Do cities create smarter animals? Behavioural monitoring of adaptive responses in urban wildlife

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Contents

Abstract

Urbanisation has transformed natural landscapes into human dominated environments and has altered ecological communities across the world. These environmental changes alter habitat structure, resource availability and ecological processes, creating both challenges and opportunities for wildlife. Although population numbers of many species are seeing steep declines in urban areas, some species seem to be stabilising under these conditions. Understanding the mechanisms that enable wildlife to persist and thrive in urban landscapes is crucial for informing conservation strategies designed to support declining urban populations.

This thesis comprised two complementary studies that investigated behavioural and physiological responses to urbanisation. Specifically, I tested the hypotheses that urban-adapted individuals exhibit greater boldness and enhanced cognitive abilities than conspecifics inhabiting less urbanised environments, and that urbanisation is associated with increased energetic demands, reflected by higher metabolic rates linked to foraging requirements. I used the European hedgehog as my study species, with individuals sampled across an urbanisation gradient.

The first study examined the relationship between uncurling behaviour (as a measure of boldness) and cognitive performance through a series of behavioural assays assessing risk taking and problem-solving abilities. The second study investigated the relationship between uncurling behaviour and metabolic rate as oxygen consumption via flow-through respirometry. Together, these approaches explored whether variation in uncurling behaviour (as a measure of boldness) across an urban gradient was associated with corresponding differences in cognitive and physiological traits.

I found that uncurling behaviour did not differ across habitats, and urbanisation did not affect overall success rate in any of the three cognitive tasks, although hedgehogs from more urbanised areas took longer to pass the first task, i.e., removal of a lid from a bowl, while performance in the subsequent tasks, i.e. the

time it took to move a panel to access food and finding an alternative entrance to the feeding station was not correlated to urbanisation. Similarly, neither uncurling nor habitat urbanisation significantly predicted variation in metabolic rate. These findings suggest that urbanisation does not appear to shape boldness, cognitive performance or metabolic rate in the study species. Furthermore, boldness was not associated with either cognitive performance or metabolic rate, indicating that these behavioural, cognitive and physiological traits may vary independently within this species.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Introduction

The global human population is expected to grow exponentially (Ahmad, 2001), with around 70% of the population predicted to live in cities by 2050 (Harris *et al.,* 2020). For wildlife populations worldwide, this expansion of urban environments will provide many challenges (Bai *et al.,* 2019) and biodiversity is often lower in urban than in rural habitats (Oertli and Parris, 2019; Uchida *et al.,* 2021). Yet, selected species, ranging from solitary bees (Persson *et al.,* 2020) to European hedgehog (*Erinaceus europaeus;* Hubert *et al., 2011)* to wild boar (*Sus scrofa;* Castillo-Contreras *et al.,* 2021), seem to thrive in urban habitats. However, urban environments differ from natural ecosystems, presenting wildlife with novel ecological challenges that may influence their behaviour, physiology and survival.

To be able to survive in urban areas, wildlife must successfully navigate human infrastructure such as roads and buildings. Infrastructure like this can expose animals to a range of anthropogenic stressors such as traffic, anthropogenic noise, artificial light, human disturbance and changes in food availability (McKinney, 2008; Marzluff, 2016). These stressors can alter movement patterns, access to refuge, foraging opportunities, predator avoidance and interactions with humans, ultimately influencing individual fitness and population persistence (Marzluff and Ewing, 2001; Ware *et al.,* 2015). Already, half of the European continent's surface is located within 1.5km from a paved road or railway line (Torres *et al.,* 2016). In Spain it was found if infrastructure continues to spread at the current rate, 46.6% of mammalian and 22.6% of bird species could be facing a decline in population numbers due to the expansion of roads, railway and urbanising areas due to the increased risk of injuries and mortality (Torres *et al.,* 2016; Brunton *et al.,* 2018). Roads often pose immediate mortality risks to animals that decide to cross them to access resources or mates (Hels and Buchwald, 2001; Glista *et al.,* 2009; Denneboom *et al.,* 2023). The necessity to cross busy roads exposes wildlife to a high risk of vehicle collisions, which contribute substantially to urban mortality rates (Eksler *et al.,* 2008; Teixeira *et al.,* 2013; Schwartz *et al.,* 2020). Roadkill is estimated to cause the deaths of

millions of vertebrates annually (Schwartz *et al.,* 2020), with vehicle collisions in the United Kingdom alone thought to kill approximately 50,000 European badgers (*Meles meles*) each year (Clarke *et al.,* 1998). However, studies have shown that some animals can adjust their crossing behaviour based on traffic patterns or time of day, illustrating behavioural adaptations to mitigate these dangers (Grilo *et al.,* 2015; Bissonette and Adair, 2008). Understanding how animals navigate these hazards is crucial for understanding how some species are able to thrive in urban areas (Adams, 2005).

Challenges posed by urbanisation extend beyond navigating roads and avoiding mortality. Urban development's alter and fragment landscapes, creating environments that may lack the vegetation, and habitat features necessary to support wildlife populations (McKinney, 2002; Grimm et al., 2008). Urban habitats may be devoid of natural vegetation (Lerman *et al.,* 2020) reducing abundance and availability of natural resources for many species including food resources. Private domestic gardens constitute a significant portion of urban green space, accounting for between 35% and 47% of green areas in many British cities (Loram *et al.,* 2007) and collectively covering over 430,000 hectares across the UK (Davies *et al.,* 2009). These gardens play a crucial role in supporting urban biodiversity by providing food resources, shelter, and connectivity for a variety of species (Gaston *et al.,* 2005; Smith *et al.,* 2006). However, approximately 10% of UK households have replaced natural lawns with synthetic turf as of 2022, and a further 29% considering similar changes to reduce garden maintenance (AVIVA, 2022). Artificial grass reduces populations of soil invertebrates and creates a physically impermeable foraging surface, limiting the ability of ground foraging insectivores such as hedgehogs and thrushes to access prey as they are unable to break this barrier to access a large portion of their natural diet, thereby contributing to declines in urban food web connectivity (Gaston *et al.,* 2007; Alberti *et al.,* 2008; Hof and Bright, 2009; Robbins *et al.,* 2009; Takeuchi *et al.,* 2012; Prasad *et al.,* 2014; Seress and Liker, 2015; Francis, 2018). Foraging on artificial grass can increase energetic costs for insectivorous species, as prey may be detected through olfactory or auditory cues but remain inaccessible beneath

the impermeable surface. This reduced access to natural food resources may ultimately affect body condition and reproductive success by limiting energy and nutrient intake over time (Jones and Leather, 2012). Such effects are particularly relevant for urban adapted insectivores such as hedgehogs, where reduced access to soil invertebrates has been linked to declines in urban populations (Hof and Bright, 2009). More broadly, this effect is amplified in urban landscapes that are already highly fragmented or lack continuous natural vegetation, which reduces overall habitat quality and food availability for many species (Beninde *et al.,* 2015; Lerman *et al.,* 2020).

In many countries, private households have started to provide supplementary food to support wild animals in urban areas (Jones and Reynolds, 2008; Murray *et al.,* 2016; Tryjanowski *et al.,* 2018). Although this supplementation food is often of lower nutritional value than natural food (Wist *et al.,* 2023), many species have taken advantage of this increased availability of food supplied by humans and eat this supplementary food instead of using energy to find more natural food resources (Contesse *et al.,* 2004). This can potentially lead to changes in physiology, cognition and behaviour as food abundance is a major factor in determining how a wild animal utilises their home range (Jones and Reynolds, 2008; Reynolds *et al.,* 2017; Hansen *et al.*, 2020). In Eurasian red squirrels (*Sciurus vulgaris*), access to abundant food resources was associated with minimal seasonal variation in resting metabolic rate, suggesting that supplemental food in addition to adjustments in activity may help squirrels cope with changing environmental conditions (Turner *et al.,* 2017). Furthermore, Egyptian fruit bats (*Rousettus aegyptiacus*) expand their home range by nesting in rural areas but foraging in urban areas due to the higher abundance of food in urban habitats (Egert-Berg *et al.,* 2021). This could also have the potential to select for certain traits in wild animals, rewarding those individuals that are able to adapt better to the altered environment and to retrieve food from close proximity of humans. Previous studies have suggested that urban environments often favour individuals that exhibit behavioural flexibility, including boldness and cognitive problem solving, because these traits allow animals to navigate the

novel challenges and exploit the opportunities presented by human altered landscapes, ultimately influencing survival and reproductive success (Sol *et al.,* 2013; Ducatez *et al.,* 2020).

Among UK mammals, the European hedgehog *(Erinaceus europaeus*) population numbers have undergone substantial decline across rural areas in the UK, however urban populations have remained more stable in some urban areas (Hubert *et al.,* 2011; Williams *et al.,* 2018). Urban environments can provide abundant supplementary food, suitable nesting sites within gardens and reduced predation pressure due to lower densities in hedgehog predators such as badgers *(Meles meles)* (Hubert *et al*., 2011; Yarnell and Pettett, 2020). However, urban habitats also present numerous challenges for hedgehogs. The European hedgehog feeds primarily on soil dwelling and surface active invertebrates such as earthworms (*Clitellata*), beetles (*Coleoptera*), caterpillars (*larval Lepidoptera*). Changes in habitat structure and reduction is accessible foraging habitats associated with urbanisation may alter the availability of natural prey, potentially increasing reliance on supplementary food provided in residential gardens (Reeve *et al.,* 2024). However, the ability to access these gardens can be challenging with ever changing maintenance in gardens and surrounding areas.

Successfully exploring urban environments may depend on behaviour traits that enable individuals to respond to novel and rapid changing conditions. Personality traits such as boldness may facilitate exploration and risk taking, while cognitive abilities may improve their ability to locate and exploit new resources. In addition, physiological traits such as metabolic rate have been proposed to influence behavioural variation by affecting energetic demands and activity levels although the evidence for these relationships remains mixed (Biro and Stamps, 2010; Sol *et al.,* 2013; Griffin *et al.,* 2017).

Therefore, in this thesis I will be using the European Hedgehog to investigate if urban adapters are bolder and have better cognitive abilities than animals living in less urbanised areas, and that urbanisation is related to an increased need for foraging due to high energetic demands. Finding this out will help understand what factors are contributing to this species success in more urbanised areas. To

do this, I worked with European hedgehogs along an urbanisation gradient throughout this thesis.

In this thesis, I have a literature review were I summarise what is known about behavioural and cognitive adaptions of wild animals that allow them to survive and thrive in urban spaces. In the first study, I investigate the influence of urban habitats on personality and cognition of hedgehogs and test the hypothesis that urban adaptors are bolder and have better cognitive abilities than animals living in less urbanised areas. In the second study, I investigate whether variation in urbanisation is associated with differences in metabolic rate and whether this is linked to personality traits. I then conclude with a general discussion of my thesis.

Literature Review

Behavioural adaptations in urban animals

Understanding the link between boldness and cognition in urban wildlife is critical for explaining patterns of urban adaptation, species persistence and ecological interactions in urban environments. Boldness, commonly defined as an individual's willingness to take risks or explore novel environments, is a key personality trait that can influence how animals respond to environmental change (Réale *et al.,* 2007). In urban habitats, bold individuals may be more willing to exploit unfamiliar resources, tolerate human disturbance and nest in novel environments, although increased risk taking may also expose them to greater mortality from threats such as road traffic or human activity (Sol *et al.,* 2013). Cognition, including learning, memory and problem solving enables individuals to acquire and use information to respond to changing environmental conditions (Shettleworth, 2010). Enhanced cognitive abilities may improve an individuals' efficiency to locate food, navigate complex urban landscapes and adjust behaviour in response to novel challenges (Griffin *et al.,* 2017). Examining boldness and cognition together may help clarify why some individuals are more

able to persist in urban environments than others. If boldness influences an individual's willingness to approach novel stimuli, while cognition affects how effectively information is acquired and used, then the two traits may jointly shape responses to urban change. Therefore, in this literature review I will summarise what is known about behavioural and cognitive adaptions of wild animals that allow them to survive and thrive in urban spaces.

Urban and rural environments differ substantially in the ecological conditions they present to wildlife. Urbanisation transforms natural landscapes into human dominated ecosystems characterised by increased habitat fragmentations, greater levels of anthropogenic disturbances, artificial light and changes in the abundance of resources (Grimm *et al.,* 2008; Sol *et al.,* 2013; Alberti, 2015). In contrast, rural habitats are generally characterised by lower levels of human disturbance, greater habitat connectivity and resource distribution that are more strongly influenced by natural seasonal processes (McKinney, 2006). Consequently, animals inhabiting urban environments are often exposed to greater environmental unpredictability and may need to rapidly gather, learn and use information to locate resources to avoid risks and respond more often than rural individuals due to the rapidly changing conditions.

Cognition

The ability to learn, remember and solve problems plays a crucial role in enabling animals to cope with challenges of urbanised environments (Lee and Thornton, 2021). Animal cognition refers to the mental process by which an animal acquires, processes, retains and use information from its environment to guide behaviour and decision making (Healy and Braithwaite, 2000; Dukas, 2004). Investigating cognition in animals is essential for understanding how individuals perceive and respond to their environmental change, as cognitive abilities can influence behavioural flexibility, resource use, survival and ultimately an individual's ability to persist in rapidly changing urban environments. By altering resource availability, habitat structure and ecological pressures, urban landscapes

can favour individuals capable of flexibly adjustment their behaviour and exploiting new resources (Sol *et al.,* 2013). An innovate strategy that an animal may use in an urban environment is trial and error learning, whereby individuals repeatedly test different behaviours until they discover a successful solution. This form of learning can enable animals to exploit novel food resources, overcome unfamiliar obstacles and adapt to changing environmental conditions (Thornton and Samson, 2012; Chow *et al.,* 2016). Therefore, gathering information from environments is an important trait that enables individuals to make both immediate and future decisions (Dall and Johnstone, 2002). To respond appropriately to environmental challenges, animals must acquire, retain and use information from previous experiences to guide future behaviour (Shettleworth, 2010). Species that rely on patchy distributed resources are predicted to require well developed spatial memory to efficiently locate and revisit profitable foraging sites (Clutton-Brock and Harvey, 1980; Milton, 1981). Animals can employ different cognitive mechanisms to solve problems depending on the context. For example, trial and error learning enables individuals to acquire successful behaviours through repeated attempts, whereas spatial memory allows them to remember and relocate reliable food patches. (Mou and McNamara, 2002; Hampton *et al.,* 2004; Burgess, 2008; Packard, 2010). For example, Lee and Thornton (2021) demonstrated that spatial memory and innovation enable animals to exploit patchily distributed urban resources more efficiently. Urban resources includes both natural and anthropogenic resources that wildlife can exploit, including food, water, shelter, nesting sites and movement corridors. Unlike many natural habitats, these resources are often spatially fragmented and influenced by human activity, requiring animals to continually acquired and update information about their availability. Resources include supplementary food, compost heaps, artificial water sources, green corridors such as railway embankments. Urbanisation also alters the materials available for nest construction for wildlife. Crawford *et al.,* (2026) reported that European hedgehogs incorporated anthropogenic materials including plastic bags, duct tape, foil and expanded polystyrene, into hibernation nests. This suggests that wildlife such as hedgehogs may modify their nesting behaviour in response to

human altered environments, although the fitness consequences of using these materials remain unknown. Although cognition is widely considered to facilitate adaptation to urban environments, evidence indicates that the effects of urbanisation on cognitive performance vary among species and ecological contexts (Sol *et al.,* 2013; Griffin *et al.,* 2017).

As cognition is thought to influence how animals respond to urban environments, researchers have developed a range of behavioural tests to assess cognitive performance. Because cognitive processes cannot be observed directly, they are inferred through an individual's performance in standardised behavioural tasks that measure abilities such as learning, memory, problem solving, innovation and cognitive flexibility (Shettleworth, 2010; Thornton *et al.,* 2014). These experimental approaches enable researchers to compare cognitive performance both within and between species, providing insight into how cognitive abilities may contribute to adaption in changing environments.

One of the most common approaches for assessing cognitive performance involves presenting animals with novel food access problems. These experiments often referred to as puzzle tasks or problem-solving tasks. Puzzle tasks require animals to manipulate objects or solve novel challenges to obtain rewards providing a direct measure of problem solving, innovation and cognitive flexibility (Auersperg *et al.,* 2011; Benson-Amram and Holekamp, 2012). Performance in these tasks is often measured using latency to solve a task, number of successful trials or efficiency of solutions which can be across repeated trials. For example, Eurasian red squirrels have been used as a model species to investigate how urban conditions influence problem solving abilities (Chow *et al.,* 2021). Squirrels were presented with novel food extraction puzzles across multiple urban sites to assess how variation in local environmental conditions affected their cognitive performance. Their findings revealed that squirrels inhabiting areas with higher levels of human disturbance and greater conspecific density solved tasks more quickly and efficiently. This suggests that urban environments may select for enhanced problem solving and persistence. However, performance can be

influenced by prior experience, motivation or neophobia (Greggor *et al.,* 2015; van Horik and Madden, 2016; Ebel and Call, 2018).

Problem solving tasks are designed to assess an individual's ability to find solutions to novel challenges. These tasks require animals to manipulate objects, navigate obstacles or solve puzzles to obtain a reward and thereby measuring multiple cognitive abilities simultaneously including innovation, learning, memory and behavioural flexibility (Auersperg *et al.,* 2011; Benson-Amram and Holekamp, 2012). In urban areas, great tits (*Parus major*) solved detour reaching tasks and learned colour reward associations quicker than rural birds, reflecting enhanced inhibitory control, associated learning and behavioural flexibility in response to urban environmental challenges (Audet *et al.,* 2015). Similar, urban house sparrows (*Passer domesticus*) outperformed rural counterparts in novel food extraction tasks, demonstrating greater problem-solving ability and reduced neophobia likely due to repeated exposure to human modified environments (Papp *et al.,* 2014). Together these findings indicate that urban populations can exhibit improved learning and efficiency and cognitive flexibility and potentially supporting survival and resource in challenging urban habitats (Papp *et al.,* 2014; Audet *et al.,* 2015)

While these cognitive task types provide valuable insights into various cognitive abilities, it is important to recognise that performance can be strongly influenced by animals' willingness to engage and its motivation to participate. Voluntary participation ensures that animals are actively choosing to perform task (Fischer *et al.,* 2021). However, research indicates that voluntary engagement does not always reflect intrinsic motivation as some individuals may participate for reasons unrelated to cognitive interest which highlights the need to carefully interpret results in the context of both participation and motivation (Meagher *et al.,* 2020; Mátrai *et al.,* 2022).

Enhanced cognitive abilities in urban environments may not only facilitate resources more efficiently, but may also influence individual risk taking and boldness, as animals must balance the potential rewards of exploiting novel or hazardous resources against the likelihood of harm. Therefore, in the first study

of my thesis, I will be investigating whether there is a correlation between cognition and risk-taking abilities in the European hedgehog along an urban gradient. By measuring boldness and cognitive performance in urban hedgehogs, we aim to test whether individuals that are bolder show enhanced problem solving which may help explain their success in urban environments.

Comparing individuals across an urbanisation gradient provides an opportunity to investigate whether exposure to contrasting environmental conditions is associated with variation in cognitive performance. Urban environments may act as ecological filter, whereby individuals processing behavioural and cognitive traits that improve their ability to exploit anthropogenic habitats are more likely to survive and reproduce (Sol *et al.,* 2013; Alberti, 2015). Alternately, differences in cognitive performance may arise through behavioural plasticity, with individuals adjusting their behaviour and learning in response to the environmental challenges they experience (Sol *et al.,* 2013; Lee and Thornton 2021). Distinguishing between these possibilities is important for understanding how wildlife respond to increasing urbanisation and whether cognitive traits contribute to the success in urban environments.

Boldness

Urban environments present wildlife with selection pressures that are different to those that animals experience in their natural habitat. As selection will affect an animal's survival and fitness, i.e. the likelihood of transferring their genes into a new generation, individuals that can adjust to these new selection pressures by changes in behaviour should have greater success in urban habitats. This will eventually cause evolutionary alterations in species that have acclimated to urban environments. This has been referred to as urban wildlife syndrome (Parker and Nilon, 2008; Ritzel and Gallo, 2020). The urban wildlife syndrome is driven by resources such as food and habitat availability (Warren *et al.*, 2006) and suggests that individuals that adapt to urban life show increased aggression and

a reduced fear of humans. This consistent personality trait, often referred to as 'boldness' is describing an individual's tendency to take risks, i.e. approach novelty and potential danger situations (Réale *et al.,* 2007). While bold individuals are more likely to engage in risky behaviours, even shy individuals may take risks when the potential reward is high or under strong motivational pressures, such as hunger or reproductive opportunity (Brown and Braithwaite, 2004; Cole and Quinn, 2014). Individual boldness can substantially influence survival outcomes, especially in urban environments where hazards are frequent and unpredictable (Atwell et al., 2012; Sol *et al.,* 2013; Baxter-Gilbert *et al.,* 2019)

Boldness allows animals to tolerate frequent human presence and approach resources in risky areas, such as roads (Møller, 2009). Exploratory behaviour enables individuals to locate an exploit novel food sources, artificial feeders, or alternative nesting sites in fragmented or altered habitats (Sol *et al.,* 2013). Tolerance of human disturbance helps animals maintain normal activity patterns despite urban disturbances (Lowry *et al.,* 2012). It is widely agreed that bolder individuals are more likely to explore environments, access more food and thrive in high risk, high reward environments (Azevedo and Young, 2006; Sih and Del Giudice, 2012; Mazza *et al.,* 2020). These traits align closely with the characteristics of the urban wildlife syndrome in which behavioural flexibility, boldness and exploratory tendencies are repeatedly favoured in urban populations. Animals living in cities frequently exhibit increased boldness, altered behavioural syndromes, and enhanced exploratory behaviour compared to their rural counterparts (Møller 2009; Evans *et al.,* 2010; Lowry *et al.,* 2012). For example, Myers and Hyman (2016) demonstrated that urban song sparrows (*Melospiza melodia*) display greater boldness than birds of the same species in rural areas, as evidenced by reduced flight initiation distances and distinct responses to alarm calls, although the correlation between boldness and aggression differed between urban and rural populations. Complementing this, Eastern grey squirrels (*Sciurus carolinensis*) in urban areas exhibit higher levels of activity and exploration than those in rural settings, further reflecting bold personality traits can be beneficial to urban survival (Tranquillo *et al.* 2024).

Boldness in urban animals often provides important adaptive benefits, helping them survive and reproduce in human-dominated environments. For example, bolder individuals are more willing to approach novel objects or areas of human activity, which allows them to exploit anthropogenic food resources such as bird feeders or hedgehog feeding stations (Møller, 2009; Cox and Gaston, 2016; Jones and Reynolds, 2008). This increased access to high calorie food can improve energy intake and overall fitness, giving bold individuals a competitive advantage in urban habitats (Cox and Gaston, 2016). This access to reliable, high calorie resources can improve nutritional status and energy reserves, supporting higher reproductive output and survival. In wood storks (*Mycteria americana*), urban food subsidies have been shown to impact foraging behaviour as when food was scarce, urban storks included human-provided food in their diet, which boosted their productivity. (Evans and Gawlik 2020). This flexibility in feeding shows boldness, as it reflects a willingness to explore and use new food sources in human-dominated areas.

Boldness may also facilitate the use of novel shelters and anthropogenic habitats in urban environments. Individuals that are more willing to tolerate human disturbance and explore unfamiliar environments may gain access to resources and refuges that are unavailable or avoided by more cautious conspecifics (Beck *et al*., 2019; Biondi *et al.,* 2020). Urban wildlife frequently exploit human made structures, such as buildings, bridges and rooftops for nesting and shelter. For example, gull species have increasingly established breeding populations in urban areas across Europe, utilising rooftops, quays and other artificial structures that provide nesting opportunities and access to anthropogenic food resources (Soldatini *et al.,* 2008; Spelt *et al.,* 2019; Goumas *et al.,* 2024). Successfully exploiting these habitats requires individuals to tolerate novel and potentially risky stimuli, including human activity, traffic and altered environmental conditions. Consequently, traits associated with boldness, such as reduced neophobia and an increased willingness to explore novel environments, may confer adaptive advantages by enabling individuals to exploit urban resources and habitats more effectively (Møller, 2009; Atwell *et al.,* 2012; Baldassarre *et al.,*

2024). These findings highlight the potential role of boldness in facilitating wildlife persistence and success within human modified landscapes.

While boldness can enhance access to resources and improve survival in urban environments, it can also have significant costs. By engaging in riskier behavouirs, bold individuals may experience increased exposure to predators and other human associated threats, potentially resulting in high mortality rates (Lind and Cresswell 2005). For example, bolder incubating female birds are more likely to remain on the nest or actively defend their nests when predators approach, potentially increasing their exposure to predation risk (Pöysä *et al.,* 2025). Similarly, urban Eurasian red squirrels allow potential threats to approach more closely before becoming alert or fleeing compared to their rural counterparts, indicating reduced vigilance in response to potential threats (Uchida *et al.,* 2019). However, this reduction in vigilance increases the potential for conflicts and predation in urban areas, particularly from domestic pets. Domestic cats are a key source of bird mortality, killing an estimated 1.3 – 4 billion birds annually in the United Sates of America alone (Loss *et al.,* 2013). Studies suggest urban cats may impose particularly strong predation pressure in bird populations due to high cat densities near human settlements and greater avian prey use in urban habitats (Baker *et al.,* 2005; Krauza-Gryz *et al.,* 2017).

One cost related to boldness in urban environments is the increased encounters with humans and domestic predators (Uchida *et al.,* 2019; Brooks *et al.,* 2020). Bolder individuals are more likely to enter gardens, parks, and recreational areas where conflicts with humans or pets are common which can elevate the risk of injury or mortality (Bateman and Fleming, 2012; Padovani *et al*., 2020; Morton *et al.,* 2023). Fences add an additional challenge as navigating barriers by climbing, squeezing through or rerouting around requires an animal to weigh the benefits of accessing food, mates or shelter against the risk of injury, predation or exposure (Gates *et al*., 2011; Jakes *et al*., 2018).

To cope with the risks and uncertainties of urban life, many species modify their natural behaviours, whether by changing when they forage, how they assess risks, or what resources they use (Evans *et al.,* 2020; Kittendorf and Dantzer,

2021; Diaz *at al.,* 2022). These adaptations can improve their chances of finding food and surviving in an environment that can be dangerous and unpredictable (Diaz *et al.,* 2022; Morelli *et al.,* 2018). Studies of urban wildlife consistently show that animals weigh foraging opportunities against risks, but the cues and thresholds they use often differ from those in non-urban settings. For example, urban birds such as pigeons and house sparrows adjust their vigilance and proximity to humans depending on food availability, tolerating closer approach when resources are abundant (Møller, 2008; Díaz *et al.,* 2022). Similarly, urban squirrels and corvids have been observed to exploit food in high-disturbance areas, suggesting that repeated exposure to humans reduces perceived risk (Bateman and Fleming, 2012; Lowry *et al.,* 2013). However, not all behavioural changes are clearly beneficial, and understanding the balance between risk taking and caution (Evans *et al.,* 2020; Kittendorf and Dantzer, 2021).

Collectively, these studies highlight that boldness can influence how individuals exploit resources, respond to environmental challenges and persist within urban environments. However, individuals differ consistently in their willingness to take risks, suggesting that boldness may be linked to underlying physiological and life-history strategies. Understanding why some individuals adopt bolder behavioural strategies than others is therefore important for explaining variation in responses to urbanisation.

The pace-of life-theory

Interestingly, bold individuals have often been found to also have a faster pace of life, with earlier date of reproduction, faster life history and higher metabolic rates (Réale *et al.,* 2010; Gopal *et al*., 2023). These traits may increase energetic demands, influencing foraging behaviour and resource use (Careau and Garland, 2012), which may untimely affect the persistence and demographic composition of wildlife populations in urban environments (Sol *et al.,* 2013). Individuals with higher metabolic rates have greater energetic demands and may therefore need to forage more frequently or over larger areas to meet their energy requirements

(Biro and Stamps, 2010; Careau and Garland, 2012). Increased foraging activity may increase encounters with unfamiliar habitats with anthropogenic hazards, which can in turn shape exploratory and risk-taking behaviour (Sih *et al*., 2004; Tuomainen and Candolin, 2010). In contrast, individuals with lower metabolic rates have reduced energetic demands and may be under less pressure to exploit novel resources or engage in risky foraging behaviours, potentially adopting more cautious behavioural strategies (Biro and Stamps, 2010; Careau and Garland, 2012). Consequently, metabolic rate has been proposed as a physiological mechanism underlying consistent variation in boldness, although support for this relationship remains mixed across species (Careau and Garland, 2012; Mathot & Frankenhuis, 2018). Understanding whether metabolic traits are associated with boldness is therefore important for determining how behavioural and physiological variation may contribute to adaptation in urban environments.

Bolder animals often have a shorter lifespan compared to shyer animals (Fichtel *et al.,* 2023). Bold or proactive individuals tend to priorities current over future reproduction and investing more energy into growth and reproductive output at the expense of longevity (Montiglio *et al.,* 2018; Eckerström-Liedholm *et al.,* 2019). This is known as the pace of life syndrome. This idea links life history theory to consistent behavioural and physiological trait differences (Réale *et al.,* 2010; Dammhahn *et al.,* 2018). The pace of life syndrome hypothesis proposes that variation among individuals fall along a slow-fast-continuum (Réale *et al.,* 2010; Dammhahn *et al.,* 2018). Fast individuals show faster growth, earlier reproduction, higher metabolic rate, bolder/riskier behaviour and shorter lifespan continuum while slow individuals show the opposite pattern (Réale *et al.,* 2010; Dammhahn *et al.,* 2018). The main idea is that differences in metabolism and how organisms allocate resources. Higher baseline energy favours bolder, higher investment in behaviours and a faster life history while lower baseline energy favours longevity and caution (Dammhahn *et al.,* 2018; Gopal *et al.,* 2023).

In urban environments, these pace of life differences may be particularly important, as bolder individuals with faster life histories may be more willing to

take risks, such as crossing roads or exploiting gardens influencing their survival and reproductive success in urbanised areas. Urban environments impose higher energetic demand than rural areas on wildlife due to the combined effects of increased movement, fragmented habitats and human disturbance (Samia *et al.,* 2015; Patten and Burger, 2018). Animals often need to travel more frequently or further to access food, navigate barriers or avoid humans or domesticated predators (Beckmann and Berger, 2003; Lowry *et al.,* 2012). Urban raccoons (*Procyon loto*) have been found to exhibit larger home ranges and have an increased movement distances compared to rural counterparts (Prange *et al.,* 2004). This increase in activity is thought to result from that patchy distribution of anthropogenic food sources which has forced individuals to travel further. This increased movement through fragmented land can increase the energic demand on species. Locomotion can significantly increase energy expenditure with metabolic rates increasing during periods of intense searching for mates, resources or nesting sites (Pontzer, 2025) which can happen when animals travel long distance or navigate obstacles. Additionally, urban environments often present novel challenges which requires animals to adapt their behaviour and physiology which can further impact their energy budgets (Carnahan *et al.,* 2021; Vardi *et al.,* 2023). These increased energetic demands from extended movement and navigation of urban environments are likely linked to elevated metabolic rates meaning that urban wildlife must balance high energy expenditure with sufficient food intake to maintain overall fitness (Careau and Garland, 2012; Speakman, 2008).

Metabolism is the way the body converts food to energy. Resting metabolic rate is a measure of the rate of energy expenditure to maintain the balance of energy during resting (Ricklefs *et al.,*1996) while aerobic metabolism is the process of energy production within cells using oxygen to covert glucose into energy to sustained activities such as running and sleeping. Open flow respirometry measures oxygen uptake with a common non-invasive method. It can act as a proxy for an organism's energy expenditure that is measured directly in real time. It enables the quantification of oxygen consumption or of carbon dioxide

production, and then this quantification provides valuable perceptions into patterns that are of metabolic rate. This non-invasive method has been used on a variety of species (Wilson *et al.,* 2011; McNab and Weston, 2018*;* Lucchini *et al.,* 2025; Thirkell *et al.,* 2025).

Therefore, in the second study I will be looking at the link between boldness and resting metabolic rate along an urban gradient. By looking at this link, we can better understand how animals balance the trade-off between energy use, risk taking and survival in urban areas.

Urbanisation imposes a range of ecological challenges that may influence multiple aspects of an individual's phenotype. Successfully exploiting human modified environments is likely to depend on a combination of behavioural and physiological traits rather than any single characteristics alone. Cognitive abilities may enable individuals to learn, remember and solve novel problems, while boldness influences the willingness to explore unfamiliar environments and take risks. These behavioural traits may also be linked to physiological characteristics, such as metabolic rate, through differences in energetic demands and foraging behaviour (Réale *et al.,* 2010; Careau and Garland, 2012).

Collectively, the literature suggests that cognition, boldness and metabolic rate may each contribute to how wildlife respond to urbanisation. However, relatively few studies have investigated these behavioural and physiological traits in wild mammals, particularly across an urbanisation gradient. Furthermore, evidence remains inconsistent regarding whether urban environments influence cognition, personality or metabolic traits, highlighting the need for further species-specific research. This thesis addresses these knowledge gaps by examining cognitive performance and boldness in one population of wild European hedgehogs and the relationship between boldness and metabolic rate with another set of European hedgehogs providing complementary insights into the behavioural and physiological mechanisms that may facilitate persistence in urban environments.

The European hedgehog represents an excellent model species for investigating behavioural responses to urbanisation. Despite a decline in population numbers, urban population numbers have remained comparatively stable, suggesting that soe individuals may possess behavioural or physiological traits that facilitate persistence in human modified environments (Hubert *et al*., 2011). Although hedgehogs are amount UK's most studied mammals from a conservation perspective, relatively little is known about how cognitive performance, personality traits or metabolic characteristics vary across an urbanisation gradient. This combination of ecological relevance, conservation concern and behavioural knowledge gap males the European hedgehog an ideal model species for investigating mechanisms of urban adaption.

General Methods

Ethics

The experimental procedures were reviewed by the Ethical Committee of Liverpool John Moores University, and ethical approval was given and was followed throughout (JN_KB/2024-7).

The Study Specie

Throughout this thesis, the study species is the European hedgehog (*Erinaceus europaeus*). The European hedgehog is a widespread insectivorous mammal found across Europe. Although traditionally associated with rural habitats, hedgehogs have experienced population declines in these areas, while numbers in urban environments appear to be stabilising (Hubert *et al.,* 2011; Wembridge *et al.,* 2022; Gazzard *et al.,* 2022). Hedgehogs frequently utilise private urban gardens where supplementary feeding, nesting opportunities and suitable habitat features resources that support their survival and reproduction in urban environments (hereafter referred to as urban resources) (Gazzard *et al.,* 2022). Like many mammals, hedgehogs hibernate during the winter due to limited food availability (Bearman-Brown *et al.,* 2020a). Notably, shifts in hibernation timing linked to changing environmental conditions suggest that hedgehogs are adapting to urban environments (Crawford *et al.,* 2025). This adaptability makes the European hedgehog a compelling model for investigating how cognitive abilities and behavioural tendencies may be influenced by habitat location.

The hedgehogs used throughout this thesis have all be rehabilitated from one rescue centre, Haydock Hedgehog Helpers Rescue (Lat: 53.468, Long: -2.682) between November 2024 and January 2025. All hedgehogs were from the wild and were not reared in captivity. Hedgehogs were handed over to the rescue centre from members of the public when found the public believed the hedgehog needed medical attention. The location where the hedgehog was found was provided by the members of public that found the hedgehog. The rescue centre

conducts a health check where they also sex the hedgehog prior to treatment if required. The hedgehogs are then housed individually. Only animals that were admitted with no physical injuries and that had completed their treatments for parasites prior to being used in the study, confirmed by at least one parasite-free faecal sample, were used for this study; body condition was determined based on weight with individuals weighing more than 450 g and less than 1300 g (Jensen, 2004; Bellini *et al.,* 2019) with the average weight being 753.8g. Hedgehogs below this weight tend to be juveniles and therefore not used in this study. Hedgehogs over this weight may struggle to enter the feeding station and therefore not used. Throughout the whole thesis a total of 30 hedgehogs were used (Male: 15 Female:15). Figure 2 shows the urbanised gradient for all individuals involved in this thesis.

Urbanisation gradient

Hedgehogs can travel up to 2km a night for foraging (Morris, 1988; Kristiansson, 1990; Reeve, 1998; Patrick *et al*., 2008), so we used a 2km diameter around the midpoint of the postcode of the location where the hedgehogs were found to determine the urbanisation gradient level of their natural habitat. The 2km buffer was created around the midpoint of each hedgehog's recorded location in QGIS using the UK Centre for Ecology & Hydrology Land Cover Map 2023 (LCM2023). The 'zonal statistics' tool was used to calculate the proportion of each land cover class within the buffer. This generated a score for the cover of urban, suburban and other habitat types (e.g., arable land, grassland and water), from which the percentage of urbanisation (urban + suburban land cover) was calculated for each individual and therefore created an urbanisation score. Please see figure 1 below which shows an example of the urban gradient. This method has been used for Western European hedgehogs (*Erinaceus europaeus)* in urban landscapes (Turner *et al.,* 2026). In Chapter 1 hedgehogs ID 1 - ID 16 took part in the cognition portion.

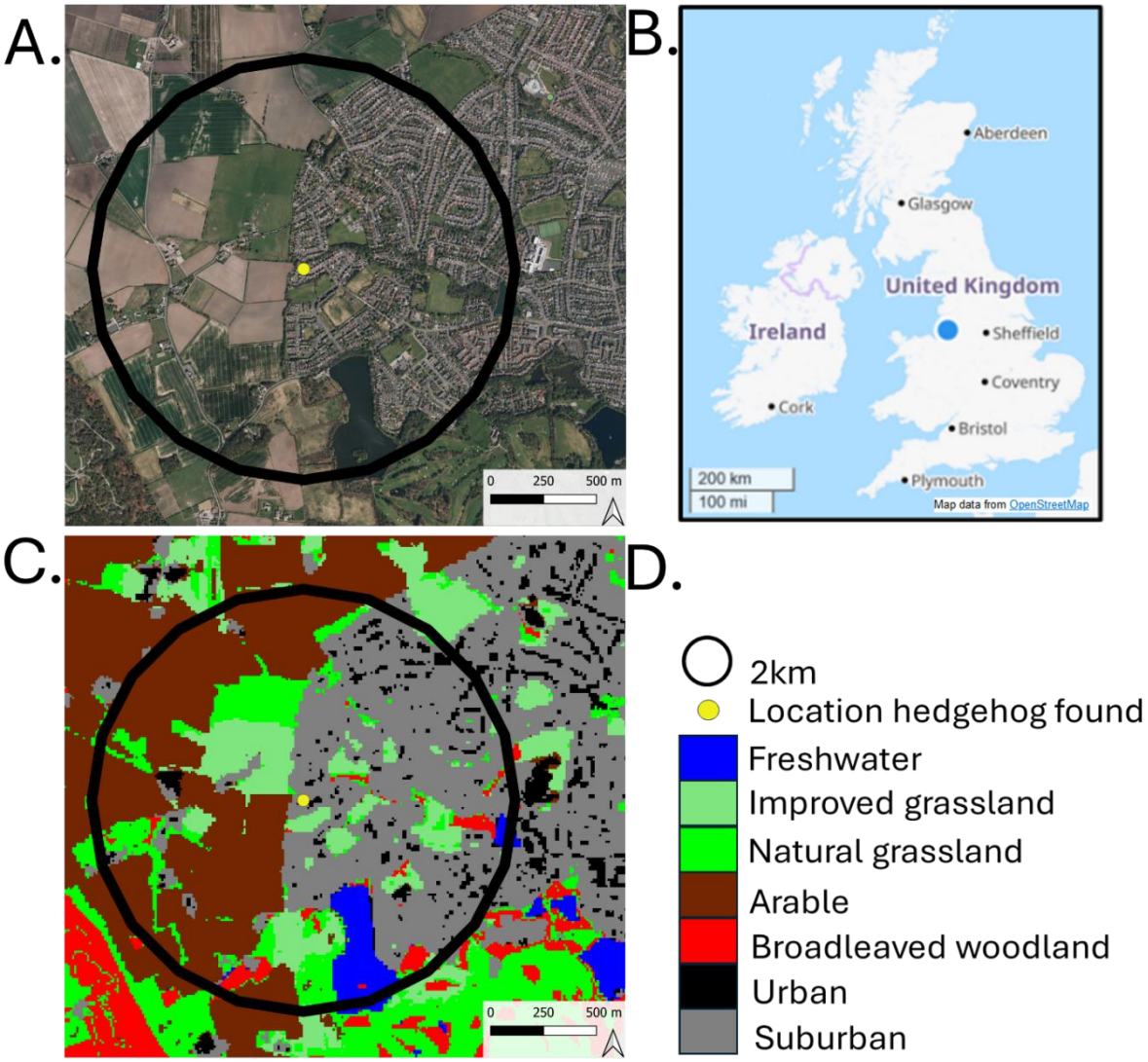

Figure 1: A: Location of a hedgehog with a 2km diameter. B: Map of the UK showing the study location. C: UK Centre for Ecology & Hydrology (UKCEH) Land cover Map 2023 (LCM2023) of location 53.454851, -2.786009. The urbanisation level for this location is 39.59. D: figure legend.

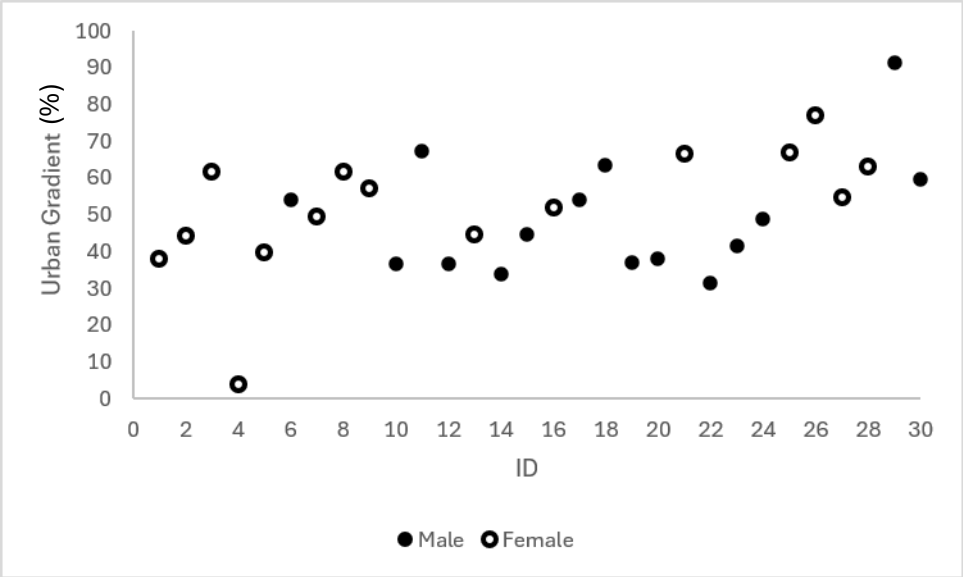

Figure 2: Urbanisation gradient percentage for all individuals involved in this thesis (n=30).

Boldness

Three tests were made to test boldness. Firstly, Uncurling was used as a proxy of boldness, (1) fully uncurl with all four feet on the ground, and (2) move all four feet from the position in which they were uncurled, was measured. Figure 3 shows an example of how the boldness was conducted. If the hedgehog made no attempt to uncurl or move after 5 minutes, 300 seconds was recorded. Limited sound or movement from the observer was made. The hedgehogs were not touched and were unrestricted. This proxy measure of boldness is based on the finding that if a hedgehog is startled, they will use the curl up response and tighten into a ball and only uncurl when they believe the threat is gone (Bearman-Brown *et al.,* 2020b; Rasmussen *et al.,* 2023). For uncurling test hedgehogs ID 1 - ID 16 plus ID 19 - ID 30 excluding ID 17 and 18 hedgehogs took part.

Boldness measures in chapter 1, hedgehogs ID 2 - ID 15 took part as well as hedgehogs ID 18 - ID 30. Hedgehogs ID 19 - ID 29 took part in the uncurling portion of the chapter 2. Figure 4 shows the urbanised gradient for the individuals that took part in this section of the thesis.

Figure 3: Example of how the boldness test was conducted. (A) Fully curled up at the start of the uncurling assay, and (B) all four feet on the ground preparing to move all four feet in a walking/ running motion.

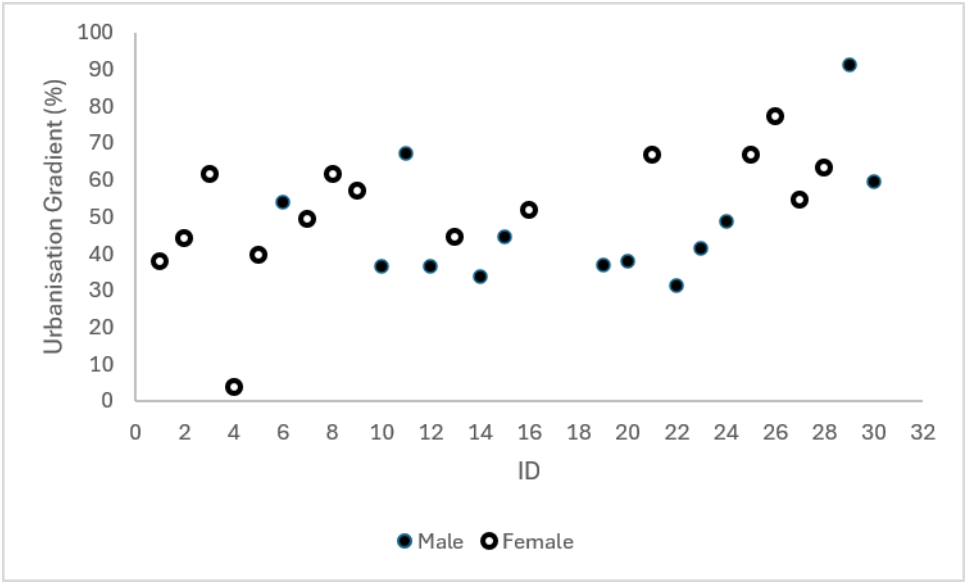

Figure 4: Urbanisation gradient percentage for all individuals involved in the Uncurling measure which was used a proxy for boldness in this thesis (n=28).

Repeatability

We investigated whether boldness, measured as the latency to uncurl (boldness test 1) and to move away following handling (boldness test 2), was repeatable over time and whether it correlated with the urbanisation level (measured as the percentage of urban and suburban land cover in each individual's habitat, see above). We estimated repeatability using the R package rptR (v 0.9.23; Nakagawa & Schielzeth 2010; Stoffel *et al*. 2017), specifying individual identity as a random effect in a linear mixed-effects model with Gaussian error distribution. We used 1,000 parametric bootstraps to calculate confidence intervals and 1,000 permutations to determine statistical significance of repeatability estimates. Fixed effects test number and urbanisation level were included where relevant to control for systematic variation. All models were fitted using the lme4 (v 1.1-37, 2025; Bates *et al*., 2015) and lmerTest (v 3.1-3, 2020; Kuznetsova *et al*., 2017) packages version and diagnostic plots confirmed that residuals met assumptions of normality.

For all models, model assumptions (linearity, normality of residuals, and homoscedasticity) were checked using qqplots. Summary statistics (minimum, maximum, mean, and standard deviation) were calculated using the dplyr package (v 1.1.4, 2023; Wickham *et al*., 2023).

P-values for model terms were calculated using a permutation test with 10,00 randomisations which compares the observed test statistic to its null distribution generated by permuting the response variable.

Chapter 1

Urban Minds, Wild Instincts: Do Hedgehogs (*Erinaceus europaeus*) Adapt Behaviourally and Cognitively to the City?

Abstract

The growing human population has led to increased urbanisation, resulting in fragmented environments, increased exposure to pollution and limited resources for wildlife. However, many species, including the European hedgehog (*Erinaceus europaeus*), are increasingly colonising in human settlements and we do not yet understand the factors that enable them to thrive in urban areas. As individual variation in behaviour and cognition are likely key factors to predicting how species adapt to rapidly changing environments, this study investigated whether consistent differences in behaviour, e.g. boldness, and cognitive performance are affected by urbanisation using European hedgehogs (*Erinaceus europaeus*) as a model species. Our study found boldness did not differ across the urban gradient, and urbanisation did not affect overall success of completion rate for three cognitive tasks. However, hedgehogs with a higher urbanisation gradient took longer to remove the lid from the bowl in the first problem solving task. Urbanisation did not influence an individual's ability to complete the remaining problem-solving tasks or their overall cognitive performance across all tasks. These findings highlight the importance of considering behavioural traits when assessing how wildlife responds to urbanisation. Improving our understanding of the cognitive and behavioural mechanisms that facilitate persistence in urban environments will help inform conservation strategies for wildlife like the European hedgehog, including management of green spaces and the provision of resources that promote natural foraging behaviours and long-term population persistence.

Introduction

Urban environments present challenges and opportunities for wildlife, requiring individuals to adapt to novel and often unpredictable environments and conditions. It is thus not surprising that urbanisation is one of the major threats to biodiversity (Sanderson *et al.*, 2018; Fenoglio *et al.,* 2020) and biodiversity is often lower in urban than in rural habitats (Urban *et al.,* 2024; Piano *et al.,* 2020; Oertli and Parris, 2019; Uchida *et al.,* 2021). With urban environments being subject to frequent anthropogenic modifications, it is important for wildlife to adapt to these changes (Lowry *et al.,* 2012). Human activities such as residential construction, garden maintenance and the installation of modern fences can rapidly alter the distribution of resources and movement opportunities available to wildlife. These changes may place greater demands on an individual's ability to locate resources and adapt its behaviour accordingly. Cognitive ability and personality traits such as boldness are increasingly being recognised as factors influencing how animals navigate and thrive in these human altered environments (Mazza and Šlipogor, 2024; Mettke-Hofmann, 2014) and several studies suggest that bolder individuals are more likely to explore new environments, access a wider variety of foods and thrive in high risk, high reward environments (Sih and Del Giudice, 2012; Mazza *et al.,* 2020). However, urban environments are not exclusively characterised by unpredictability. Many urban resources are relatively stable and predictable, including supplementary feeding provided by garden owners, anthropogenic heat sources and reduced predation pressure (Lowry *et al.,* 2012). The availability of these resources may reduce the cognitive and energetic demands associated with locating food and shelter compared with more natural environments. Consequently, urbanisation may impose both novel challenges and novel opportunities for wildlife, making it difficult to predict how behavioural traits such as cognition and boldness will vary across urban gradients.

The contrasting characteristics of urban environments suggest that urbanisation may influence behavioural traits in multiple ways. Individuals inhabiting more urbanised habitats may benefit from enhanced cognitive abilities and greater

boldness when exploiting novel or fragmented resources, whereas predictable resource availability may reduce the need for such traits. Consequently, understanding how cognition and boldness vary across an urbanised gradient is essential for determining the behavioural mechanisms that facilitate persistence in human modified landscapes.

Therefore, in this study, we aimed to investigate the influence of urban habitats on personality and cognition of the European hedgehogs and test the hypothesis that urban adaptors are bolder and have better cognitive abilities than animals living in less urbanised areas. We predict (1) hedgehogs from a more urban area would be faster problem solvers than hedgehogs from a less urban area and (2) that bolder individuals will come from more urbanised areas.

Methods

Ethics

Please see General Method Section for more details.

The study took place between May - November 2024 in a private garden in St Helens, UK (53.448, -2.743). We used European hedgehogs from a rescue centre, Haydock Hedgehog Helpers Rescue. Hedgehogs were transported 4 miles by car from the rescue centre to the private garden where they were kept in a rabbit run (2.35L x 1.2W x 0.48H m; predator-proof) on grass, with a small wooden nesting box with hay as bedding used during resting. The enclosure was moved roughly 1m at 90 degrees to a new patch of grass in the same garden before each hedgehog to eliminate potential effects of olfactory cues and ground disturbance from previous individuals. Only hedgehogs brought to the rescue centre as adults were used and the total sample size was N= 16 (females=10, males=6). Hedgehogs were weighed using a digital scale (Nutmeg Home Digital Scales) before and after the experiment (average weight: 981g ± 166g, range: 663g - 1288g). Please see General Methods for more details on the study species.

Urbanisation gradient

Please see General Method Section for more details on the Urbanisation gradient. For chapter 1, the Urban gradient average percentage was 45.3 ± 3.6 (average ± SE, range: 3.73 - 67.28). Figure 1 shows an example of a map for one of the hedgehog locations of the area they were found. Figure 3 shows the distribution of the 16 study hedgehogs along the urbanisation gradient.

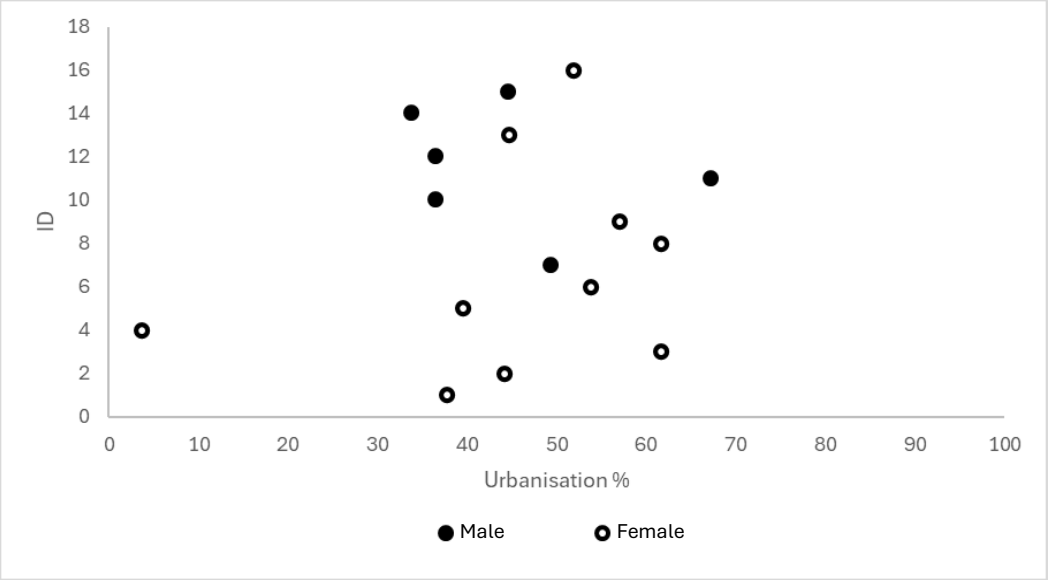

Figure 3: Distribution of the n=16 study hedgehogs along the urbanisation gradient. Each point represents an individual hedgehog and is positioned according to the percentage of urban land cover associated with the found location. Different symbols indicate the sex of each individual. These individuals took part in the cognition section of this chapter.

Boldness

Please see General Method Section for more details for the methods of uncurling. 16 hedgehogs who conducted the cognition test completed this task as well as an additional 11 hedgehogs took part in this boldness test.

Test 1 and 2 were completed twice, first before They are placed inside the enclosure and second after the last problem-solving task (Task C: Alternative entrance). Uncurling, a proxy of boldness, was measured as the latency to uncurl (boldness test 1) and to move away on all four feet (boldness test 2).

Test 3 was conducted with the same set-up as used for the cognition tasks (see cognition methods below). The first interaction with the feeding station was measured as risk taking. The first interaction including a sniff, touching was counted.

Cognition experiment

The cognitive abilities of 16 rehabilitated hedgehogs were assessed using a series of problem-solving tests based on Mazza and Guenther (2021) and Morton *et al* (2023). Hedgehogs were presented with one task per night over consecutive nights (Figure 5). In each task, individuals were required to access a food reward located within a feeding station. Night temperature and sunset time were recorded before each testing night using data obtained from the Met Office (Met Office, 2024).

On the first night, a bowl containing 40g of dry high protein cat food (Lifestage Kitten Dry Food, Chicken with Fish & Rice) was placed on the ground of the enclosure. This acclimatisation period allowed hedgehogs to become familiar with both the experimental environment and the food reward prior to cognitive testing, thereby minimising any potential stress associated with being housed in a novel environment. High protein cat food was selected as it more closely reflects

the natural diet of the European hedgehog, which predominantly is protein rich (Gimmel *et al.,* 2021).

On the second night, the feeding station was presented for the first time to the hedgehog (figure 6a). The feeding station was constructed from transparent plastic (Height =34cm, width = 58cm, depth = 34cm) and contained two alternative entrances (Entrance 1 and 2; each measuring 13 x 13cm). Latency to approach the feeding station was measured as the time between the first interaction with the feeding station until they entered (boldness test 3). An interaction included touching or sniffing any part of the feeding station.

During nights 3, 4 and 5 hedgehogs were presented with three consecutive problem-solving tasks designed to assess cognitive performance. Individual performance was quantified using accumulated attempt time. An attempt was defined as an interaction with the feeding station, including sniffing or touching any part of the apparatus. For each attempt, duration from the initial interaction with the feeding station until the hedgehog either successfully completed the task or stop interacting with the feeding station. When individuals made multiple attempts, the duration of each attempt was summed to provide a total accumulated attempt time, representing the overall effort invested in solving the task. Hedgehogs that did not engage with or attempt a task were excluded from the analysis.

The three cognitive tasks were as follows:

Task A (Lid removal): the feeding station was presented with entrance 1 open and entrance 2 closed, however the food bowl (diameter 7.62cm, weight 112g without food, Figure 6a,) that was covered with a removable lid (diameter 10.16cm, weight 11g), that the hedgehog had to remove to get access to the food (Figure 6d). A hedgehog was successful when they entered the feeding station, went to the bowl and the lid was removed or lifted so the food could be accessed. The timer was stopped when the hedgehog started to eat the food inside the feeding station.

Task B (Door movement): entrance 1 of the feeding station was partially blocked with a section of fence panel which was able to swing to open (L20 x W11 x D1.8cm and weighs 216g when wet, Figure 6b) that needed to be moved to the side to gain access to the feeding station (Figure 6 and 6b). A hedgehog was successful when they were able to get past the fence panel and enter the feeding station. This could be achieved by pushing under the panel or by nudging the panel to the side. The timer was stopped when the hedgehog started to eat the food from the bowl inside the station.

Task C (Alternative entrance): entrance 1 was fully blocked, and the animal needed to access the feeding station via entrance 2 accessible with a ramp (Figure 6d). A hedgehog was successful when they went up the ramp (18cm higher and to the right of entrance 1; height a highest point 16.9cm, at lowest point 1.1cm, width = 13.2, length of ramp = 30.6cm; additional ramp on the inside the station; height at highest point = 16cm, lowest = 1.2cm, width = 13cm, ramp length =26cm) and used the alternative entrance into the feeding station. The time stopped when the hedgehog started to eat the food inside the feeding station.

Each task requires a different motor behaviour to solve a problem and gain access to the food bowl, testing the ability of individuals to adapt to environmental changes. To ensure the animals were not disturbed, no observer was present during the tests and data was recorded via remote video cameras (3 Reolink Go Plus, Wireless, Model SFNS1008). If a task was not completed successfully, the hedgehog received food with lower protein content rather than the reward (20g of low meat protein cat food; Riley's chicken, beef & vegetable dry cat food) at 1am; this happened on 8 occasions. This was the only time a human would disturb but the official experimental has stopped and no other measurements were being made. This lower quality of food was used to improve motivation to participate in the task, which can be a key driver of success in completing cognition tasks (van Horik and Madden, 2016). Water was available *ad libitum* through the test.

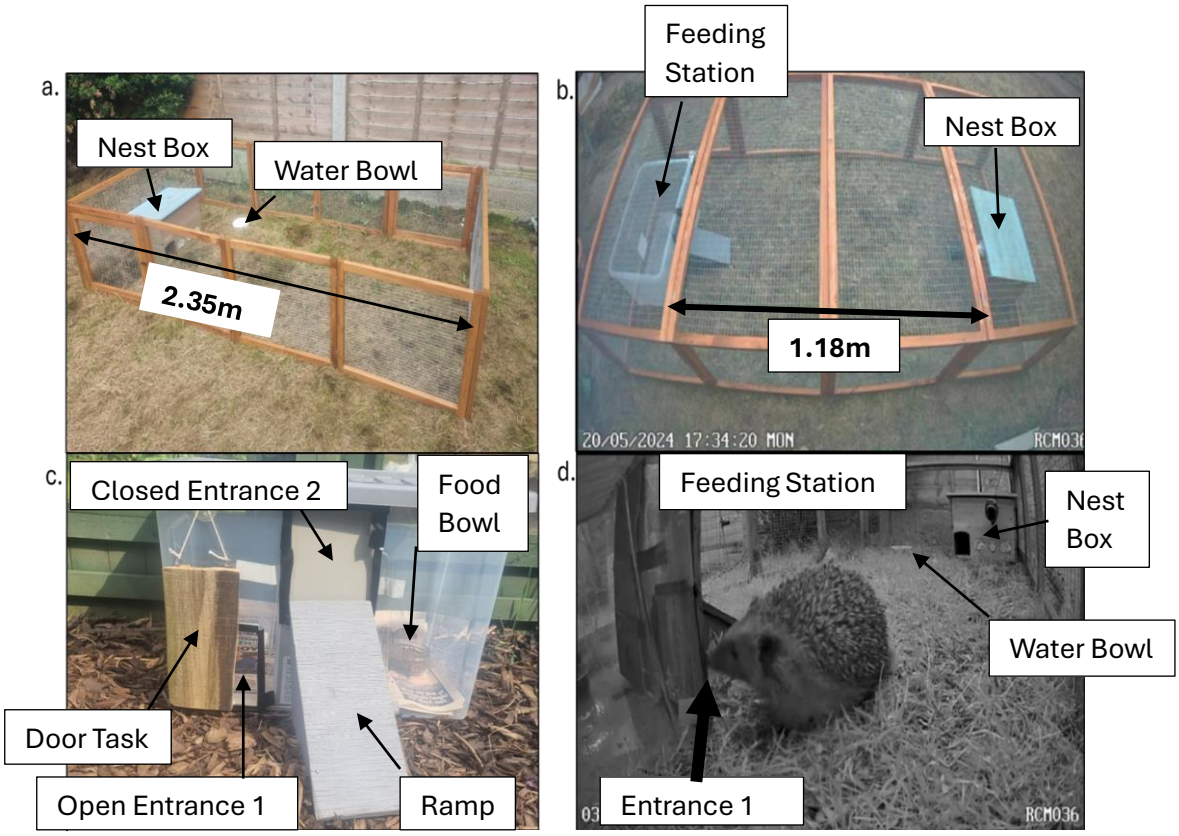

Figure 5: a. the 2.35m enclosure with the nest box and water bowl inside. b. the enclosure with the predator proof lid onto and the nest box, water bowl and feeding station inside. c. the feeding station set up for task 3 (Door Task). d. a still from footage of a hedgehog attempting the Door Task.

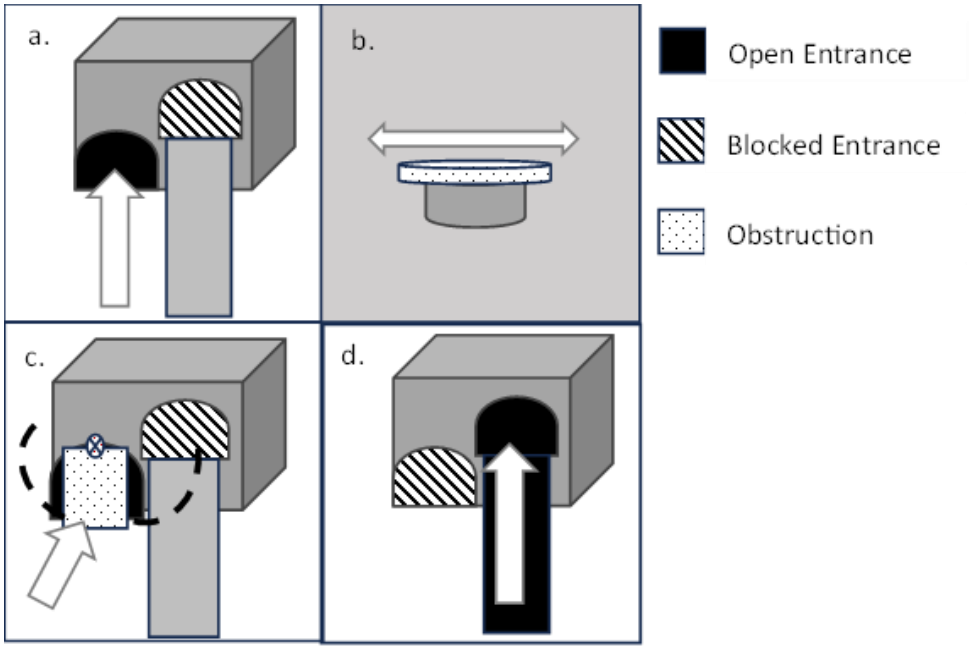

Figure 6: (a) Basic setup of the feeding station with Entrance 1 open and Entrance 2 closed. (b) Lid Removal Task: Inside the feeding station, task requires removal of a lid to access food. (c) Door Movement Task: Wooden panel blocking Entrance 1.
(d) Alternative Entrance Task: Entrance 1 is closed and Entrance 2 is open, accessed via a ramp.

Statistical Analyses

All statistical analyses were conducted in R version 4.5.0 (V4.5.1: R Core Team, 2025).

Boldness

We investigated whether boldness, measured as the latency to uncurl (boldness test 1) and to move away following handling (boldness test 2), was repeatable over time. We estimated repeatability using the R package rptR (v 0.9.23; Nakagawa & Schielzeth 2010; Stoffel *et al*. 2017), specifying individual identity as a random effect in a linear mixed-effects model with Gaussian error distribution. We used 1,000 parametric bootstraps to calculate confidence intervals and 1,000 permutations to determine statistical significance of repeatability estimates. Fixed effects test number and urbanisation level were included where relevant to control for systematic variation. All models were fitted using the lme4 (v 1.1-37, 2025; Bates *et al.,* 2015) and lmerTest (v 3.1-3, 2020; Kuznetsova *et al.,* 2017) packages version and diagnostic plots confirmed that residuals met assumptions of normality. Boldness test 3 was not repeated and thus could not be tested for repeatability.

For all models, model assumptions (linearity, normality of residuals, and homoscedasticity) were checked using qqplots. Summary statistics (minimum, maximum, mean, and standard deviation) were calculated using the dplyr package (v 1.1.4, 2023; Wickham *et al*., 2023), with missing values excluded.

To increase sample size for repeatability analyses, we also re-ran the tests by including a small number of additional hedgehogs from a separate boldness test in which both uncurling and movement were recorded (N=11). Hedgehogs were tested within a familiar room, and both tests were run on the same day, on average 6 hours apart. To correct for differences in the experimental design, the subset origin (dataset 1/2) was included as a factor in the model.

Finally, we also tested the relationship between the three variables that we measured in the three boldness tests (latency to uncurl, latency to move and latency to enter the feeding station) using a Spearman's rank correlation test. In this test only the original dataset was used. Missing values were handled using pairwise deletion, so that each correlation used all available pairs of observations (n=14).

Correlation between Boldness and urbanisation

The effect of urban gradient on uncurling was assessed using a generalised linear model using glm() function (McCullagh and Nelder, 2019), with individual ID included as a random effect to account for repeated measures.

Cognition

We assessed the relationship between the time taken by individuals to successfully complete a given task and the urbanisation level using generalised linear models (GLMs) with appropriate error structures for each response variable. Fixed effects in the full model included sex (male or female), night temperature (°C), time since sunset (minutes), uncurl as a proxy of boldness, and the number of attempts an animal needed to complete a task. Separate models were fitted for each of the three tasks to evaluate task-specific responses across the urban gradient. Individuals which did not completed the respective task were excluded from the analysis. Model selection and diagnostics followed standard procedures to ensure appropriate fit and to verify assumptions (see above). We started with the global model and then removed the variables that were not significant while retaining the urbanisation gradient. The last model for all three tasks only included the number of attempts.

We used a generalised linear mixed-effects model (GLM) with a binomial error distribution and logit link function to test whether the probability of successfully solving the tasks (success/failure) was influenced by the urban gradient level and the different task types (lid removal, door movement, and alternative entrance).

The fixed effects included urbanisation level and task type. Individual identity was included as a random effect to account for repeated measures from the same individuals. The model was fitted using the glmer function from the lme4 package (v 1.1-37; Bates *et al*., 2015). The binary response variable indicated whether an individual successfully completed a task (1 = success, 0 = failure). Model assumptions were checked by examining residual plots and assessing overdispersion. No significant deviations from model assumptions were detected, confirming the suitability of the model.

Results

Boldness

Uncurling behaviour after handling was found to differ significantly between individuals and was repeatable 156.8 ± 13.0 (mean ± SE; range: 47.33 – 300 s). The repeatability of uncurling was 0.469 (SE ± 0.155), with a 95% confidence interval of 0.121, 0.726. This indicates that approximately 47% of the variance in uncurling could be attributed to consistent differences among individuals. The result was statistically significant based on both a likelihood ratio test (p = 0.012) and a permutation test (p = 0.011), suggesting that individual hedgehogs consistently differed in their uncurling behaviour across repeated measures. Re-running the test with the bigger dataset improved repeatability. We Included an additional 11 hedgehogs from a separate test increased the sample size to n=27. For the larger dataset, repeatability for uncurling behaviour was 0.47 (SE ± 0.16), with a 95% CI of 0.09, 0.72. The result was significant (permutation: p = 0.013).

Moving after uncurling (n=16) was significantly repeatable across individuals, with the estimated repeatability of 0.41 (SE ± 0.19) with a 95% confidence interval of 0, 0.73 with permutation of 0.038 and respectively p=0.048. When adding an additional 11 hedgehogs to make the sample size 27, moving after uncurling was not Repeatable and was non-significant 0.121 (SE ± 0.144), with a 95% confidence interval of 0, 0451 (likelihood ratio test, p = 0.303, permutation

test p = 0.266). The relationship between urbanisation level and boldness measures in hedgehogs was measured. None of the behaviours varied significantly with urbanisation (all p>0.05) (Figure 7).

We also assessed boldness as the time it took hedgehogs from their first approach to the feeding station until they entered the feeding station. It took hedgehogs 13.17 ± 6.53 minutes (mean ± SE; range: 0.1 -71.16 mins) to have their first interaction with the feeding station until they entered the station. Only

14 hedgehogs completed this task. Using a linear model, we found no significant association between the latency to uncurl or move and the time it took a hedgehog to enter the feeding station for the first time ($F(1,14) = 0.441$, $p = 0.517$ and $F(1,14) = 0.210$, $p = 0.654$).

The Spearman's rank correlations test revealed that uncurling behaviour was positively correlated with the latency to move ($p = 0.568$, $p = 0.034$). Uncurling behaviour was negatively correlated with the latency to approach the feeding station ($p= -0.627$, $p = 0.016$). The latency to move and the latency to approach the feeding station were negatively correlated, but this relationship was not significant ($p = -0.398$, $p = 0.159$).

To explore the potential influence of habitat urbanisation on boldness and task performance, we fitted separate models for each behavioural measure. None of these models revealed significant effects indicating no detectable relationship between urbanisation level and these behavioural traits or task outcomes. Further, we examined whether urbanisation influenced latency to approach the feeding station, a potential indicator of boldness. Although the mean latency was 8.27 ± 25.82 minutes (mean ± SE, range: 0.13 – 169.65 minutes), there was no significant effect of urban gradient on this measure ($F(1,58) = 2.47$, $p = 0.121$). We found no significant effect of urban gradient level on uncurling behaviour ($F(2,13) = 0.205$, $p = 0.817$), indicating that hedgehog boldness did not vary consistently with urbanisation in our sample.

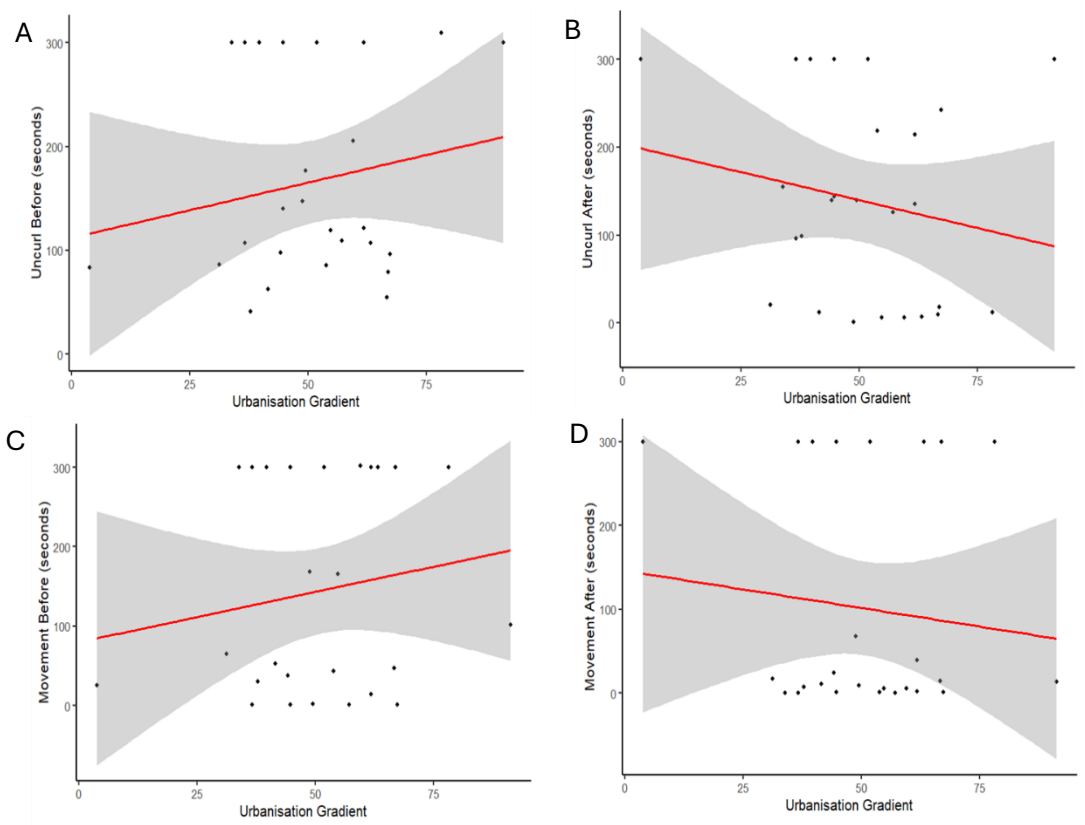

Figure 7: Relationship between urbanisation level and boldness measures in hedgehogs. None of the behaviours varied significantly with urbanisation (all $p>0.05$). A: Seconds it took each individual to uncurl before completing any task along the urban gradient. B: Seconds it took each individual to uncurl after they had completed the last task. C: Seconds it took each individual to Move before completing any task along the urban gradient. D Seconds it took each individual to Move after they had completed the last task.

Cognition

Neither the urban gradient (β = -0.004 ± 0.071, z = -0.06, p = 0.954, N=16) nor the type of task (β = -0.604 ± 0.432, z = -1.40, p = 0.162, N=16) had a significant effect on task success. The result did not change when we re-ran the test without including individuals that did not attempt the task (urban gradient: β = 0.007 ± SE = 0.037, z = 0.19, p = 0.848, task: β = -0.326 ± SE = 0.380, z = -0.86, p = 0.392).

For Lid removal task, on average it took 1.5 ± 1.3 mins (mean ± SE; range: 0.2 – 4.5 mins, N=15 individuals attempted the task) to solve the task. One individual needed 10 attempts; the other 14 individuals took 1 attempt to pass. A generalised linear model including urbanisation, sex, night temperature, activity before sunset and number of attempts as predictors. The final model included the urbanisation gradient as well as the number of attempts and explained 66.17% variation (adjusted R^2 = 0.4737). Hedgehogs from areas with higher levers of urbanisation required significantly more attempts to successfully complete the task than individuals from less urbanised areas (β = 23.39 ± 0.96 SE, p = 0.028) (Figure 8). No other predictors had significant effects.

Individuals on average took 4.6 ± 5.0 mins (mean ± SE; range: 0.4 - 17.7 mins) to solve the door movement task (N=14 individuals attempted the task). 12 individuals passed (range: 1 - 10 attempts and passed) with 2 failing (range: 12 - 18 attempts but failed). The final model included the urbanisation gradient as well as the number of attempts. Urbanisation level had no significant effect on the number of attempts (Figure 8) (β = 4.20 ± 3.55 SE, p = 0.261) however number of attempts had a positive effect (β = 40.89 ± 10.28 SE, p = 0.002)

Individuals took 6.3 ± 4.8 mins to solve the alternative entrance task (mean ± SE; range: 0.6 – 18.7 mins, N=15 individuals attempted the task). 12 individuals passed (range: 1 - 13 attempts to pass) with 3 failing (range: 2 - 12 attempts but still failed) the task. The model included urbanisation level and number of attempts. Its showed only number of attempts was significantly predicted the number of attempts (β = 62.04 ± 12.75 SE, p <0.001. Urban gradient had no significant effect (β = - 5.08 ± 3.11 SE, p = 0.129), please see figure 8.

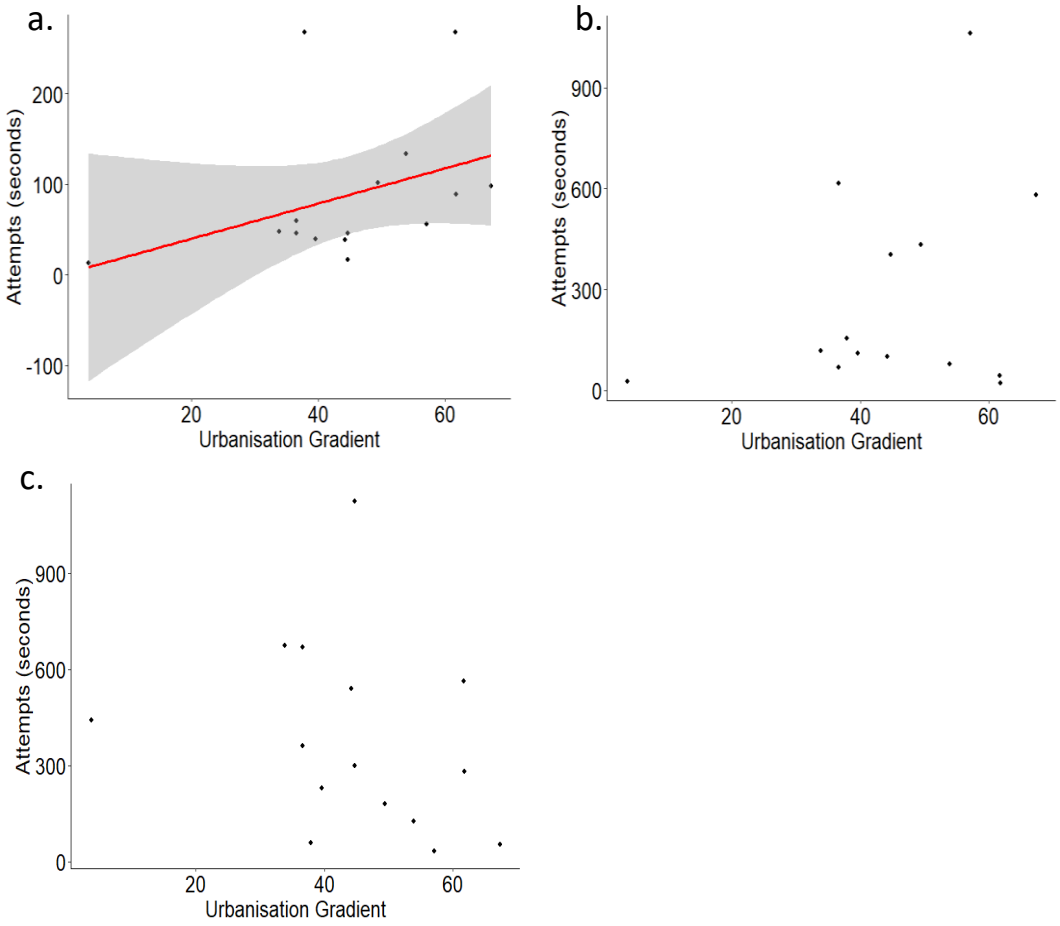

Figure 8: Generalised linear mixed-effects model (GLM) showing the accumulative number of seconds it took each individual to complete the task along the urban gradient score (n=16). A. Lid Removal Task B. Door Movement Task. C. Alternative entrance Task.

Discussion

The aim of this study was to test whether risk taking, and cognition abilities of European hedgehogs differ in relation to the urbanisation level of their habitat. Our overall hypothesis that urban adaptors are bolder and have faster cognitive abilities than animals living in less urbanised areas was not supported by our findings. We found that boldness of hedgehogs in our population did not differ from habitats of differing urbanisation level. Furthermore, the urban gradient also had no significant effect on task success. However, when considering performance across the individual tasks, hedgehogs from more urbanised habitats took significantly longer to successfully complete the first cognitive task, which required them to remove the lid from the food bowl. In contrast, urbanisation level was not associated with the time taken to complete the door movement or alternative entrance task.

Our findings for cognition indicate that individual variation in problem solving success among hedgehogs was only partly influenced by urbanisation level. Across all tasks, there was no significant effect of urban gradient or task type on the likelihood of task completion, suggesting that cognitive performance in these problem-solving tasks did not differ between individuals from more or less urbanised environments. This was consistent even when excluding individuals that failed to attempt the tasks, highlighting that task engagement alone did not explain performance differences. Hedgehogs from more urbanised habitats took significantly longer to successfully complete the first task, which required them to remove the lid from the food bowl. This suggests when individuals have to complete physical problem-solving tasks that involve object manipulation, hedgehogs in more urbanised environments were less efficient at solving this novel problem. One explanation for this may be that in urban areas, hedgehogs may be more used to convenient food such as food from feeding stations in private gardens (Murray *et al.,* 2016) whereas less urbanised hedgehogs may depend more on naturally occurring food resources obtained through foraging. The relationship between urbanisation and performance was not evident in the other two tasks in which they needed to move pasted an obstacle (door

movement) or solve a navigation problem and find an alternative entrance. These results suggest that while some tasks may reveal an urban-related gradient in cognitive efficiency, this effect is not consistent across different types of cognitive challenges.

Unlike existing literature (Lee *et al.,* 2021; Vincze *et al.,* 2022), we found that higher levels of urbanisation were associated with poorer performance in the first cognitive task, which may be linked to the availability of supplementary food in urban gardens (Steyaert *et al.,* 2014; Fehlmann *et al.,* 2021) and the fact that hedgehogs preferentially use gardens offering artificial feeding (Gazzard *et al.,* 2022; Turner *et al*., 2022). The extended latencies observed on the first task may reflects animal's initial caution and reluctance to engage with novel objects, rather than differences in cognitive or problem-solving abilities. Previous studies have shown that approach hesitation can strongly influence first trail performance across taxa (Benson-Amram and Holekamp, 2012; Griffin and Diquelou, 2015; Griffin *et al.,* 2015; Thornton and Lukas, 2012). Racoons (*Procyon lotor*) often hesitated before engaging with a puzzle box and the success probability increased over trials (Lazure and Weladji, 2024). This is in line with a study by Mazza *et al.,* (2020) that found that rural animals in captivity were consistently shyer and less exploratory than they were in the wild. It suggests that urban populations may be more flexible in their behaviour which could explain the variable responses we saw across tasks in our study. Additionally, individual hedgehogs varied widely in the time they took to solve tasks and in the number of attempts needed. This suggests individual differences in problem-solving behaviours or motivation. Nevertheless, these differences were not consistently predicted by urbanisation level or boldness measures. The lack of consistent cognitive differences across habitats contrasts with findings in other urban-adapted species, such as great tits (*Parus major*), where urban individuals often outperform rural conspecifics in problem-solving tasks (Audet *et al.,* 2015). This may suggest that urban hedgehogs do not face the same cognitive pressures as other species or that urbanisation has not yet strongly shaped cognitive traits in this population.

One important limitation of this study is that the urbanisation gradient was relatively narrow, with the majority of individuals originating from moderately urbanised habitats and very few represented extremes of the gradient. In particular, no truly rural hedgehogs were included in this study. This was largely a consequence of the sampling strategy, as individuals were sourced from a rescue centre rather than being actively sampled across predetermined urbanisation categorised. Although this approach provided access to wild hedgehogs suitable for behavioural testing over a few days, it limited the representation of individuals from higher and lower urbanised areas. The limited variation in urbanisation levels may therefore have reduced the ability to detect relationships between urbanisation, cognition and boldness. Ecological studies have demonstrated that behavioural responses to urbanisation are often species specific and may only become apparent when individuals are sampled across sufficiently broad urbanisation gradients (McDonnell and Hahs, 2008). Consequently, stronger contrast between habitat types are likely to provide greater power to detect behavioural differences associated with urbanisation. It is therefore possible that the absence of the significant effects observed throughout this study reflects limitations of the urbanisation gradient rather than a true absence of behavioural differences among individuals.

While boldness was not significantly different between hedgehogs from different urbanisation levels, our data revealed consistent individual differences in boldness, measured as latency to uncurl, between individuals. Additionally, we found no evidence that boldness was linked to how well hedgehogs performed in problem-solving tasks. Urbanisation also did not seem to affect boldness or task performance. This suggests that while some hedgehogs were consistently bolder than others, this did not help them solve the task faster or reflect the type of habitat they lived in. Our findings are supported by other studies such as Mazza and Guenther (2021) who similarly reported no differences in boldness between rural and urban individuals of 24 rural and 24 urban voles (*Microtus arvalis*) as well as 27 rural and 15 urban striped field mice (*Apodemus agrarius*). However, it is acknowledged that the main factor affecting our results may be the lack of

diversity between urban areas as all individuals used in this study came from one rescue centre and thus from similar environments.

Although boldness was not associated with urbanisation level or latency to approach the feeding station in our study, previous research has suggested that food availability can influence boldness, with individuals in more resource rich environments often display higher levels of bold behaviour (Jolles *et al.,* 2016). Our study was conducted in hedgehogs in good body condition after a stay at a rescue centre, hunger may not have been a strong motivator for these individuals.

The absence of a clear relationship between boldness and cognitive performance suggests that these traits may be shaped by different selection pressures and may not consistently covary. While some studies have found links between personality traits like boldness and cognitive ability (Sih and Del Giudice, 2012; Griffin *et al.,* 2015), other studies report weak or inconsistent relationship (Carter *et al.,* 2013; Dougherty and Guillette, 2018). Boldness may not always confer cognitive advantages, particularly in tasks that require persistence or inhibitory control rather than exploratory behaviour. Furthermore, individual differences in motivation, past experiences with feeding stations or different types of environments may influence performance independently of personality traits (Van Horik & Madden, 2016).

Urban and suburban habitats often feature a high density of supplementary feeding (Tryjanowski *et al.,* 2015; Gimmel *et al.,* 2021; Gazzard *et al.,* 2022) which can provide frequent opportunities for birds and hedgehogs to encounter and interact with novel food resources. Hedgehogs are more likely to be present in gardens where food is supplied regularly, suggesting that the availability of supplementary feeding can influence their activity patterns and habitats use (Gazzard *et al*., 2021). Consequently, individuals from more urbanised habitats may have different experiences of food resources compared to those relying in natural foraging opportunities, which could influence how they engage with novel food related tasks. Behavioural responses to cognitive tests may therefore

reflect differences in environmental experiences in addition to underlying personality traits.

My findings do not provide consistent support for the hypothesis that urban hedgehogs are bolder and have enhanced cognitive abilities than hedgehogs from less urbanised environments. Neither boldness nor task success appeared to be influenced by the urbanisation level. However, hedgehogs from more urbanised areas did take longer to complete the removing a lid from a food bowl task. Collectively, these findings suggest that urban adaption in European hedgehogs is unlikely to be driven solely by enhanced boldness or cognitive abilities. Instead, urban living may shape behavioural responses in more subtle and task specific ways, highlighting the complexity of behavioural adaptions in urban wildlife.

Chapter 2

Metabolic Rate Measurement in European Hedgehogs (*Erinaceus europaeus*)

Abstract

Urbanisation is rapidly altering landscapes worldwide and can influence the physiology and behaviour of wildlife. Metabolic rate is key physiological trait linked to life-history strategies, behavioural variation and energetic requirements. Urbanisation may influence metabolic rates by altering the energetic demands experienced by individuals through changes in habitat structure, resource availability and the energetic cost associated with foraging and movement, potentially shaping how individuals acquire and utilise energy within human modified landscapes. Understanding how animals adjust their energy use in response to urban environments is important for predicting their ability to persist and adapt to increasingly urbanised habitats. This study investigated whether variation in urbanisation is associated with differences energy expenditure in European hedgehog *(Erinaceus europaeus)*. We measured resting metabolic rate as oxygen consumption via flow-through respirometry in 13 (males= 9, females = 4) hedgehogs under laboratory conditions and assessed the relationship between the urbanisation level of their habitat and their metabolism. Furthermore, we also tested whether individual metabolic rate was influenced by consistent differences in personality, i.e. boldness. Our data suggest that while sex had a significant influence, neither boldness, nor the urbanisation level of the individual's habitat was a significant predictor of variations in metabolic rate.

Introduction

Urbanisation is rapidly transforming natural landscapes into human dominated environments, exposing wildlife to novel ecological and physiological challenges (Gallo *et al.,* 2019; Zhao *et al.,* 2020). These changes can alter the energetic demands experienced by individuals through differences in resource availability, habitat structure and movement requirements. Metabolic rate is a key physiological trait that determines how animals acquire, allocate and utilise energy and may therefore influence an individual's ability to persist within urban environments (Hou *et al.,* 2008; Careau and Garland, 2012; Réale *et al.,* 2010). Metabolic rate represents the rate at which an individual expends energy to maintain physiological process, including cellular maintenance, thermoregulation and activity. Variation in metabolic rate can influence how animals allocate its energy between competing demands such as growth, reproduction and movement which can affect how an animal, cope with environmental stressors, avoid predators and gather resources and therefore affects survival and fitness of individuals (Møller, 2009; Okuyama, 2015; Schmitz *et al.,* 2017).

A key component of metabolic rate is basal metabolic rate (BMR) which represents the minimum energy expenditure required to maintain essential physiological functions in a resting, fasting and thermoneutral conditions (McNab, 2002). Although BMR reflects only a baseline measure of energy expenditure, it provides insight into underlying physiological variation among individuals and populations (McNab, 2002). Differences in BMR may therefore influence how individuals respond to environmental challenges by affecting energetic requirements and the amount of energy available for other biological functions, including reproduction, immune function and behaviour (Speakman and Król, 2010). In urban environments, where resource availability, habitat structure and disturbance differ from natural habitats, variation in metabolic requirements may influence energetic demands and potentially shape metabolic strategies in wildlife populations (McKinney, 2002; Lowry *et al.,* 2013).

The energy expenditure of urban living wildlife remains poorly understood, yet urban environments introduce very different environmental pressures that likely

affect the energy budgets of wildlife (Lowry *et al.,* 2012). Urbanisation can alter resource availability and foraging opportunities through habitat fragmentation and supplementary feeding, which may influence individual body mass, body condition and energetic requirements (Tranquillo *et al.,* 2023a). This can, for example be due to reduced predation pressure in urban areas (Eötvös *et al.,* 2018) which can lower acute energetic demand associated with vigilance and fight-or -flight response (Clinchy *et al.,* 2012). Furthermore, research has found wildlife adapts their behaviour according to food abundance which is a major factor in how a wild animal uses their home range (Jones and Reynolds, 2008; Reynolds *et al*., 2017; Hansen *et al.,* 2020). Access to supplementary food sources such as garden feeders or anthropogenic waste may thus reduce the need for extensive foraging (Careau and Garland, 2012; Orros and Fellowes, 2015) and urban animals may thus have lower locomotion-related energy requirements than rural counterparts (Herr *et al.,* 2008). On the other hand, urban areas can also introduce novel stressors such as noise, night pollution and frequent human disturbance (Raap *et al.,* 2017; Kunc and Schmidt, 2019). This may elevate physiological stress responses and increase energetic demands (Barnett *et al.,* 2016; Kleist *et al.,* 2018).

The “pace of life syndrome” proposes that individual differences in behaviour, physiology and life history are linked along a slow fast continuum, where individuals with a higher metabolic rate are typically associated with a fast pace of life characterised by earlier reproduction, shorted lifespan and often also a bolder personality (Réale *et al.* 2010; White and Kearney, 2012). However, evidence suggests these relationships can be context dependent. For example, great white-toothed shrews (*Crocidura russula*) living in urban areas were found to be bolder and more exploratory than their rural counterparts but exhibited lower resting metabolic rates, suggesting a dissociation between behaviour and metabolism in environments with reduced predation pressure and abundant food resources (Oliveira *et al.,* 2020). Similarly, studies on Merriam’s kangaroo rats (*Dipodomys merriami*) have found that boldness and aggression were not linked to high metabolic rates in suburban environments (Hurtado and Mabry,

2017). These findings indicate that environmental factors such as urbanisation, food availability and predation risk may modify the association between boldness, metabolic rate and life-history strategies and emphasise the need to understand how urbanisation is affecting endothermic species. Addressing this question across a broader range of taxa is not only important for advancing ecological theory but also for informing conservation strategies as wildlife increasingly inhabits human dominated landscapes.

Hedgehogs in the UK have a declining population in rural areas but have stabilised numbers in urban areas (Hubert *et al.,* 2011; Wembridge *et al.,* 2022; Gazzard *et al.,* 2022). This suggests that hedgehogs may be adapting to urban life, however the behavioural and physiological adaptions that might enable hedgehogs to thrive in cities remain poorly understood. Therefore, in this study, we investigated the link between consistent differences in risk taking behaviour (i.e. uncurling as a proxy of boldness) and energetic needs of hedgehogs along an urban gradient. For urban wildlife, metabolic variation may be particularly important because individuals must balance the energetic costs of movement through fragmented landscapes, thermoregulation and foraging against availability of anthropogenic resources. We hypothesise that individuals from more urbanised habitats have higher energetic needs and are bolder than animals inhabiting less urbanised areas. To test this hypothesis, we quantified metabolic rate and risk-taking abilities of rescued hedgehogs prior to their return to the wild.

Methods

Ethics

Please see General Method Section

Metabolic measurements

We measured metabolic rate in 13 Western European hedgehogs (4 females, 9 males) at a Hedgehog Rescue Centre in the UK in November 2024 and January 2025. Please see General Method Section for more details.

Individuals remained in their familiar holding cage during the experiment (615 x 320 x 310 mm) to minimise stress associated with relocation. Each cage was divided into two sections: one sections contained food and water (375 x 320 x 310 mm) and the other section was fitted with a modified plastic nest box with bedding (hay), which acted as the metabolic chamber (Figure 9).Individuals were able to freely enter and exit the nesting box throughout the measurement period. Similar approaches have previously been used to measure metabolic rate for wild animals, including wild swallows (Wellbrock *et al.* 2022). Metabolic rate was estimated as oxygen consumption (VO_2) by measuring the difference in O_2 concentration between incurrent and excurrent air from the animals' nest boxes. Measurements were conducted using an oxygen analyser (FoxBoxC, Sable Systems International, USA), with airflow maintained at approximately 1500 $mL \cdot min^{-1}$ for both baseline and animal channels. A gas multiplexer (RM8, Sable Systems International, USA) was used to alternate between baseline (i.e. Nowack *et al.,* 2020) air and air drawn from the nest box, with baseline measurements recorded every 5 minutes (Please see figure 9 and 10). Fresh air was pulled from the outside into the holding cage outside of the metabolic chamber. Metabolic rate for each individual was monitored for 4 to 6 hours during the resting period of the animals between 12pm and 5pm. Measurement time varied due to the measurement taking place inside an active rescue centre meaning external factors affected measurement times. The metabolic chamber was connected to the analyser (pull mode; order: metabolic chamber, pump, Scrubbers, needle valve, flow meter, oxygen analyser) with airtight tubes (Figure 10). Air was dried and scrubbed of CO_2 before entering the analyser. Oxygen consumption was recorded at a measuring interval of one sample every 10 seconds. For each bout, we calculated the metabolic rate by selecting the lowest stable 10-minute period of oxygen consumption within the bout. This approach reduces the influence of short-term fluctuations or activity related spikes and provides a more accurate estimate of the animal's resting energy expenditure.

During the measurements, ambient temperature inside the holding cage was recorded using an iButton (Hygrochron iButtons/DS1923, Dallas Semiconductor,

USA; programmed to log every 30 minutes) which was placed on top of lid of the modified nest box. Room temperature was measured using a room thermometer at the beginning and end of each metabolic rate recording session. Temperature was recorded immediately after data was being measured and again upon end of recording, approximately 4-6 hours later. The average room temperature in was 13.7 ± 0.9 °C (Average ± SE, range = 7.1 - 18.4). The average cage temperature using the ibutton was 15.2 ± 0.7 °C (Average ± SE, range = 10.0 - 19.4).

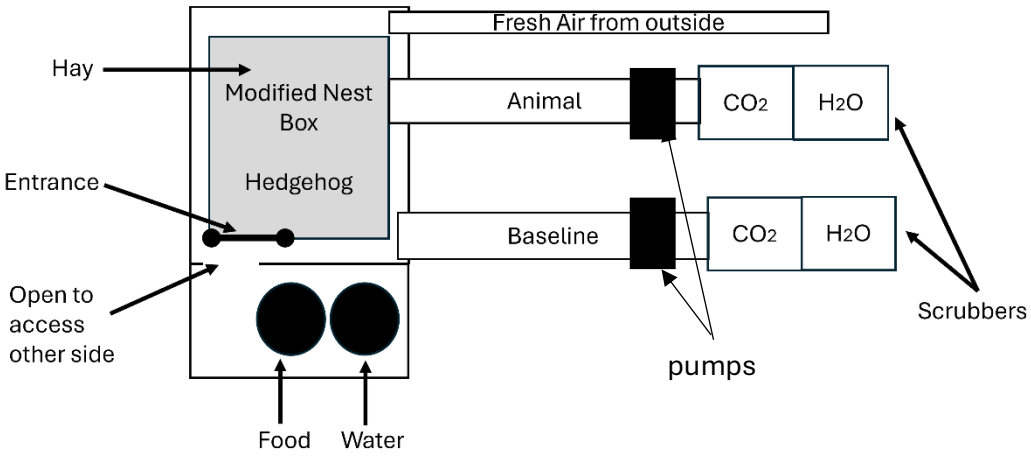

Figure 9: Diagram showing the Metabolic Champer. A modified nest box was filled with bedding for the hedgehog to demonstrate natural day time behaviour, sleep. The hedgehog could leave at any point through the entrance. They had access to food and water at all ties. Air was pulled from the modified nest box. Baseline air was pulled from the metabolic chamber.

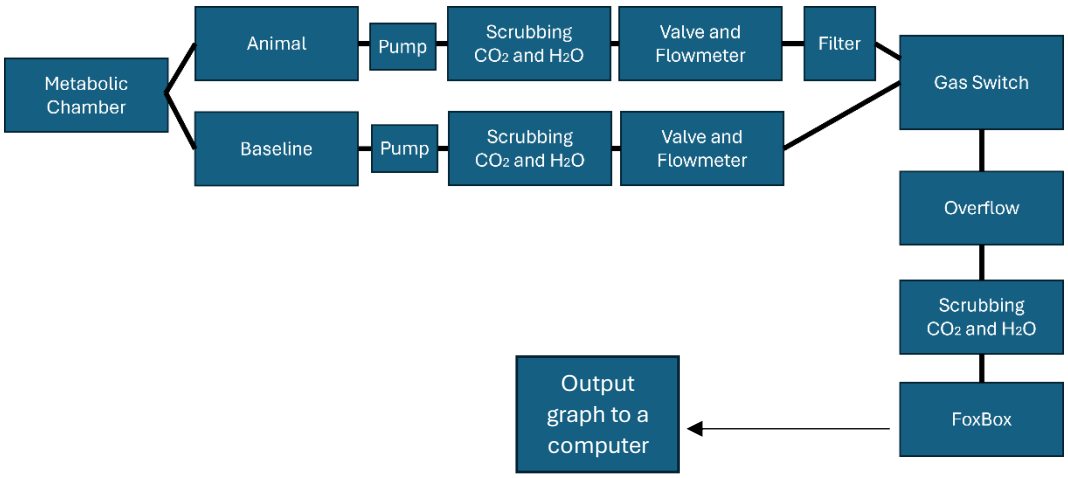

Figure 10: Diagram showing the whole open flow respirometry process.

Boldness

Please see General Method Section

Urbanisation

Please see General Method Section for more details (n=13) 55.95 ± 4.77 % (average ± SE, range: 31.22 - 91.29). Please see figure 11.

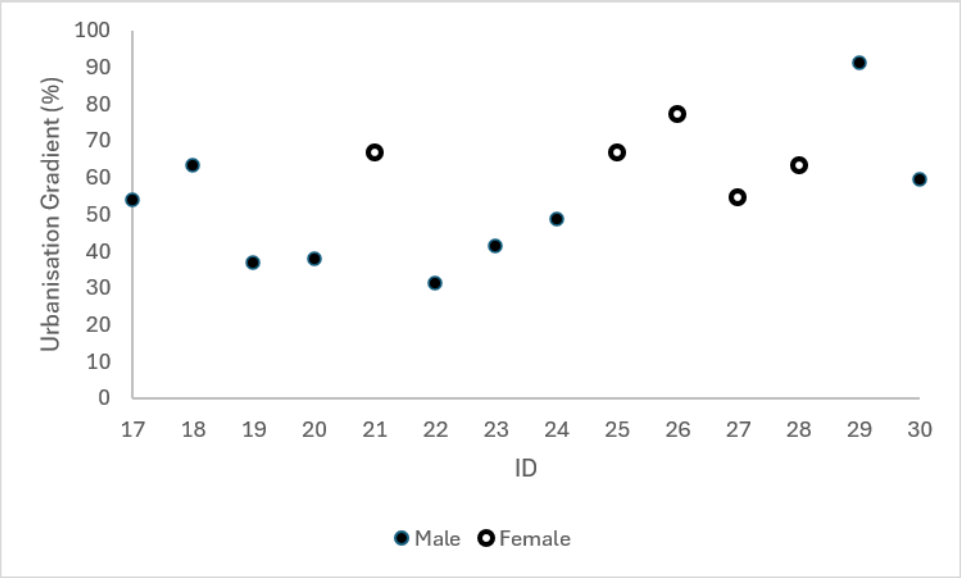

Figure 11: Distribution of the n=14 study hedgehogs along the urbanisation gradient. Each point represents an individual hedgehog and is positioned according to the percentage of urban land cover associated with the found location.

Data analysis & Statistical analysis

All statistical analyses were conducted in R (V4.5.1, 2025). Data are presented as mean and SE.

Repeatability

Please seen General Method Section for more details.

Metabolic rate

Stepwise model selection using Akaike's Information Criterion was used to identify the most informative predictors of metabolic rate from an initial set including boldness (uncurl from before the test, N=11), sex, body mass, urban gradient and ambient temperature. The sample size for the model selection was reduced to 11 individuals due to the lower sample size for the boldness variable. Model assumptions of normality, homogeneity of variance and independence were checked using diagnostic tests. No violations were detected.

For metabolic rate, we worked with two parameters. First, we calculated the absolute minimum metabolic rate by identifying the lowest 10-minute average of oxygen consumption value observed during the measurement period. This approach reduces the influence of short-term fluctuations or drops that may not reflect the animal's baseline (Chabot *et al.,* 2016). We also calculated the mean of the three consecutive lowest bouts (i.e. average resting metabolic rate) which helps provide a more robust measure that accounts for consistency over a time rather than relying on a single minimum value. Minimum metabolic rate was strongly correlated with the average of three lowest metabolic rates (Spearman rank test, $p=0.962$, $p<0.001$), indicating strong agreement between the two measures (Killen *et al.,* 2021). We thus only report the data for the model including average of the three lowest metabolic rate below. Hedgehogs taking part in Metabolic Rate reading are ID 17 – ID 29 excluding ID 25. Figure 12 shows an example of the output given from the software ExpeData to measure metabolic rate. The peaks show the baseline. Measurements between peaks provided a metabolic reading, this calculation between the peaks gave the bouts. This is repeated between all bouts. When a measurement between peaks dropped, indicated the hedgehog left the nest box and the reading between these two peaks were excluded.

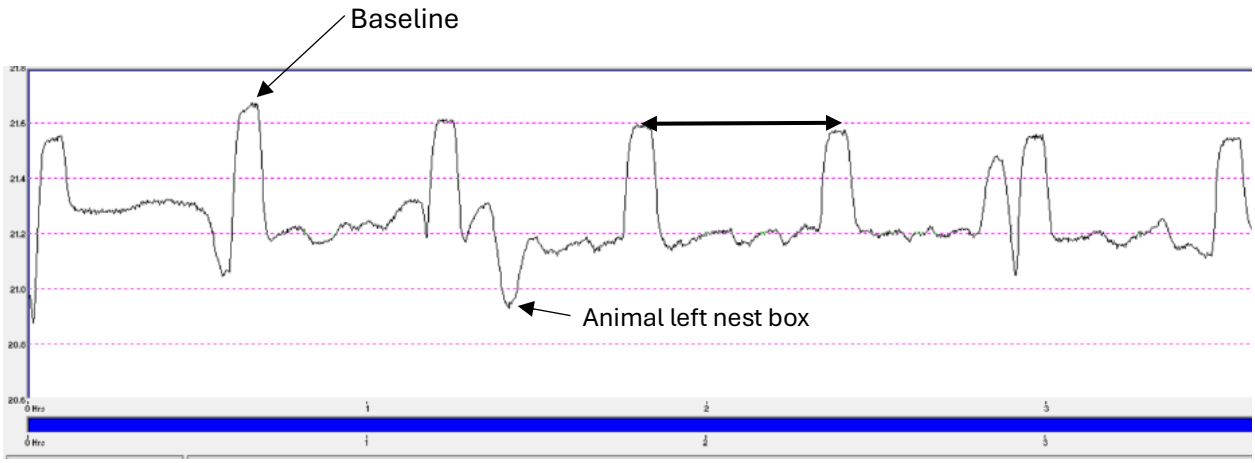

Figure 12: Example of the output given from the software ExpeData to measure metabolic rate. The peaks is the baseline reading. Measurements between peaks provided a metabolic reading. When a measurement between peaks dropped, indicated the hedgehog left the nest box and the reading between these two peaks were excluded.

As ambient temperature was recorded using two methods, we first tested whether the two measurements (room and cage temperature) were correlated using a Spearman rank correlation. Temperature recorded by iButton in the cage was strongly correlated with room temperature ($p=0.96$, $p < 0.001$). We thus only included the cage temperature in the model.

To identify the most informative set of predictors we applied stepwise model selection based on Akaike's Information Criterion (AIC) (Akaike, 1974) using stepAIC function from the MASS package (7.3-65, 2025: (Ripley and Venables, 2009). Following recommendations that models within $\Delta AIC \leq 2$ are similarly supported, we selected the most parsimonious model excluding predictors that contributed little explanatory power.

Metabolic rate measurements were successfully obtained for nine of the eleven individuals. Data from two individuals were excluded due to a technical malfunction of the respirometry system that produced unreliable metabolic rate recordings.

Results

Repeatability

The time that it took the individuals to uncurl varied among individuals and showed moderate repeatability across repeated trials (N=9; R= 0.486 ± SE 0.243). The 95% confidence interval ranged from 0 to 0.842 (permutation p = 0.084).

The time it took a hedgehog to move after being placed on their backs was not repeatable across trials (N=9; R= 0 ± SE 0.184). The 95% confidence interval ranged between 0 to 0.621 (permutation p = 1).

In contrast, latency to uncurl showed moderate repeatability and was therefore selected as the measure of boldness for all analysis.

Metabolic Rate Variation

The average body mass of hedgehogs was 829 ± 54 g (average ± SD, range = 566 - 1206g, N=13; females: average ± SE, range = 708 – 1206g, males: average ± SD, range = 566 - 962g).

Minimum resting metabolic rate varied among individuals, ranging from 2.35 to 7.84 ml O_2 g^{-1} h^{-1} (mean ± SD, 4.76 ± 0.492), average resting metabolic rate (average of the three lowest consecutive measurements) displayed a wider range from 2.58 to 10.73 ml O_2 g^{-1} h^{-1} (mean ± SD, 5.52 ± 0.699).

Stepwise model selection identified a model including urbanisation level, body mass, and sex as the best-supported model, explaining 54% of the variation in metabolic rate. However, the urbanisation level was not a significant predictor (urbanisation: β = 0.043 ± SE 0.027, *p* = 0.16) and only increased the model slightly (Table 1) as the model including only body mass and sex explained 46% of the variation. Body mass and sex had a significant effect on metabolic rate (body mass: β = 0.007, p = 0.055; sex: β = 2.85, p = 0.042) with males having higher metabolic rates than females (Figure 13). Including cage temperature and boldness did not improve the model (Table 1). As boldness was not included in

the final model, we re-ran the model with the full sample size (N=13), this did not lead to any changes in the overall outcome (F 3,9 = 4.32, p = 0.038).

Model	Predictor	AIC	Delta AIC
Average MR ~ urbanisation gradient + body mass + sex		10.788	0
	+ boldness	11.564	0.776
	- urbanisation level	12.168	1.38
	+ cage temp	13.53	2.74

Table 1: Stepwise model selection using Akaike's Information Criterion was used to identify the most informative predictors of metabolic rate from an initial set including boldness (uncurl from before the test, N=11)

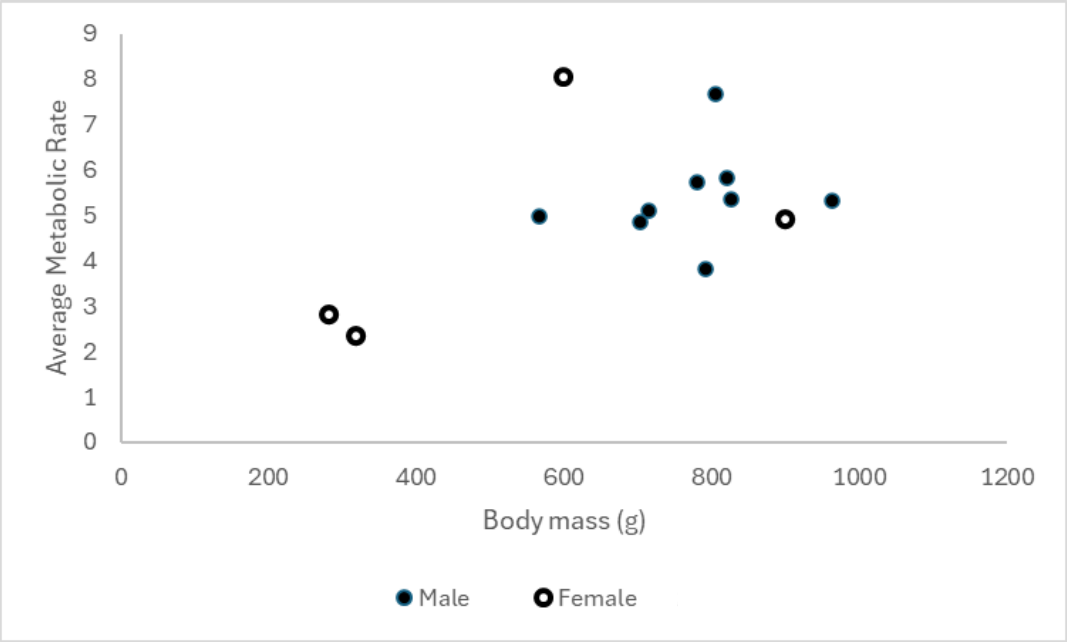

Figure 13: Relationship between body mass and metabolic rate (MR). Filled circles represent males (n = 9) and open circles represent females (n = 4). Each point represents a single individual.

Discussion

In this study, we hypothesised that hedgehogs from a high urbanised area would have a higher energetic demand than individuals from less urbanised areas. We found that metabolic rate was not affected by the level of urbanisation in an individual's habitat. Our results also showed sex and body mass were important predictors of metabolic rate, with males and larger individuals exhibiting higher rates. Interestingly, uncurling did not influence the metabolic rate, suggesting that personality and energy expenditure are not linked for hedgehogs, as would be predicted based on the pace of life concept, or that our sample size was too small to detect such a relationship.

Although our findings did not reveal a significant relationship between urbanisation and metabolic rate, similar studies have previously demonstrated that the urbanisation level and habitat features can influence small mammal energetic responses (Merritt and Zegers, 2014; Wist *et al.,* 2023). For example, urban squirrels exhibited a reduced metabolic response to colder ambient temperatures compared to counterparts that were living in woodland (Wist *et al.,* 2023). Similarly, Pettett *et al.* (2017) investigated the daily energy expenditure of European hedgehogs in rural UK landscapes, with a focus on predation risk. Using the doubly labelled water method, they measured daily energy expenditure across four predominantly arable sites, comparing areas with and without badger (*Meles meles*) presence as a proxy for predation risk. They found that hedgehogs used more energy in areas with higher predation risk, suggesting that environmental pressures, such as the threat of predators, can significantly influence small mammal energy budgets in the wild. However, the absence of a relationship between urbanisation and metabolic rate in my study differs from Pettett (2017). This study measured different aspects of energetic expenditure. Daily energy expenditure reflects the cumulative energetic costs of movement, foraging and behavioural responses to environmental pressures in free ranging individuals, whereas metabolic rate using respirometer provides a measure of baseline energetic expenditure under standardised conditions. Consequently, urbanisation may influence the daily energetic demands experienced by

hedgehogs without necessarily altering their underlying metabolic rate. Furthermore, urban environments may simultaneously impose energetic costs and provide energetic benefits, such as supplementary food resources, which could obscure any detectable relationship between urbanisation and metabolic rate.

A limitation of this study is the relatively narrow urbanisation gradient represented within the sample population. No individuals originated from habitats with less than 30% urbanisation, only two individuals came from highly urbanised habitats (>70% urbanisation), and the rest of the sample (n=12) originated from habitats between 30 % and 70% on the urbanisation gradient. Consequently, the study primarily compared individuals from moderately urbanised environments, limiting the ability to detect physiological differences across the full spectrum of urbanisation. It is therefore possible that stronger relationships between urbanisation and metabolic rate may emerge when comparing truly rural and highly urbanised populations.

The pace of life syndrome hypothesis predicts that individuals with a fast behavioural strategy such as high boldness or exploration, will also exhibit elevated metabolic rates and associated life history traits (Réale *et al.,* 2010; Biro and Stamps, 2010). In our study, we found moderate repeatability in uncurling behaviour, suggesting that individual hedgehogs consistently differ in this trait over time, which aligns with the concept of animal personality (Biro and Stamps, 2010). However, we did not find a significant relationship between uncurling and metabolic rate. This result is consistent with the idea that the pace of life syndrome may not always be evident when considering resting metabolic rates alone (Mathot *et al.,* 2018). One important limitation of linking resting metabolic rate and personality is that resting metabolic rate does not capture the full energy cost associated with bold behaviour as is more likely to happen during active periods rather than at rest (Careau *et al.,* 2012). Consequently, the absence of a link between uncurling and resting metabolic rate in our study reflects this limitation rather than a true lack of relationship between personality and energy expenditure. Additionally, the use of rescued hedgehogs may

influence the expression of behavioural and physiological traits measured in this study. The location of the study was familiar to the hedgehogs. This environment may have reduced behavioural variation among individuals as they knew they were in a safe location. This may potentially limit the ability to detect subtle relationships between metabolic rate and behaviour as individuals may not exhibit the same behaviours in an unknown location. However, captivity alone is unlikely to completely obscure biological differences between individuals. These findings align with other evidence suggesting relationships between metabolic rate and behaviour are context dependent which varies across taxa, behaviour types and environmental conditions (Mathot *et al.,* 2018; Royauté *et al.,* 2018; Arnold *et al.,* 2021). This highlights the importance of considering both ecological context as well as life history traits when testing predictions of pace of life syndrome in wild mammals.

Our study did not find a significant effect of urbanisation on resting metabolic rate in hedgehogs. This suggests that hedgehogs may cope with urban environments through behavioural flexibility rather than physiological changes in resting metabolism. Urban areas can impose energetic constraints through altered landscapes, food availability, noise and temperature variation, all of which can influence wildlife behaviour and energy budget (Lowry *et al.,* 2012; Murray *et al.,* 2019). Behavioural adjustments, such as shifts in inactivity patterns and foraging strategies may allow hedgehogs to maintain energy balance without substantially altering their metabolism. These findings highlight the importance of considering behavioural plasticity in urban wildlife. Animals may rely more on flexible behaviours than physiological changes to cope with anthropogenic pressure. Behavioural plasticity has been proposed as an important mechanism enabling wildlife to cope with anthropogenic change, potentially allowing individuals to respond rapidly changing environments without requiring underlying physiological adaptations (Sih *et al.,* 2011; Lowry *et al.,* 2013; Sol *et al.,* 2013).

Our results highlight the importance of species-specific physiology and life history traits in shaping energy expenditure and suggests that environmental factors

such as urbanisation may interact with characteristics rather than determining metabolic rate alone (Réale *et al.,* 2010; Biro & Stamps, 2010; Montiglio *et al.,* 2018).

Conclusion

Adapting to the City

This thesis investigated whether urban adapted European hedgehogs exhibit differences in cognition, boldness and metabolic rate across an urbanised gradient. By examining behavioural and physiological responses to urbanisation, this thesis aimed to identify the factors that may contribute to the success of the European hedgehogs in urban environments. The overall aim of this thesis was to test the hypothesis that urban adapters are bolder and have better cognitive abilities and higher energetic demands than animals living in less urbanised areas. To test this, I conducted two studies using the European hedgehogs from a range of urbanised areas in the Northwest of England. Study one assessed how individuals' differences in boldness related to cognitive performance, whereas study two examined the relationship between metabolic rate and boldness along an urban gradient. Overall, the findings of this thesis provide limited evidence that urbanisation consistently influences cognition, boldness or metabolic rate in European hedgehogs. While urbanisation was associated with longer latencies to complete the first problem solving task, no relationship was found with overall cognitive performance across subsequent tasks.

Urban environments provide both challenges and opportunities for wildlife (Shochat *et al.,* 2006; McDonnell and Hahs, 2015). While urban habitats may increase fragmentation and alter natural resource availability, they can also provide predictable anthropogenic resources such as supplementary feeding (Shochat *et al.,* 2006; Lowry *et al.,* 2012). One possible explanation for the latency to remove a lid from bowl, is that urban environments may alter the selective pressure and experiences associated with foraging (Sih *et al.,* 2011; Sol

et al., 2013). Individuals inhabiting less urbanised environments may rely more heavily on natural foraging behaviours such as searching and digging for prey, were as individuals from a higher level of urbanisation may have greater access to predictable anthropogenic food resources (Hubert *et al.,* 2011; Pettett *et al.,* 2017). Consequently, differences in foraging experience could influence how individuals respond to novel food related challenges, rather than reflecting differences in cognitive ability. This suggests that urban adaption in European Hedgehogs may not necessarily involve enhanced problem-solving abilities but instead may be facilitated by behavioural flexibility that allows individuals to adjust their responses and exploit opportunities within human modified landscapes (Lowry *et al.,* 2012; Sol *et al.,* 2013).

This thesis found limited evidence that urbanisation influenced metabolic rate in European hedgehogs. Urban environments can impose energetic challenges through habitat fragmentation, altered movement patterns and changes in resource distribution which could theoretically increase energy expenditure (Lowry *et al.,* 2012). However, urban habitats may also provide energetic benefits, including predictable anthropogenic food resources and reduced investment in some behaviours such as foraging (Shochat *et al*., 2006; Lowry *et al.,* 2012). The absence of a relationship between urbanisation and metabolic rate may therefore reflect a balance between the energetic costs and benefits associated with urban environments. Individuals living in urban habitats may experience increased challenges in navigating fragment landscapes, but these costs may be offset by increased resource availability or reduced foraging effort (Shochat *et al.,* 2006). Therefore, urban adaptation in European hedgehogs may not necessarily involve physiological changes in baseline energy expenditure but instead may rely on behavioural adjustment that allow individuals to exploit altered resource landscapes.

The findings in this thesis contrast with predictions from the pace of life syndrome framework which poses that behavioural, physiological and life history traits co-exist along a slow-fast continuum (Réale *et al.,* 2010; Santostefano *et al.,* 2017; Dammhahn *et al.,* 2018; Montiglio *et al.,* 2018). According to the pace of

life syndrome hypothesis, fast individuals are expected to be bolder, more exploratory, and exhibit higher resting metabolic rates while slow individuals show more cautious behaviours reduce energetic demands (Réale *et al.,* 2010; Dammhahn *et al.,* 2018). The absence of such correlation in the study population of hedgehogs may suggest that urban ecological conditions may weaken or disrupt the expected link between behaviour and physiology (Polverino *et al.,* 2018; Charmantier, 2024) however, several studies have reported similar findings, where no significant relationship was observed between metabolic rate and boldness (Binder *et al.,* 2016; Väätäinen *et al.,* 2018; Poranen and Ruuskanen, 2020).

Uncurling as a proxy of boldness was found to be a repeatable personality trait in European hedgehogs but not influenced by urbanisation. This suggests that the persistence of hedgehogs within urban environments is unlikely driven by the presence of consistently bolder individuals. While boldness has been associated with invasion success and the colonisation of novel habitats in other species (Pârvulescu *et al*., 2021; Bensky and Bell, 2022; Sales *et al*., 2023; Eccard *et al*., 2023), the findings presented here indicate that successful urban adaptation in hedgehogs may instead be facilitated by behavioural flexibility and the ecological opportunities provided by urban environments (Lowry *et al.,* 2012; Santini *et al.,* 2019). Urban habitats may buffer individuals against some ecological pressures through increased resource availability and reduced predation risk, potentially reducing the selective pressures favouring particular behaviour phenotypes (Hubert *et al*., 2011; Hoft and Bright, 2016; Wembridge *et al.,* 2022).

A key limitation across this thesis was the restricted range of urbanisation along the urbanisation gradient represented within the study population. As hedgehogs were sourced from a rescue centre, the urbanisation gradient represented in this thesis was determined by the individuals admitted before or during the study period, rather than by targeted sampling across rural and urban habitats. Consequently, few individuals originated from low or highly urbanised habitats, limiting the ability to detect differences at the extremes of urbanisation. Although this approach allowed investigation of variation among individuals

experiencing different levels of urban influence, stronger relationships between urbanisation and behavioural or physiological traits may emerge when comparing population across a broader environmental gradient. This approach however did ensure consistent husbandry and handling conditions across individuals prior to the studies; minimising variation associated with recent environmental experiences that may influence behavioural and physiological measures.

The findings of this thesis also contribute to broader discussions surrounding urban wildlife syndrome and the mechanisms that facilitate species persistence within urban environments. Urban wildlife syndrome predicts that urban adapted species exhibit consistent behavioural, physiological and life history traits that distinguish them from their rural counterparts (Lowry *et al.,* 2012; Alberti *et al.,* 2017). Despite the successful of European hedgehogs within urban habitats, there was limited evidence that urbanisation consistently influenced cognitive performance or metabolic rate. Instead, behavioural differences were subtle and appeared to relate more closely to how individuals initially respond to novel challenges rather than enhanced cognitive abilities.

Urbanisation is one of the most significant drivers of global environmental change (McDonnell and Hahs, 2015). However, wildlife species differ considerably in their ability to persist within human modified landscapes with responses varying according to species traits and environmental conditions including resource availability, habitat structure and human provided resources (Haight *et al*., 2023). Collectively, the findings of this thesis challenge the assumption that successful urban wildlife populations are necessarily characterised by enhanced cognitive abilities, increased boldness or altered physiological traits. Despite their successful persistence in urban environments, European hedgehogs did not exhibit clear behavioural or physiological syndromes associated with urbanisation. Instead, the findings of this thesis suggest that for urban wildlife , persistence is therefore likely shaped not only by individual behaviour or physiological traits, but also by interactions with the wider urban ecosystem, including access to resources, exposure to predators and the challenges of navigating fragmented landscapes (Lowry *et al.,* 2012; Sol *et al.,* 2013). By

improving our understanding how hedgehogs respond to urbanisation, this thesis contributes to the growing body of research investigating the mechanisms that allow some species to successfully exploit urban habitats. As urban landscapes continue to expand, understanding the behavioural and physiological traits that facilitate wildlife persistence will be essential for informing effective conservation strategies and promoting coexistence between humans and wildlife.

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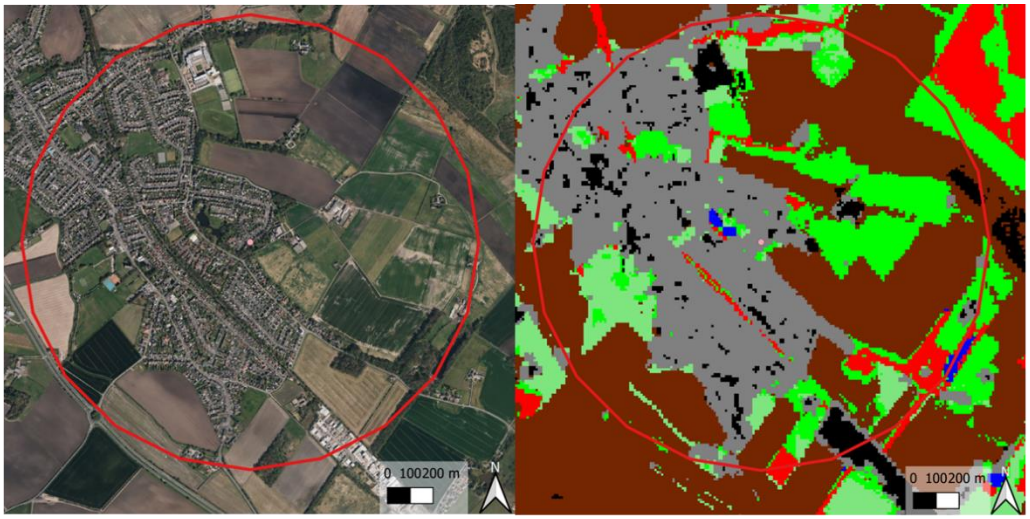
Appendix

Chapter 1: Maps of the location the hedgehogs were found



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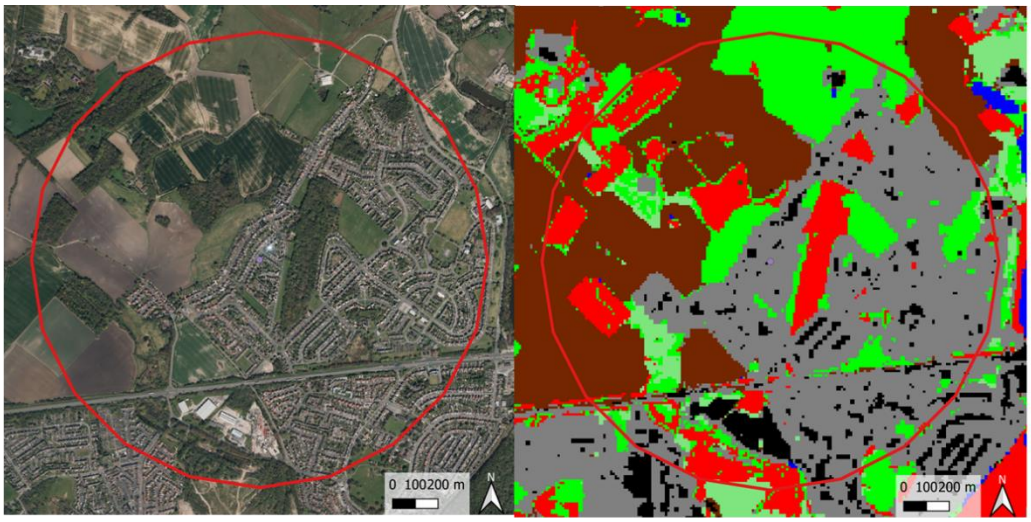
Urban Gradient Score: 37.84%



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Urban Gradient Score: 44.21%

ID: 3
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Urban Gradient Score: 61.76%

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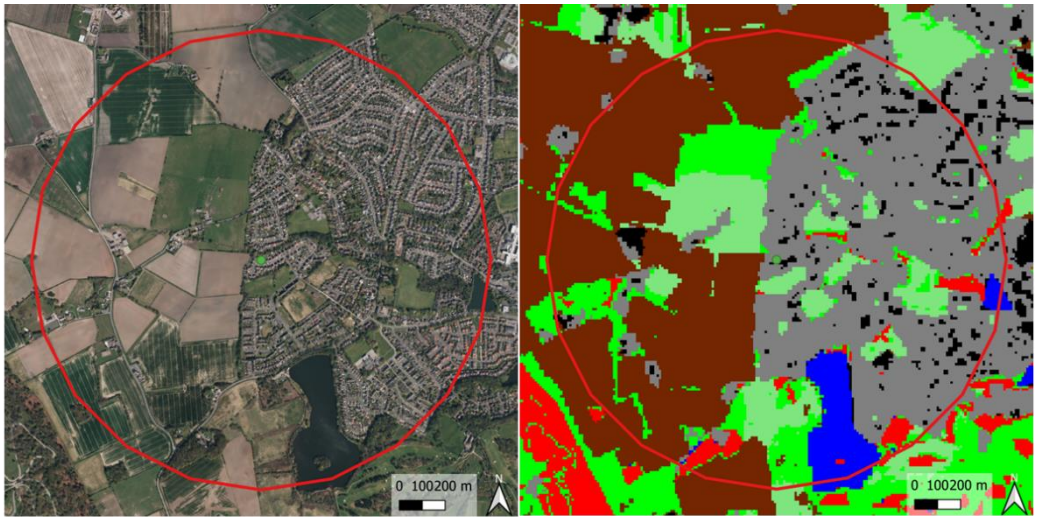

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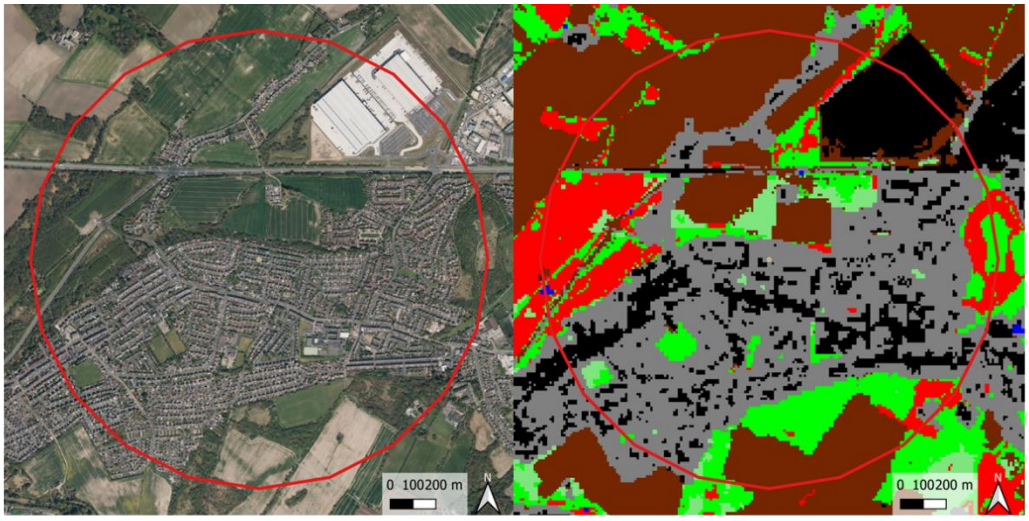

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Sex: Male
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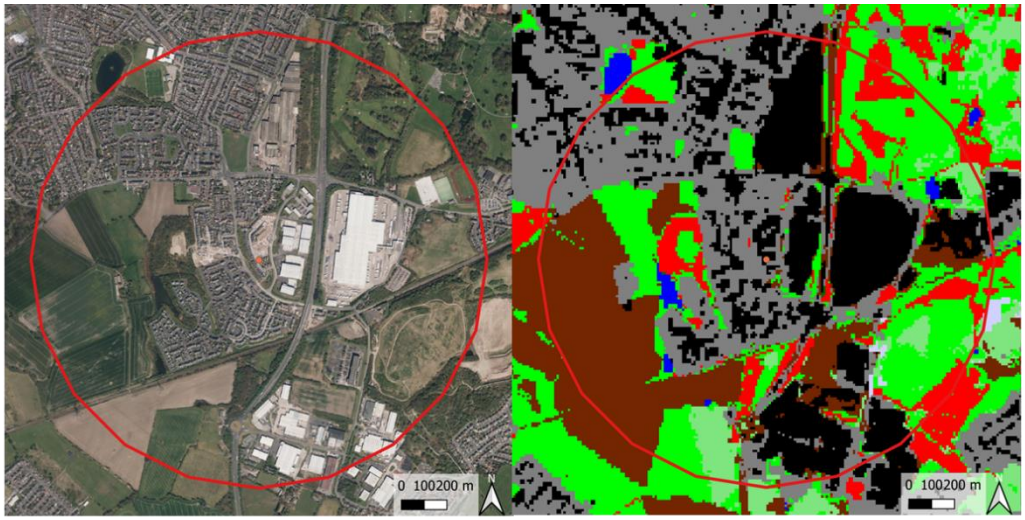

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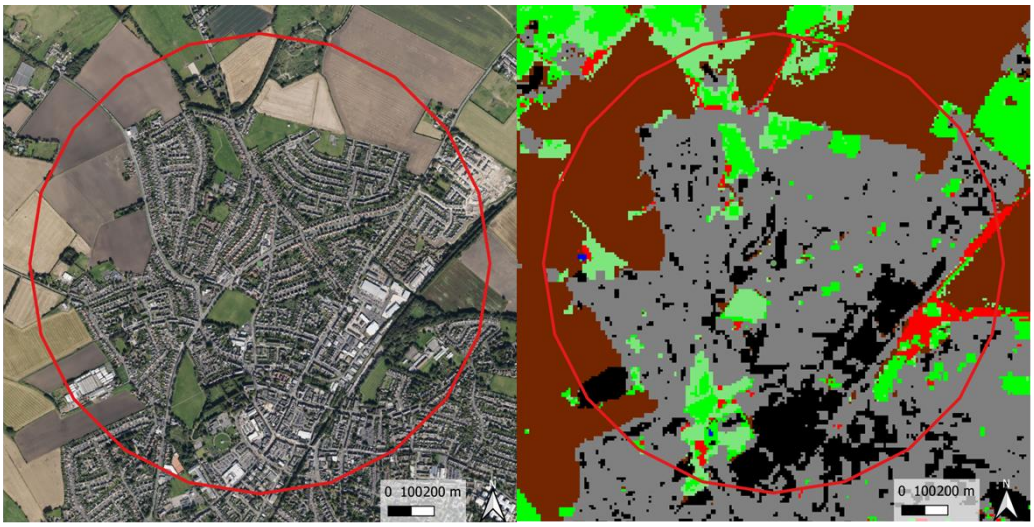
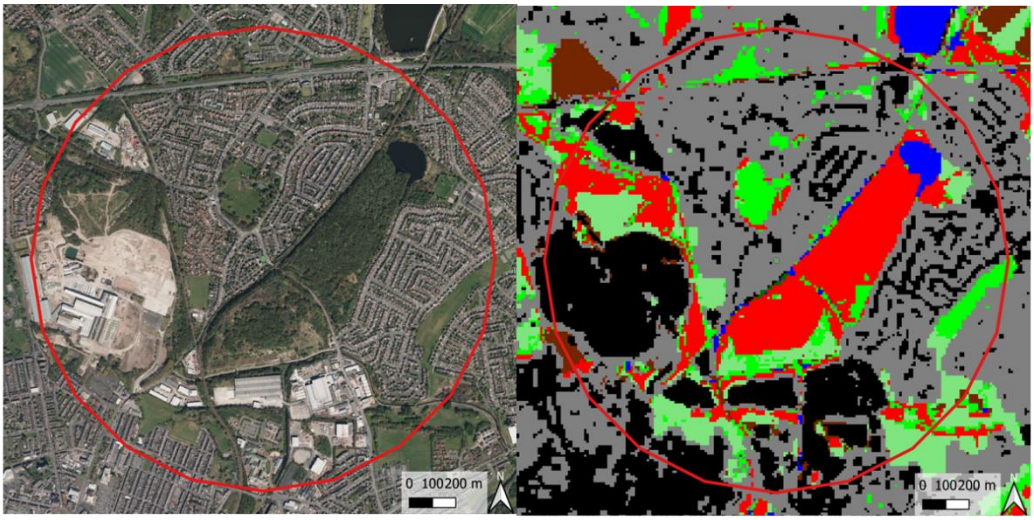
Urban Gradient Score: 49.44%



ID: 8
Sex: Female
Urban Gradient Score: 61.70%

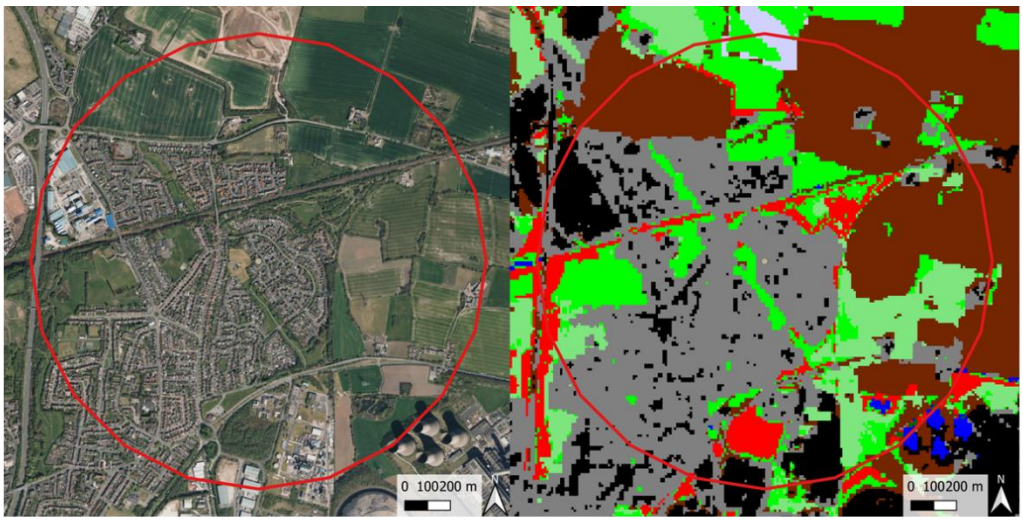
ID: 9
Sex: Female
Urban Gradient Score: 57.09%

ID: 10
Sex: Male
Urban Gradient Score: 36.57%



ID: 11
Sex: Male
Urban Gradient Score: 67.28%

ID: 12
Sex: Male
Urban Gradient Score: 36.57%



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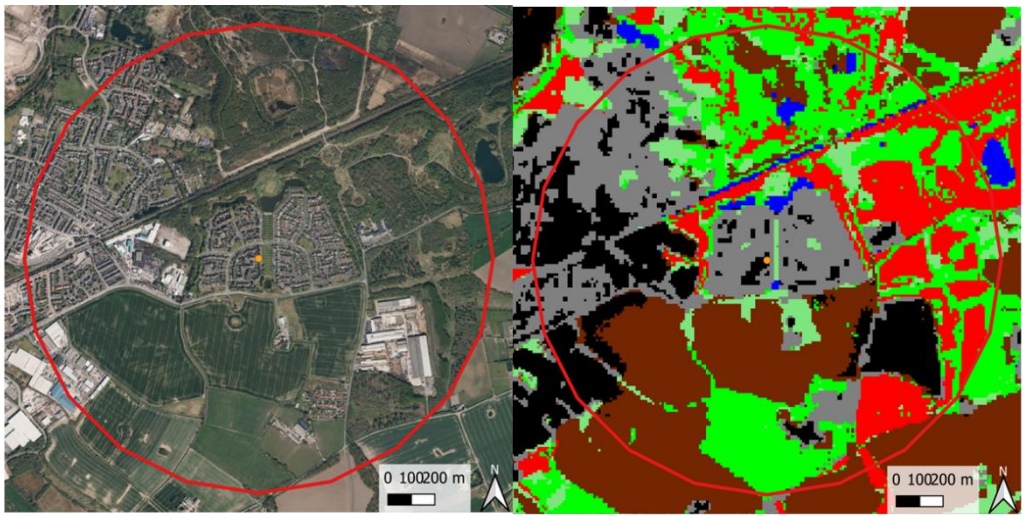

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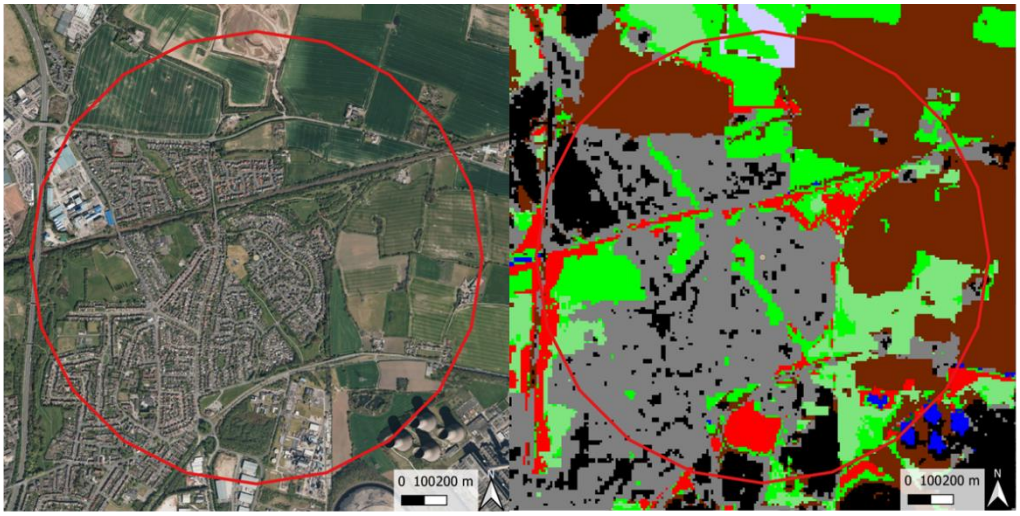

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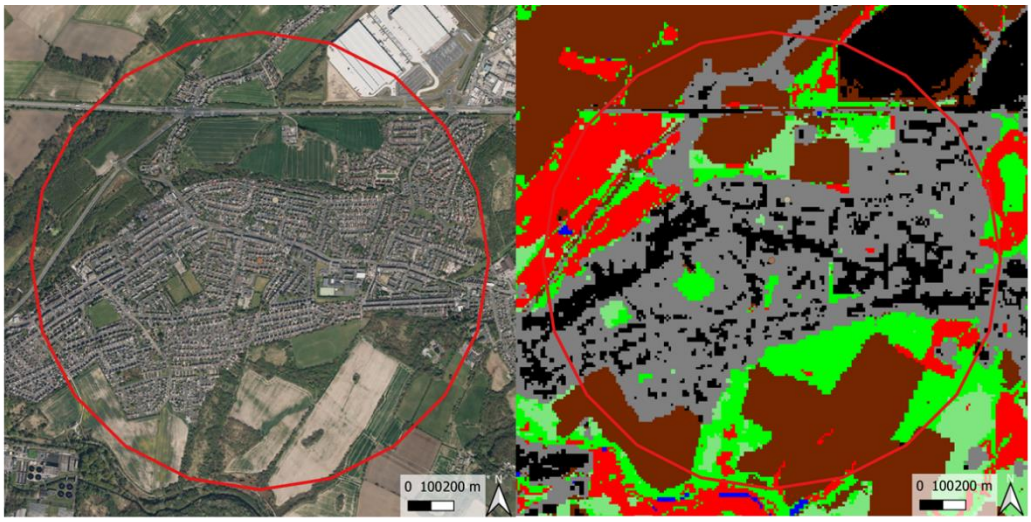
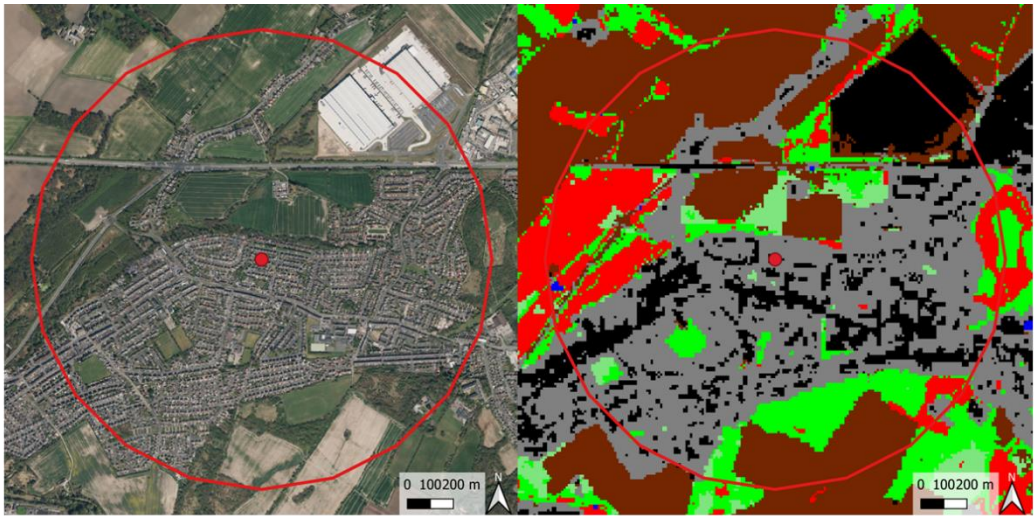
Sex: Male
Urban Gradient Score: 44.70%



ID: 16
Sex: Female
Urban Gradient Score: 51.89%

Chapter 2: Maps of the location the hedgehogs were found



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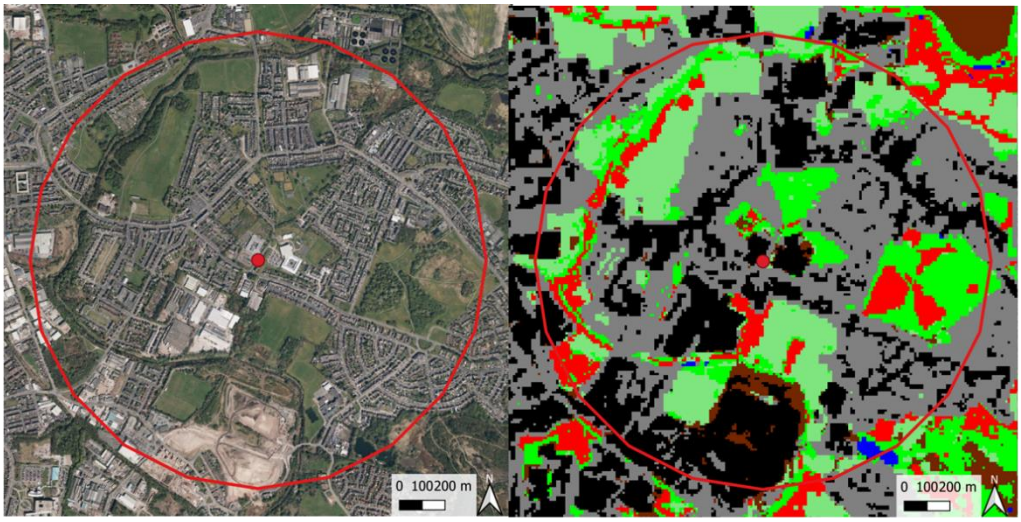
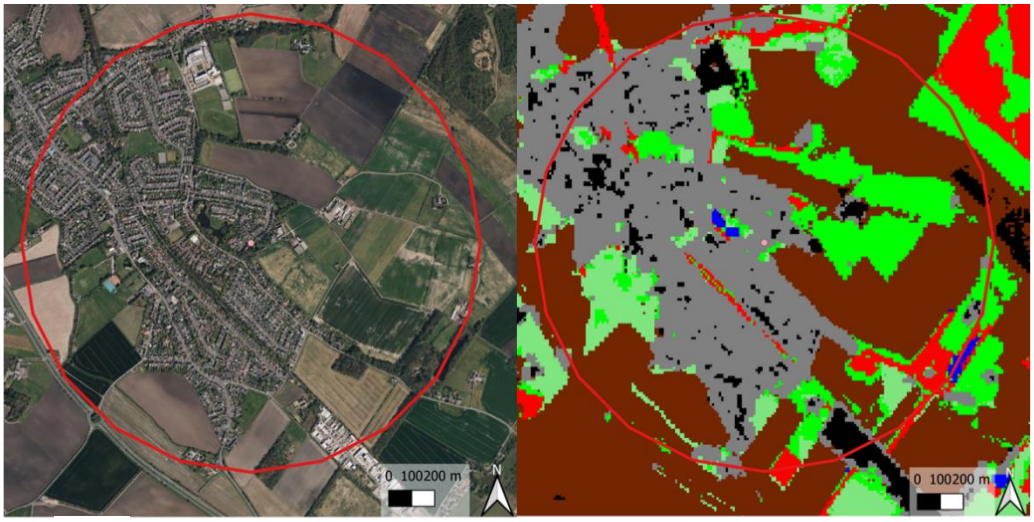


ID: 18
Sex: Male
Urban Gradient Score: 63.34%

ID: 19
Sex: Male
Urban Gradient Score: 36.97%



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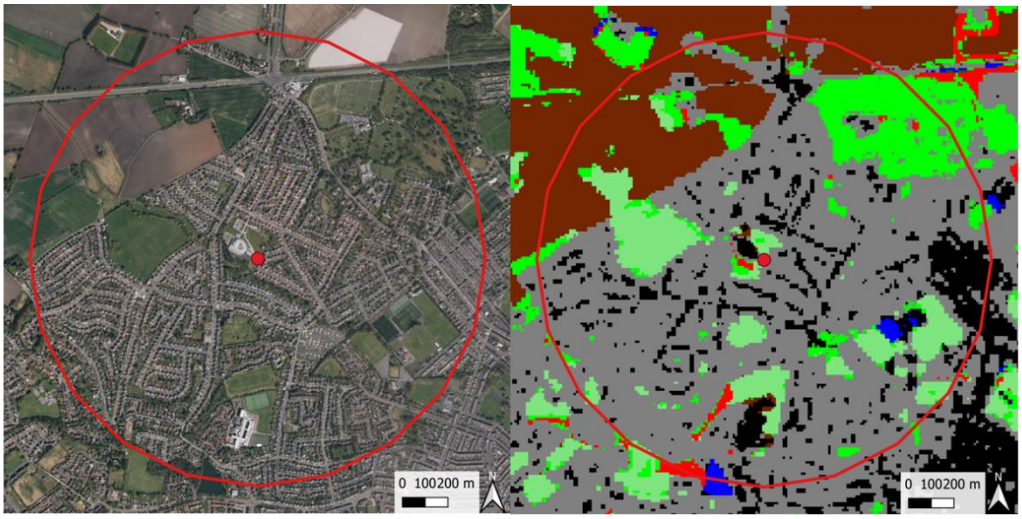

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Sex: Female
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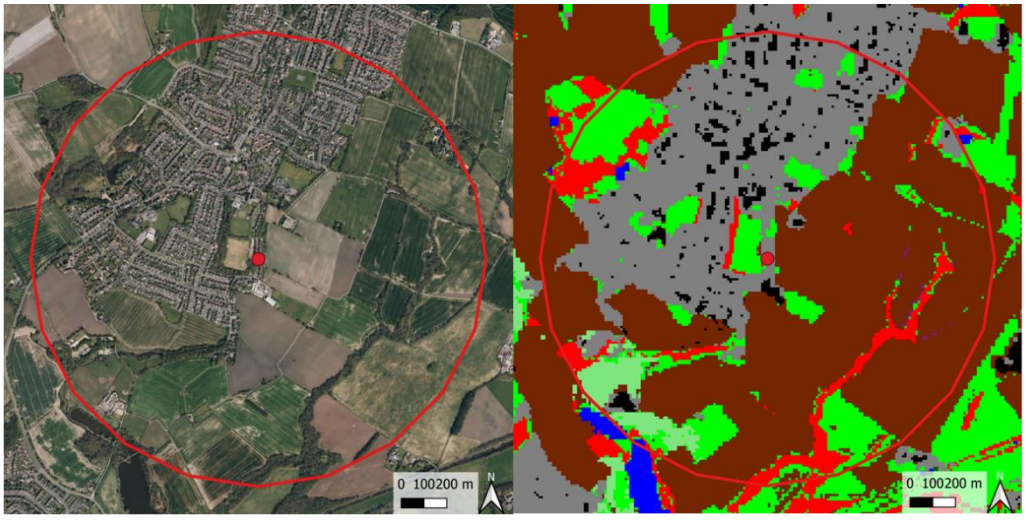

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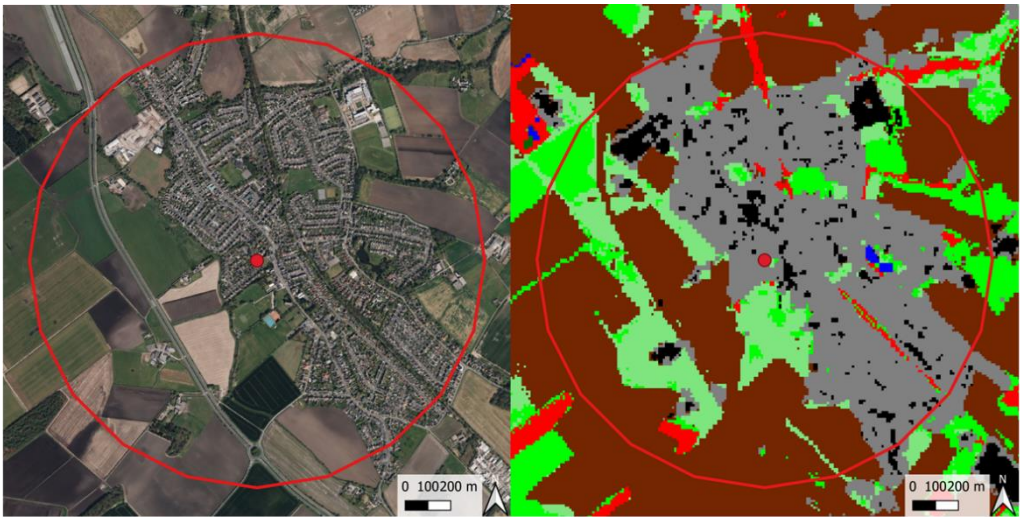

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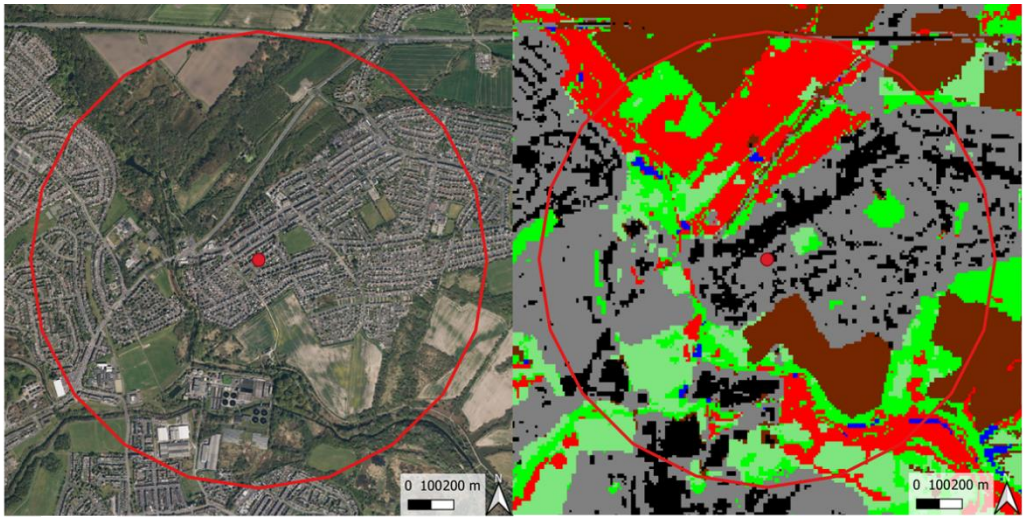

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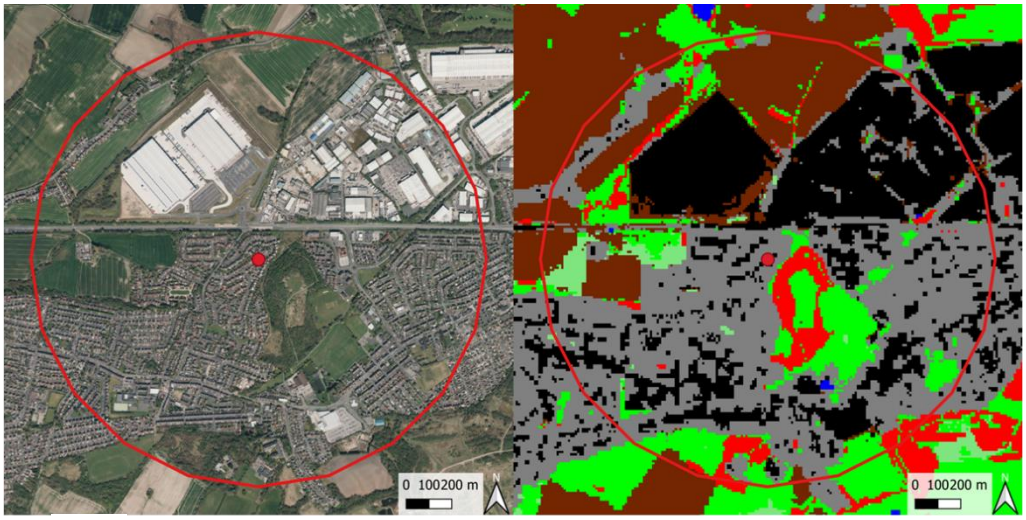

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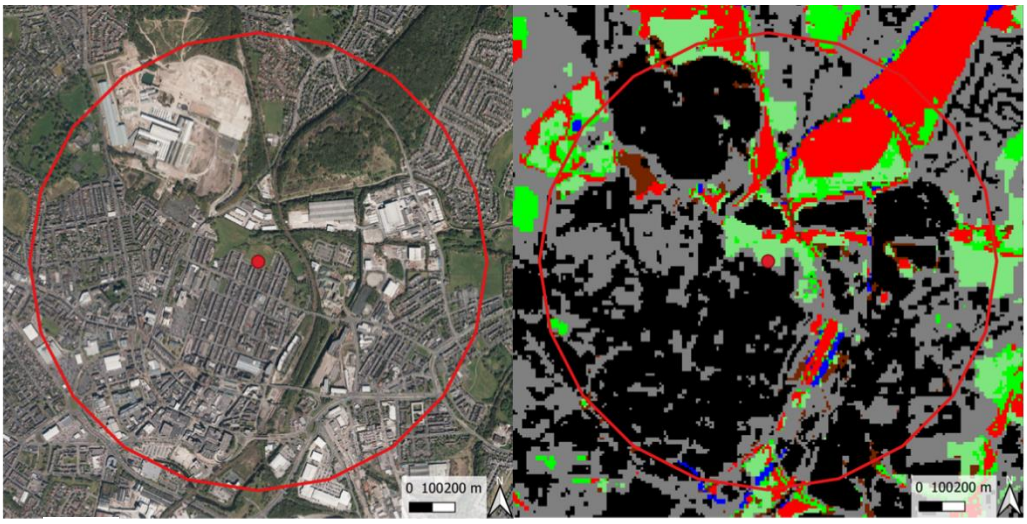

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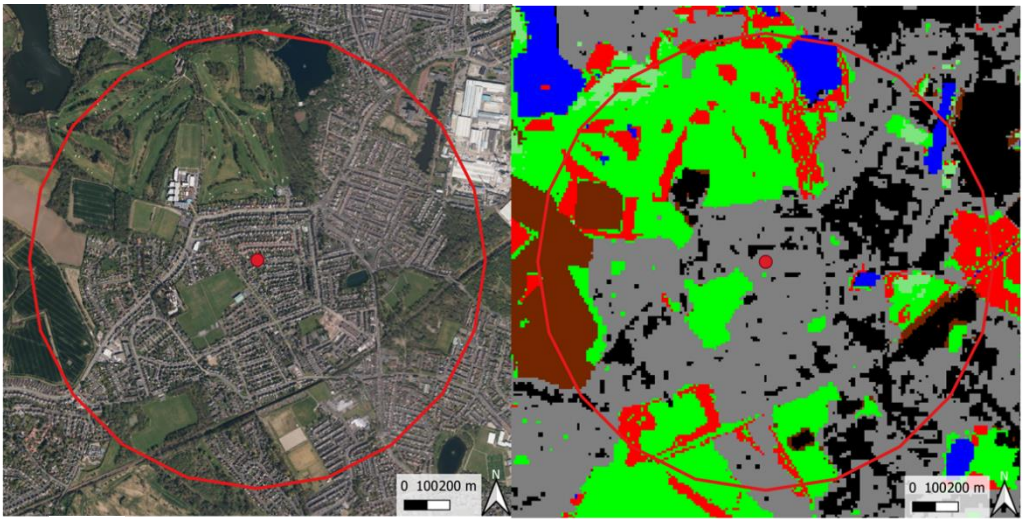

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Sex: Female
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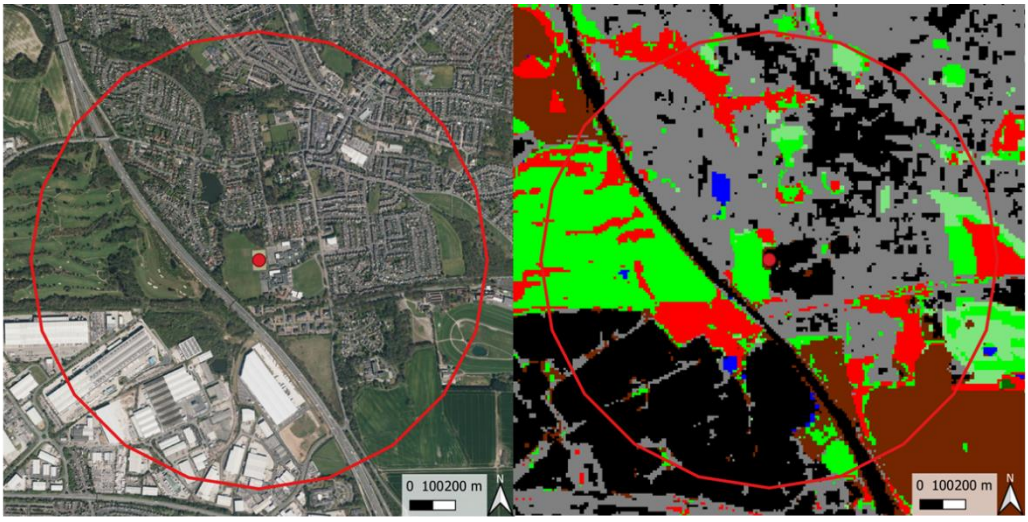

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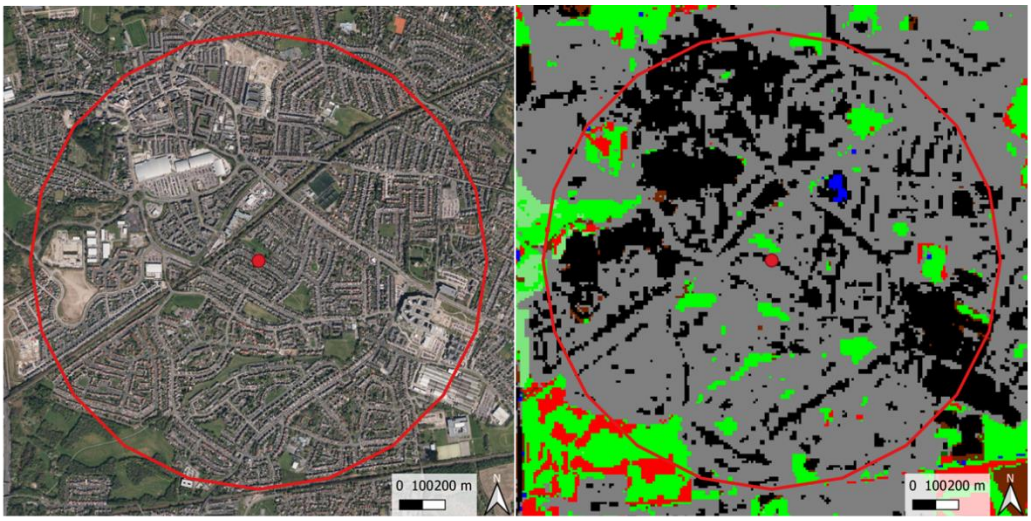

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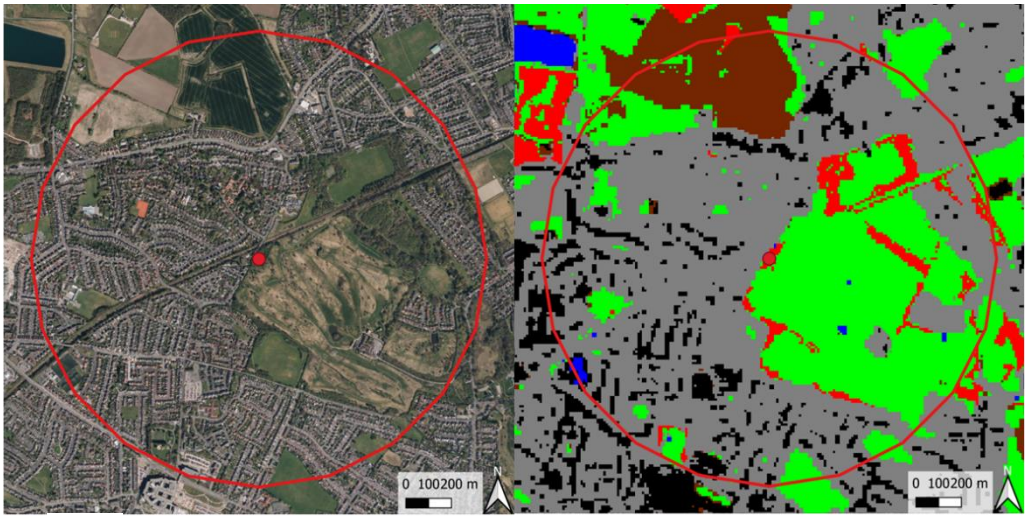

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