. https://doi.org/10.1111/ele.12573

Lapiedra, O., Chejanovski, Z., & Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, *23*(2), 592–603. https://doi.org/10.1111/gcb.13395

Laskowski, K. L., & Pruitt, J. N. (2014). Evidence of social niche construction: Persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1783). https://doi.org/10.1098/rspb.2013.3166

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The Landscape of Fear : Ecological Implications of Being Afraid, *2*, 1–7.

Le, C., Thibault, M., Pisanu, B., Thibault, S., Chapuis, J.-L., & Baudry, E. (2015). Temporally fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, *26*, 1285–1291. https://doi.org/10.1093/beheco/arv074

Le, S., Josse, J., & Husson, F. (2008). FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, *25*(1), 253–258. https://doi.org/10.1016/j.envint.2008.06.007

Lea, A. J., & Blumstein, D. T. (2011). Age and sex influence marmot antipredator behavior during periods of heightened risk. *Behavioral Ecology and Sociobiology*, *65*(8), 1525–1533. https://doi.org/10.1007/s00265-011-1162-x

Leaver, L. A., Jayne, K., & Lea, S. E. G. (2016). Behavioral flexibility versus rules of thumb: how do grey squirrels deal with conflicting risks? *Behavioral Ecology*, *00*, arw146. https://doi.org/10.1093/beheco/arw146

Lehrer, E. W., Schooley, R. L., Nevis, J. M., Kilgour, R. J., Wolff, P. J., & Magle, S. B. (2016). Happily ever after? Fates of translocated nuisance woodchucks in the Chicago metropolitan area. *Urban Ecosystems*, *19*(3), 1389–1403. https://doi.org/10.1007/s11252-016-0560-2

Liker, a, Papp, Z., Bókony, V., & Lendvai, a Z. (2008). Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *The Journal of Animal Ecology*, *77*(4), 789–795. https://doi.org/10.1111/j.1365-2656.2008.01402.x

Lilly, M. V., Lucore, E. C., & Tarvin, K. A. (2019). Eavesdropping grey squirrels infer safety from bird chatter. *PLoS ONE*, *14*(9), 4–8. https://doi.org/10.1371/journal.pone.0221279

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance : the group-size effect. *Animal Behaviour*, *49*, 11–20.

Lima, S. L., Valone, T. J., & Caraco, T. (1985). Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Animal Behaviour*, *33*, 155–165.

Lin, T., Coppack, T., Lin, Q., Kulemeyer, C., Schmidt, A., Behm, H., & Luo, T. (2012). Does avian flight initiation distance indicate tolerance towards urban disturbance? *Ecological Indicators*, *15*(1), 30–35. https://doi.org/10.1016/j.ecolind.2011.09.018

Lintott, P. R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R. J., Olley, L., & Park, K. J. (2014). City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal Society Open Science*, *1*, 1–8. https://doi.org/10.1098/rsos.140200

Lishak, R. S. (1984). Alarm Vocalizations of Adult Gray Squirrels. *American Society of Mammalogists*, *65*(4), 681–684. Retrieved from https://www.jstor.org/stable/1380852

Lowry, H., Lill, A., & Wong, B. B. M. (2011). Tolerance of auditory disturbance by an avian urban adapter, the noisy miner. *Ethology*, *117*(6), 490–497. https://doi.org/10.1111/j.1439-0310.2011.01902.x

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews of the Cambridge Philosophical Society*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Luo, J., Siemers, B. M., & Koselj, K. (2015). How anthropogenic noise affects foraging. *Global Change Biology*, *21*(9), 3278–3289. https://doi.org/10.1111/gcb.12997

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 3977–3990. https://doi.org/10.1098/rstb.2010.0207

Lyons, J., Mastromonaco, G., Edwards, D. B., & Schulte-Hostedde, A. I. (2017). Fat and happy in the city: Eastern chipmunks in urban environments. *Behavioral Ecology*, *00*(September), 1–8. https://doi.org/10.1093/beheco/arx109

Magle, S., Zhu, J., & Crooks, K. R. (2005). Behavioral Responses To Repeated Human Intrusion By Black-Tailed Prairie Dogs (*Cynomys Ludovicianus*). *Journal of Mammalogy*, *86*(3), 524–530. https://doi.org/10.1644/1545-1542(2005)86[524:brtrhi]2.0.co;2

Magnhagen, C., Hellström, G., Borcherding, J., Heynen, M., & Genner, M. (2012). Boldness in two perch populations - long-term differences and the effect of predation pressure. *The Journal of Animal Ecology*, *81*(6), 1311–1318. https://doi.org/10.1111/j.1365-2656.2012.02007.x

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/10.1111/brv.12122

Makowska, I. J., & Kramer, D. L. (2007). Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. *Animal Behaviour*, *74*(1), 153–158. https://doi.org/10.1016/j.anbehav.2006.11.019

Mangel, M., & Stamps, J. (2001). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, *3*, 583–593.

Manley, P., Horne, B. Van, Roth, J. K., Zielinski, W. J., McKenzie, M. M., Weller, T. J., … Horne, V. (2006). Multiple Species Inventory and Monitoring Technical Guide Design Team Multiple Species Inventory and Monitoring Technical Guide. *United States Department of Agriculture Forest Servive*, (August).

Martin, J. G. a, & Réale, D. (2008). Animal temperament and human disturbance: Implications for the response of wildlife to tourism. *Behavioural Processes*, *77*(1), 66–72. https://doi.org/10.1016/j.beproc.2007.06.004

Martin, J. G A, & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. *Animal Behaviour*, *75*, 309–318. https://doi.org/10.1016/j.anbehav.2007.05.026

Martin, J G A. (2008). Animal temperament and human disturbance : Implications for the response of wildlife to tourism, *77*, 66–72. https://doi.org/10.1016/j.beproc.2007.06.004

Martin, Julien G.A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, *75*(1), 309–318. https://doi.org/10.1016/j.anbehav.2007.05.026

Martin, L. B., & Fitzgerald, L. (2005). A taste for novelty in invading house sparrows, *Passer domesticus. Behavioral Ecology*, *16*(4), 702–707. https://doi.org/10.1093/beheco/ari044

Maynard-Smith, J. (1976). Evolution and the Theory of Games: In situations characterized by conflict of interest, the best strategy to adopt depends on what others are doing. *American Scientist*, *64*(1), 41–45. https://doi.org/10.2277/0521288843

Mccleery, R. a. (2009). Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landscape Ecology*, *24*(4), 483–493. https://doi.org/10.1007/s10980-009-9323-2

Mccleery, R. A., Lopez, R. R., Silvy, N. J., & Gallant, D. L. (2008). Fox Squirrel Survival in Urban and Rural Environments. *Journal of Wildlife Management*, *72*, 133–137. https://doi.org/10.2193/2007-138

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Mella, V. S. A., Ward, A. J. W., Banks, P. B., & McArthur, C. (2015). Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia*, *177*(1), 293–303. https://doi.org/10.1007/s00442-014-3110-8

Middleton, A. (1930). The Ecology of The American Grey Squirrel (*Sciurus carolinensis*) In The British Isles. *Proceedings of the Zoological Society of London*, (100), 809–843.

Minias, P. (2015). Successful Colonization of a Novel Urban Environment is Associated with an Urban Behavioural Syndrome in a Reed-Nesting Waterbird. *Ethology*, *121*, 1178–1190. https://doi.org/10.1111/eth.12433

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*, *19*(9), 2634–2644. https://doi.org/10.1111/gcb.12258

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Group, T. P. (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses : The PRISMA Statement. *PLoS Med*, *6*(7). https://doi.org/10.1371/journal.pmed.1000097

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Tans, E., Robison, T., … Moll, R. J. (2019). What does urbanization actually mean ? A framework for urban metrics in wildlife research, (August 2018), 1–12. https://doi.org/10.1111/1365-2664.13358

Moller, A. P., Grim, T., Ibanez-Alamo, J. D., Marko, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*(5), 1211–1217. https://doi.org/10.1093/beheco/art054

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology*, *21*(2), 365–371. https://doi.org/10.1093/beheco/arp199

Montiglio, P. O., Garant, D., Thomas, D., & Réale, D. (2010). Individual variation in temporal activity patterns in open-field tests. *Animal Behaviour*, *80*(5), 905–912. https://doi.org/10.1016/j.anbehav.2010.08.014

Montiglio, P., Sih, A., Mathot, K. J., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state – behaviour feedbacks : a review and guide for empiricists. *Trends in Ecology & Evolution*, *30*(1), 50–60. https://doi.org/10.1016/j.tree.2014.11.004

Morand-Ferron, J., Hermer, E., Jones, T. B., & Thompson, M. J. (2019). Environmental variability, the value of information, and learning in winter residents. *Animal Behaviour*, *147*, 137–145. https://doi.org/10.1016/j.anbehav.2018.09.008

Morosinotto, C., Thomson, R. L., & Korpimäki, E. (2010). Habitat selection as an antipredator behaviour in a multi-predator landscape: All enemies are not equal. *Journal of Animal Ecology*, *79*(2), 327–333. https://doi.org/10.1111/j.1365-2656.2009.01638.x

Morris-Drake, A., Bracken, A. M., Kern, J. M., & Radford, A. N. (2017). Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. *Environmental Pollution*, *223*, 476–483. https://doi.org/10.1016/j.envpol.2017.01.049

Moule, H., Michelangeli, M., Thompson, M. B., & Chapple, D. G. (2015). The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity-exploratory behavioural syndrome. *Journal of Zoology*, n/a-n/a. https://doi.org/10.1111/jzo.12288

Murray, M. H., & St. Clair, C. C. (2015). Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. *Behavioral Ecology*, *00*, arv102. https://doi.org/10.1093/beheco/arv102

McNamara, J. M. (1990). The policy which maximises long-term survival of an animal faced with the risks of starvation and predation. *Advances in Applied Probability*, 295-308

Newman, J. A., & Caraco, T. (1987). Foraging, predation hazard and patch use in grey squirrels. *Animal Behaviour*, *35*(6), 1804–1813. https://doi.org/10.1016/S0003-3472(87)80073-8

Newman, J. A., Recer, G. M., Zwicker, S. M., & Caraco, T. (1988). Effects of Predation Hazard on Foraging " Constraints ": Patch-Use Strategies in Grey Squirrels. *Oikos*, *53*(1), 93–97.

Newsome, S. D., Garbe, H. M., Wilson, E. C., & Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia*, *178*(1), 115–128. https://doi.org/10.1007/s00442-014-3205-2

Newson, S. E., Leech, D. I., Hewson, C. M., Crick, H. Q. P., & Grice, P. V. (2010). Potential impact of grey squirrels *Sciurus carolinensis* on woodland bird populations in England. *Journal of Ornithology*, *151*(1), 211–218. https://doi.org/10.1007/s10336-009-0445-8

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, *19*(4), 478–486. https://doi.org/10.1111/ele.12584

Olsson, O., & Molokwu, M. N. (2008). On the Missed Opportunity Cost, Gud, and Estimating Environmental Quality. *Israel Journal of Ecology and Evolution*, *53*(3), 263–278. https://doi.org/10.1560/IJEE.53.3.263

Orrock, J. L. (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology*, *15*(3), 433–437. https://doi.org/10.1093/beheco/arh031

Ovadia, O., & Zu Dohna, H. (2003). The effect of intra- and interspecific aggression on patch residence time in Negev Desert gerbils: A competing risk analysis. *Behavioral Ecology*, *14*(4), 583–591. https://doi.org/10.1093/beheco/arg031

Pack, J. C., Mosby, H. S., & Paul B. Siegel. (1967). Influence of Social Hierarchy on Gray

Squirrel Behavior. *The Journal of Wildlife Management*, *31*(4), 720–728.

Parker, T. S., Gonzales, S. K., & Nilon, C. H. (2014). Seasonal comparisons of daily activity budgets of gray squirrels (Sciurus carolinensis) in urban areas. *Urban Ecosystems*, (May 2014), 969–978. https://doi.org/10.1007/s11252-014-0371-2

Parker, T. S., & Nilon, C. H. (2008). Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems*, *11*(3), 243–255. https://doi.org/10.1007/s11252-008-0060-0

Partan, S. R., Fulmer, A. G., Gounard, M. A. M., & Redmond, J. E. (2010). Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. *Current Zoology*, *56*(3), 313–326.

Partan, S. R., Larco, C. P., & Owens, M. J. (2009). Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behaviour. *Animal Behaviour*, *77*(5), 1127–1135. https://doi.org/10.1016/j.anbehav.2008.12.029

Partecke, J., Schwabl, I., & Gwinner, E. (2006). Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology*, *87*(8), 1945–1952. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16937632

Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour*, *123*, 69–79. https://doi.org/10.1016/j.anbehav.2016.10.006

Petrelli, A. R., Levenhagen, M. J., Wardle, R., Barber, J. R., & Francis, C. D. (2017). First to Flush: The Effects of Ambient Noise on Songbird Flight Initiation Distances and Implications for Human Experiences with Nature. *Frontiers in Ecology and Evolution*, *5*(June). https://doi.org/10.3389/fevo.2017.00067

Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Boone, C. G., Groffman, P. M., Irwin, E., … Warren, P. (2011). Urban ecological systems: Scientific foundations and a decade of progress. *Journal of Environmental Management*, *92*(3), 331–362. https://doi.org/10.1016/j.jenvman.2010.08.022

Poudel, B. S., Spooner, P. G., & Matthews, A. (2016). Pastoralist disturbance effects on Himalayan marmot foraging and vigilance activity. *Ecological Research*, *31*(1), 93–104. https://doi.org/10.1007/s11284-015-1315-x

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2003). Demographic Factors Contributing to High Raccoon Densities in Urban Landscapes Author (s): Suzanne Prange , Stanley D . Gehrt and Ernie P . Wiggers Published by : Wiley on behalf of the Wildlife Society Stable URL : http://www.jstor.org/stable/3802774 A. *Wildlife Management*, *67*(2), 324–333.

Prasher, S., Thompson, M. J., Evans, J. C., El-nachef, M., & Bonier, F. (2019). Innovative consumers : ecological , behavioral , and physiological predictors of responses to novel food. *Behavioral Ecology*, 1–10. https://doi.org/10.1093/beheco/arz067

Quinn, J. L., Cole, E. F., Bates, J., Payne, R. W., & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation, (December 2011), 1919–1926. https://doi.org/10.1098/rspb.2011.2227

Rabin, L. A., Coss, R. G., & Owings, D. H. (2006). The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beechey*i). *Biological Conservation*, *131*(3), 410–420. https://doi.org/10.1016/j.biocon.2006.02.016

Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., … Thompson, R. F. (2009). Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, *92*(2), 135–138. https://doi.org/10.1016/j.nlm.2008.09.012

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Robertson, B. a, Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, *28*(9), 552–560. https://doi.org/10.1016/j.tree.2013.04.004

Rockwell, C., Gabriel, P. O., & Black, J. M. (2012). Bolder, older, and selective: Factors of individual-specific foraging behaviors in Steller’s jays. *Behavioral Ecology*, *23*(3), 676–683. https://doi.org/10.1093/beheco/ars015

Rodewald, A. D., & Shustack, D. P. (2008). Consumer resource matching in urbanizing landscapes: are synanthropic species over-matching? *Ecology*, *89*(2), 515–521. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/18409440

Rodríguez-Prieto, I., Martín, J., & Fernández-Juricic, E. (2010). Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology*, *64*(12), 1937–1945. https://doi.org/10.1007/s00265-010-1004-2

Rösner, S., Mussard-Forster, E., Lorenc, T., & Müller, J. (2014). Recreation shapes a “landscape of fear” for a threatened forest bird species in Central Europe. *Landscape Ecology*, *29*(1), 55–66. https://doi.org/10.1007/s10980-013-9964-z

Rushton, S.P, Lurz, P. W. W., Fuller, R., & Garson, P. . (1997). Modelling the Distribution of the Red and Grey Squirrel at the Landscape Scale : A Combined GIS and Population Dynamics Approach. *Journal of Animal Ecology*, *34*(5), 1137–1154.

Rushton, Steven P., Lurz, P. W. W., Gurnell, J., Nettleton, P., Bruemmer, C., Shirley, M. D. F., & Sainsbury, A. W. (2006). Disease threats posed by alien species: The role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology and Infection*, *134*(3), 521–533. https://doi.org/10.1017/S0950268805005303

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2016). Increased tolerance to humans among disturbed wildlife. *Nature*, *6*(1), 1–8. https://doi.org/10.1007/s13398-014-0173-7.2

Sandro, B. (2008). Introduction of the American grey squirrel (*Sciurus carolinensis*) in Europe: A case study in biological invasion. *Current Science*, *95*(7), 903–906.

Santicchia, F., Romeo, C., Ferrari, N., Matthysen, E., Vanlauwe, L., Wauters, L. A., & Martinoli, A. (2019). The price of being bold? Relationship between personality and endoparasitic infection in a tree squirrel. *Mammalian Biology*, *97*, 1–8. https://doi.org/10.1016/j.mambio.2019.04.007

Santos, C. D., Cramer, J. F., Pârâu, L. G., Miranda, A. C., Wikelski, M., & Dechmann, D. K.

N. (2015). Personality and morphological traits affect pigeon survival from raptor attacks. *Scientific Reports*, *5*, 15490. https://doi.org/10.1038/srep15490

Sarno, R. J., Parsons, M., & Ferris, A. (2014). Differing vigilance among gray squirrels (*Sciuridae carolinensis*) along an urban–rural gradient on Long Island. *Urban Ecosystems*, 517–523. https://doi.org/10.1007/s11252-014-0414-8

Scales, J., Hyman, J., & Hughes, M. (2011). Behavioral Syndromes Break Down in Urban Song Sparrow Populations. *Ethology*, *117*(10), 887–895. https://doi.org/10.1111/j.1439-0310.2011.01943.x

Scales, J., Hyman, J., & Hughes, M. (2013). Fortune favours the aggressive: territory quality and behavioural syndromes in song sparrows, *Melospiza melodia*. *Animal Behaviour*, *85*(2), 441–451. https://doi.org/10.1016/j.anbehav.2012.12.004

Schuett, W, Dall, S. R. X., Kloesener, M. H., Baeumer, J., Beinlich, F., & Eggers, T. (2014). Life-history trade-offs mediate “personality” variation in two colour morphs of the pea aphid, *Acyrthosiphon pisum*. *The Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.12263

Schuett, Wiebke, Delfs, B., Haller, R., Kruber, S., Roolfs, S., Timm, D., … Drees, C. (2018). Ground beetles in city forests: does urbanization predict a personality trait? *PeerJ*, *6*, e4360. https://doi.org/10.7717/peerj.4360

Schuett, Wiebke, Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews of the Cambridge Philosophical Society*, *85*(2), 217–246. https://doi.org/10.1111/j.1469-185X.2009.00101.x

Searle, K. R., Stokes, C. J., & Gordon, I. J. (2008). When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology*, *19*(3), 475–482. https://doi.org/10.1093/beheco/arn004

Selonen, V., Fey, K., & Hämäläinen, S. (2018). Increased differentiation between individuals, but no genetic isolation from adjacent rural individuals in an urban red squirrel population. *Urban Ecosystems*, *21*(6), 1067–1074. https://doi.org/10.1007/s11252-018-0794-2

Senar, J. C., Conroy, M. J., Quesada, J., & Mateos-Gonzalez, F. (2014). Selection based on the size of the black tie of the great tit may be reversed in urban habitats. *Ecology and Evolution*, n/a-n/a. https://doi.org/10.1002/ece3.999

Sepp, T., McGraw, K. J., Kaasik, A., & Giraudeau, M. (2018). A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? *Global Change Biology*, *24*(4), 1452–1469. https://doi.org/10.1111/gcb.13969

Seress, G., Lipovits, Á., Bókony, V., & Czúni, L. (2014). Quantifying the urban gradient: A practical method for broad measurements. *Landscape and Urban Planning*, *131*, 42–50. https://doi.org/10.1016/j.landurbplan.2014.07.010

Shochat, E. (2004). Credit or debit ? Resource input changes population dynamics of city-slicker birds. *Oikos*, *106*(3), 622–626. https://doi.org/10.1111/j.0030-1299.2004.13159.x

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. *BioScience*, *60*(3), 199–208. https://doi.org/10.1525/bio.2010.60.3.6

Short, K. H., & Petren, K. (2008). Boldness underlies foraging success of invasive Lepidodactylus lugubris geckos in the human landscape. *Animal Behaviour*, *76*(2), 429–437. https://doi.org/10.1016/j.anbehav.2008.04.008

Siemers, B. M., & Schaub, A. (2011). Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings. Biological Sciences / The Royal Society*, *278*(1712), 1646–1652. https://doi.org/10.1098/rspb.2010.2262

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, *15*(3), 278–289. https://doi.org/10.1111/j.1461-0248.2011.01731.x

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Smith, T. B., & Bernatchez, L. (2008). Evolutionary change in human-altered environments. *Molecular Ecology*, *17*(1), 1–8. https://doi.org/10.1111/j.1365-294X.2007.03607.x

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS One*, *6*(5), e19535. https://doi.org/10.1371/journal.pone.0019535

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*(5), 1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L. Z., & Møller, A. P. (2017). Risk-taking behavior, urbanization and the pace of life in birds. *Behavioral Ecology and Sociobiology*, in press. https://doi.org/10.1007/s00265-018-Daniel

Sol, D., Santos, D. M., Garcia, J., & Cuadrado, M. (1998). Competition for Food in Urban Pigeons: The Cost of Being Juvenile. *The Condor*, *100*(2), 298–304. https://doi.org/10.2307/1370270

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What’s your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, *20*(1), 3–18. https://doi.org/10.1111/ele.12708

Sprau, P., & Dingemanse, N. J. (2017). An approach to distinguish between plasticity and non-random distributions of behavioral types along urban gradients in a wild passerine bird. *Frontiers in Ecology and Evolution*, *5*(AUG), 1–8. https://doi.org/10.3389/fevo.2017.00092

Stamps, J. A. (2007). Growth-mortality tradeoffs and “personality traits” in animals. *Ecology Letters*, *10*(5), 355–363. https://doi.org/10.1111/j.1461-0248.2007.01034.x

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings. Biological Sciences / The Royal Society*, *272*(1581), 2627–2634. https://doi.org/10.1098/rspb.2005.3251

Stears, K., & Shrader, A. M. (2015). Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales. *Animal Behaviour*, *108*, 155–164. https://doi.org/10.1016/j.anbehav.2015.07.012

Steyaert, S. M. J. G., Kindberg, J., Jerina, K., Krofel, M., Stergar, M., Swenson, J. E., & Zedrosser, A. (2014). Behavioral correlates of supplementary feeding of wildlife: Can general conclusions be drawn? *Basic and Applied Ecology*, *15*(8), 669–676. https://doi.org/10.1016/j.baae.2014.10.002

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., … Kramer-Schadt, S. (2017). Secrets of Success in a Landscape of Fear: Urban Wild Boar Adjust Risk Perception and Tolerate Disturbance. *Frontiers in Ecology and Evolution*, *5*(December), 1–12. https://doi.org/10.3389/fevo.2017.00157

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of the human “super predator” has landscape-scale impacts from mountain lions to mice. *Ecology Letters, 22*(10), 1578-1586 https://doi.org/10.1111/ele.13344

Swan, G. J. F., Redpath, S. M., Bearhop, S., & McDonald, R. A. (2017). Ecology of Problem Individuals and the Efficacy of Selective Wildlife Management. *Trends in Ecology and Evolution*, *32*(7), 518–530. https://doi.org/10.1016/j.tree.2017.03.011

Tadesse, S. A., & Kotler, B. P. (2012). Impact of tourism on Nubian ibex (*Capra nubiana*) revealed through assessment of behavioral indicators. *Behavioral Ecology*, *23*(6), 1257–1262. https://doi.org/10.1093/beheco/ars110

Thompson, D. C. (1977). Reproductive behavior of the grey squirrel. *Canadian Journal of Zoology*, *55*(7), 1176–1184. https://doi.org/10.1139/z77-152

Thompson, D. C. (1978). The Social System of the Grey Squirrel. *Behaviour*, *64*, 305–328.

Thompson, D. C., & Thompson, P. S. (1980). Food habits and caching behavior of urban grey squirrels. *Canadian Journal of Zoology*, *58*(5), 701–710. https://doi.org/10.1139/z80-101

Thompson, K. A., Rieseberg, L. H., & Schluter, D. (2018). Speciation and the City. *Trends in Ecology & Evolution*, *33*(11), 815–826. https://doi.org/10.1016/j.tree.2018.08.007

Thompson, M. J., Evans, J. C., Parsons, S., & Morand-Ferron, J. (2018). Urbanization and individual differences in exploration and plasticity. *Behavioral Ecology*, *29*, 1415–1425. https://doi.org/10.1093/beheco/ary103

Tryjanowski, P., Møller, A. P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M., … Dulisz, B. (2016). Urbanization affects neophilia and risk-taking at bird-feeders. *Scientific Reports*, *6*, 28575. https://doi.org/10.1038/srep28575

Tsurim, I., Abramsky, Z., & Kotler, B. P. (2008). Foraging Behavior of Urban Birds: Are Human Commensals Less Sensitive To Predation Risk Than Their Nonurban Counterparts? *The Condor*, *110*(4), 772–776. https://doi.org/10.1525/cond.2008.8572

Tüzün, N., Müller, S., Koch, K., & Stoks, R. (2017). Pesticide-induced changes in personality depend on the urbanization level. *Animal Behaviour*, *134*, 45–55. https://doi.org/10.1016/j.anbehav.2017.10.007

Twining, J. P., Montgomery, W. I., Price, L., Kunc, H. P., & Tosh, D. G. (2020). Native and invasive squirrels show different behavioural responses to scent of a shared native predator.

Twining, J. P., Montgomery, W. I., & Tosh, D. G. (2020). Declining invasive grey squirrel populations may persist in refugia as native predator recovery reverses squirrel species replacement. *Journal of Applied Ecology*, (December 2019), 1–13. https://doi.org/10.1111/1365-2664.13660

Uchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2015). Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habiUchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2015). Seasonal variation of flight initiation distance in Eurasian red squirrels in u. *Journal of Zoology*, n/a-n/a. https://doi.org/10.1111/jzo.12306

Uchida, K, Suzuki, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2015). Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat, 225–231. https://doi.org/10.1111/jzo.12306

Uchida, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2020). Comparison of multiple behavioral traits between urban and rural squirrels. *Urban Ecosystems*, 1-10

Uchida, Kenta, Suzuki, K. K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2019). Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology*, 1–8. https://doi.org/10.1093/beheco/arz117

Valcarcel, A., & Fernández-Juricic, E. (2009). Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? *Behavioral Ecology and Sociobiology*, *63*(5), 673–685. https://doi.org/10.1007/s00265-008-0701-6

Van Der Merwe, M., Brown, J. ., & Jackson, W. M. (2005). The coexistence of Fox (*Sciurus niger*) and gray (*S. caroliniensis*) squirrels in the Chicago metroplitan area. *Urban Ecosystems*, *8*, 335–347.

Van Dongen, W. F. D., Robinson, R. W., Weston, M. A., Mulder, R. A., & Guay, P. J. (2015). Variation at the DRD4 locus is associated with wariness and local site selection in urban black swans. *BMC Evolutionary Biology*, *15*(1), 1–11. https://doi.org/10.1186/s12862-015-0533-8

van Oers, K., & Mueller, J. C. (2010). Evolutionary genomics of animal personality. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 3991–4000. https://doi.org/10.1098/rstb.2010.0178

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, *60*, 457–464. https://doi.org/10.1007/s00265-006-0172-6

Viblanc, V. A., Smith, A. D., Gineste, B., & Groscolas, R. (2012). Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC Ecology*, *12*(1), 10. https://doi.org/10.1186/1472-6785-12-10

Warren, P. S., Katti, M., Ermann, M., & Brazel, A. (2006). Urban bioacoustics: It’s not just noise. *Animal Behaviour*, *71*(3), 491–502. https://doi.org/10.1016/j.anbehav.2005.07.014

Wauters, L. A., & Lens, L. (1995). Effects of food availability and density on red squirrel (Sciurus vulgaris) reproduction. *Ecology*, *76*(8), 2460–2469. https://doi.org/10.2307/2265820

Wauters, L. a., Lurz, P. W. W., & Gurnell, J. (2000). Interspecific effects of grey squirrels

(Sciurus carolinensis) on the space use and population demography of red squirrels (Sciurus vulgaris) in conifer plantations. *Ecological Research*, *15*, 271–284. https://doi.org/10.1046/j.1440-1703.2000.00354.x

Wauters, L., & Dhondt, A. A. (1989). Body Weight , Longevity and Reproductive Success in Red Squirrels (Sciurus vulgaris). *Journal of Animal Ecology*, *58*(2), 637–651.

Weaver, M., Ligon, R. A., Mousel, M., & McGraw, K. J. (2018). Avian anthrophobia? Behavioral and physiological responses of house finches (*Haemorhous mexicanus*) to human and predator threats across an urban gradient. *Landscape and Urban Planning*, *179*(July), 46–54. https://doi.org/10.1016/j.landurbplan.2018.07.001

West-Eberhard, M. J. (1989). Phenotypic Plasticity and the Origins of Diversity. *Annual Review of Ecology and Systematics*, *20*(1), 249–278. https://doi.org/10.1146/annurev.es.20.110189.001341

Weston, M. A., Fitzsimons, J. A., Wescott, G., Miller, K. K., Ekanayake, K. B., & Schneider, T. (2014). Bark in the park: A review of domestic dogs in parks. *Environmental Management*, *54*(3), 373–382. https://doi.org/10.1007/s00267-014-0311-1

Wheeler, H. C., & Hik, D. S. (2014). Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour*, *95*, 1–8. https://doi.org/10.1016/j.anbehav.2014.06.005

Williamson, M. H., & Fitter, A. (1996). The characters of successful invaders. *Biological Conservation*, *78*, 163–170. Retrieved from http://eprints.whiterose.ac.uk/60266/

Williamson, R. D. (1983). Identification of urban habitat components which affect eastern gray squirrel abundance. *Urban Ecology*, 345–356.

Wolf, M., Doorn, G. S. Van, Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *44*(7144), 581–584. https://doi.org/10.1038/nature05

Wolf, M., & McNamara, J. M. (2012). On the evolution of personalities via frequency-dependent selection. *American Naturalist*, *179*(6), 679–692. https://doi.org/10.1086/665656

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3959–3968. https://doi.org/10.1098/rstb.2010.0215

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001
