Foraging Behaviours in Urban Wildlife: Squirrel Route Choices and Wildlife Trash Foraging

Ariana Moin Kenary

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By: Ariana Moin Kenary

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Signed by the final examining committee:

____Chair
Dr. Craig Townsend

____External Examiner
Dr. Carly Ziter

____Examiner
Dr. Julie Teichroeb

____Thesis Supervisor
Dr. Sarah E. Turner

Approved by ____
Dr. Pascale Biron, Graduate Program Director

August 29th, 2024 ____
Dr. Pascale Sicotte, Dean of Faculty

ABSTRACT

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Ariana Moin Kenary

Urbanization impacts wildlife survival by altering foraging decisions and introducing anthropogenic food sources, like waste. Foraging behaviours are critical to animal survival, and understanding these decisions provides insights into species adaptation and resilience, which can inform biodiversity conservation strategies. While the physical impacts of ingesting waste are well-documented, the nuanced behavioural aspects are often overlooked. This thesis explored foraging route choice among Eastern gray squirrels (*Sciurus carolinensis*) through an experimental field study on wild urban squirrels, compared these data with Japanese macaques (*Macaca fuscata*), and investigated how anthropogenic food sources alter foraging strategies in urban vertebrates through a literature review. In Chapter 2, I used a 1mx2m multi-destination, Z-shaped foraging array to collect 62 foraging trials on squirrels at Mount Royal Park in Montreal. Comparing these data with macaque data from Joyce et al. (2021), I found that squirrels (1) foraged more slowly, (2) exhibited a higher rate of platform revisiting, and (3) chose routes consistent with heuristic use at a similar rate to macaques. Observations also indicated that garbage and human food waste were an important part of the squirrels' diet, leading to Chapter 3's exploration of how urban trash affects wildlife behaviour. I found that urban species foraging on waste modify their behaviours in various ways, including adopting new behaviours, changes in foraging methods, timing, energy budgets and social behaviours. My research enhances our understanding of urban mammal foraging behaviour and my literature review highlights the specific behaviours urban species adopt to thrive in urbanized settings.

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DEDICATION

I dedicate this thesis to my loved ones. Nobody achieves anything in a vacuum, and I am grateful to have a long list of people to thank.

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CONTRIBUTION OF AUTHORS

This project was conceptualized by Sarah Turner and myself, with valuable input from Megan Joyce, and based on primate research methods developed by Julie Teichroeb. I was responsible for the data collection, preparation, and analysis, as well as the writing of the first version of the thesis manuscript. Sarah Turner supervised the project, co-developed field methods and logistics, conducted some data collection, provided funding support, and reviewed drafts of the analyses and thesis text. Megan Joyce provided data from her MSc research on Japanese macaques (Joyce, 2021; Joyce et al. 2023), and contributed to methods conception and data analysis, particularly with ideas for the interspecies comparison sections of the thesis. Ivan Miloslavov provided assistance with technological and statistical aspects, and wrote the program for used for field data collection.

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List of Abbreviations

ADM	Animal decision making
NN	Nearest neighbor heuristic
OFT	Optimal foraging theory
SP	Shortest path heuristic
SW	Sweep heuristic
TSP	Traveling salesperson problem

Chapter 1: Introduction

Urban environments present unique and multifaceted challenges for wildlife, necessitating decision-making in new contexts and behavioural plasticity to exploit the available resources and navigate the complex landscapes. The rapid expansion of urban areas globally has led to significant habitat fragmentation and the creation of novel ecological niches, thereby exerting powerful selective pressures on urban-dwelling species. Understanding how wildlife species adjust their behaviours and adapt to these environments is crucial for developing effective conservation strategies and ensuring biodiversity in urban settings. The primary focus of this thesis is to explore the foraging route choice decisions and foraging strategies of urban wildlife, particularly for Eastern gray squirrels (also spelled 'grey squirrels'), *Sciurus carolinensis*. By examining the foraging behaviours of this species, comparing them to published data on Japanese macaques, and examining the broader context of urban wildlife foraging on human food wastes, garbage and other trash through a literature review, this thesis aims better understand how species thrive foraging in urban settings.

This thesis is structured into several chapters, each addressing a specific aspect of urban wildlife foraging behaviour. In Chapter 2, I provide a general review of the literature on animal foraging behaviour and a detailed examination of urban squirrels and their foraging behaviour. I review the literature on urban squirrel foraging behaviour, and how certain individual and social factors can impact how these animals modify their foraging strategies. In this chapter, I also review the literature on foraging patterns, route selection and heuristics to provide context for my hypotheses and data presented in Chapter 3, and my systematic literature review in Chapter 4.

In Chapter 3, I address two research questions: how squirrels navigate a foraging array in an urban environment, and how the foraging of Eastern gray squirrels compares to that of Japanese macaques on a foraging array. This chapter presents data and results from field experiments conducted on wild squirrels living in Mount Royal Park, Montreal, QC. This chapter presents the findings from a multi-destination foraging experiment using a Z-shaped array. Given the difficulty of collecting data on these wild squirrels, I then compared my results directly with similar data collected on Japanese macaques (*Macaca fuscata*) by Megan Joyce for her MSc Thesis (Joyce, 2021; Joyce et al. 2023), highlighting the similarities and differences in foraging strategies between the two species. I found significant differences in foraging patterns, route choice selection, and I discussed the implications of these findings.

During my field research on urban squirrels, in addition to collecting quantitative data for my foraging trials, I spent time qualitatively observing urban squirrel behaviour. My observation that they spend considerable time foraging on human food waste and other garbage in the park, lead me to wonder what impacts urban trash and waste could have on foraging behaviour. In order to address this research question, I conducted a review of the literature on the relationship between urban wildlife foraging behaviour and trash. In Chapter 4, I present this review of the literature. I synthesized findings from various studies, providing a broader context for understanding how different species adapt to urban environments. In this review, I identified key themes, such as social learning, adaptation mechanisms, and ecological impacts, drawing connections between the experimental findings and existing literature.

Lastly, I summarized the overall findings and contributions of the thesis in Chapter 5. The findings from this research highlight the importance of behavioural plasticity in enabling wildlife to thrive in urban environments and underscore the need for continued investigation into the interactions between urbanization impacts, animal behaviour, and human-wildlife coexistence. This thesis reflects on the importance of understanding urban wildlife behaviour in the context of increasing urbanization and provides recommendations for future research. The chapter emphasizes the need to integrate animal behavioural studies into urban planning and conservation strategies to foster coexistence between human development and wildlife populations, and reduce human-wildlife conflicts.

Chapter 2: Literature Review: Urban Squirrel Foraging

2.1 Introduction

Urban land use is one of the fastest-growing forms of human spatial development, expanding rapidly across the globe (Deng et al., 2009; Vitousek et al., 1997). Urbanization is defined as the mass movement of populations from rural to urban settings and encompasses the consequent physical changes to these expanding urban settings, such as an increase in roads, buildings and other infrastructure (Kuddus et al., 2020). Urbanization has dramatic impacts on local environments and is considered one of the biggest threats to biodiversity and ecosystems worldwide, as a primary driver of habitat degradation and fragmentation (Bai et al., 2019; Haddad et al., 2015; Liu et al., 2016). Habitat degradation has important impacts on local biota, subjecting them to new powerful pressures which often have negative long-lasting effects, ranging from modification of species assemblages to complete loss of local species, threatening the integrity of ecosystems worldwide (Bonnington et al., 2014; Eötvös et al., 2018; Haddad et al., 2015; Ibáñez-Álamo & Soler, 2010; Lyons et al., 2016; Sovie et al., 2020). Research on urban wildlife has not increased as fast as the expansion of urban areas, leading to gaps in the literature concerning the behaviours and habitat needs of species that share urban space with humans (Magle et al., 2012). As anthropogenic activities continue to expand, it becomes increasingly important that we improve our understanding of the other organisms on the planet in order to conserve biodiversity, reduce negative human impacts on wildlife, and encourage human-wildlife co-existence.

Animals that have adjusted to urban landscapes have been able to do so in part by modifying their behaviour, often leading to behavioural variation between them and their wild counterparts (Anderson, 2012; Birnie-Gauvin et al., 2016; Jokimäki et al., 2017; Sol et al., 2013). A literature review of research conducted between 1987 and 2020 on behaviour changes in wild urban mammals found that urban environments drive adaptive responses in a diversity of species (Ritzel & Gallo, 2020). Behavioural changes associated with urban species include changes in diet preference, shifts in activity budget and decreased in flight initiation distance (Ritzel & Gallo, 2020).

Squirrels (species in the *Scuridae* subfamilies *Callosciurinae* and *Sciurinae*) represent an important taxon impacted by urban expansion. Globally, squirrel species have been affected by human activities, and impacts include: shifts in population dynamics (*Sciurus niger* & *Sciurus carolinensis,* Sovie et al., 2020); shifts in behaviour (*S. niger, S. carolinensis & S. vulgaris,* Uchida et al., 2020); negative effects of environmental pollution (*Callosciurus erythraeus* , Suzuki et al., 2006); habitat fragmentation (*Sciurus anomalus*, Khalili et al., 2018; *Petaurus norfolcensis* Sharpe & Goldingay, 2010); and other direct effects such as road mortality (Mccleery et al., 2008). These small mammals are present in almost every urban setting in North America, yet we still lack information about how they survive in and make use of urban habitats, especially how their foraging behaviour influences their use of urban habitats (Mccleery et al., 2008; Parker et al., 2014). Squirrels live among humans across urban landscapes; their presence is not limited to parks, and they can also thrive in the most developed areas within a city. Moreover, increased proximity between squirrels and other wildlife has the potential to lead to increased human-wildlife conflicts, as squirrels can cause damage to human structures and vegetation, disrupt human activities and cause road accidents (Anderson, 2012; Fingland et al., 2021; Kenward, 2008; Lurz et al., 2001; Shuttleworth, 2001; Uchida et al., 2020). The potential for negative human-squirrel interactions is likely to increase as greenspaces become limited or fragmented, pushing existing squirrel populations into closer contact with people (Anderson, 2012; Birnie-Gauvin et al., 2016; Cooper et al., 2008).

2.2 Animal decision making and foraging

Research on foraging behaviour in animals is a cornerstone of ecology studies. Foraging encompasses all the methods and actions by which an organism acquires and uses food, and is an essential activity for all animals (Koy & Plotnick, 2007; Stephens et al., 2008). This has always been a "central concern" of ecology, as advancing our understanding of how species acquire nutrition allows for a more complete understanding of the larger environment, and is relevant across multiple disciplines (Kamil et al., 1987). To that end, understanding how animals make foraging decisions and predicting the outcomes of potential foraging tradeoffs can inform our understanding of survival and reproductive success (Pyke et al., 1977).

Multiple hypotheses have been proposed to predict and explain how and where an individual (or group of animals) will choose to forage, most suggesting that individuals should seek to minimize or optimize energy expenditure to obtain the greatest net benefit from the activity (Owen-Smith et al., 2010). The animal decision making (ADM) process is an important component of foraging behaviours. I will use the definition of ADM provided by Blumstein and Bouskila (1996) as "the process of selecting a behaviour while a subject weighs the costs and benefits of alternative behaviours" (Blumstein & Bouskila, 1996, p. 569). ADM is impacted by an individual's physiology, as well as social and environmental factors and can change throughout an individual's life (Blumstein & Bouskila, 1996; Owen et al., 2017). Foraging decision-making behaviours have been studied and identified in multiple species across many taxa (for review see Budaev et al., 2019). For example, Lihoreau's work with bees, in which he and colleagues identified a foraging optimization pattern known as "trap lining" (Lihoreau et al., 2010, 2011, 2013).

One of the most robust bodies of work in studying foraging can be found in the study of human and non-human primates. Experiments on decision making have been conducted with wild and laboratory populations of many non-human primate species. These have identified the ability of individuals to not only find the shortest path while foraging, but also behavioural flexibility allowing them to make use of context dependent strategies to improve foraging outcomes (Carter et al., 2013; Chapman et al., 2012; Janson, 2019; Joyce et al., 2023; Teichroeb & Smeltzer, 2018; Trapanese et al., 2019).

Route choice problems in ecology are similar to the *Travelling Salesperson Problem* (TSP). TSP is a theoretical mathematical problem that consists of selecting the shortest path through a series of set points and returning to the origin (Macgregor & Ormerod, 1996). This approach would in theory maximize the rewards while minimizing the distance travelled, making it the most effective route to take. TSPs become more complex and difficult to solve as the number of points increases, with simple algorithms failing in experimental situations where humans can find near-optimal routes (Macgregor & Ormerod, 1996). This can be accomplished in part using certain fixed strategies such as heuristics, or "rules of thumb" to simplify decision-making.

2.2.1 Optimal foraging theory

Optimal Foraging Theory (OFT) is a model used in ecology to predict organism behaviours as they search for food, proposed by MacArthur and Pianka (1966). OFT predicts that an organism will make decisions to maximize their net energy gain by optimizing energy expenditure and foraging time during food acquisition activities, choosing the shortest routes that lead to the most and best quality food (Hopkins, 2016; Joyce, 2021; MacArthur & Pianka, 1966; Pyke et al., 1977; Pyke & Starr, 2021). This theory has provided explanations about foraging behaviour for over 50 years (Pyke et al., 1977; Pyke & Starr, 2021). OFT predicts that animals will forage as efficiently as possible. However, assessing how effective or impactful a foraging strategy is over the course of an organism's lifetime can be a difficult task. Houston & McNamara (2014) describe a way around this: the identification and use of a criterion(s) that has a direct relationship to a behaviour can provide a quantifiable way to study a behaviour of interest. In the context of foraging, these criteria are usually time and energy (Houston & McNamara, 2014). Recent literature reveals the use of foraging efficiency as a valid unit used to study optimal foraging behaviours (Nolet, 2002). Here I define foraging efficiency as the number of food items acquired per unit of time (s) or unit of distance (m).

Optimal foraging and other optimality models have worked well for and predicted behaviour in some species of insects, large herbivores, and primates (Cramer & Gallistel, 1997; Lihoreau et al., 2010; Owen-Smith & Novellie, 1982). However, overall, the application of optimization principles has shown mixed results in squirrel species. For example, while optimization theories (such as OFT) successfully predicted diet and foraging selection in Columbian ground squirrels, *Spermophitus coiumbianus* (Ritchie, 1991), and some caching decisions such as food item size and distance caching in American red squirrels, *Tamiasciurus hudsonicus* (Hurly & Robertson, 1987), they did not predict nut or patch selection in eastern gray squirrels *S. carolinensis* (A. R. Lewis, 1980, 1982) or foraging patterns in eastern fox squirrels, *S. niger* (Tatina, 2007).

2.2.2 Route and choice

Traveling to and from resource patches is one of the most important elements of foraging behaviour (Marshall et al., 2012). Terminology in varied publications have used the *route* and *path* interchangeably to refer to a direct linear movement between two points (Hastings et al., 2010; Hopkins, 2016; Joyce, 2021; Shaffer, 2014; Trapanese et al., 2019). I will use the term *route* from Joyce (2021) to mean “direct, linear, goal-oriented travel between two (or more) positions. A route could be limited to a single segment between two points, or it could be the total accumulated distances of a series of segments” (Joyce, 2021).

There is some variability in the literature concerning the interpretation of decision-making processes; while some argue that animals use calculated approaches (Gigerenzer & Gaissmaier, 2011), others suggest that organisms are simply demonstrating ingrained, or stereotypic responses to familiar scenarios (Owen et al., 2017). The concept of choice is fundamental to the discussion of foraging behaviour in animals (Barnard, 2004), involving the identification and selection of a specific behavioural or cognitive option among several possibilities. Choice involves processing various types of information and weighing the value of these outcomes to determine the best option for the organism (Budaev et al., 2019). Animals are bombarded with inputs and stimuli from multiple sources as they navigate their environments. In order to conserve energy and make decisions in an effective way, individuals need a way to sort through these inputs and inherent sensory noise (Budaev et al., 2019; Faisal et al., 2008). Although natural environments are complex and stochastic, certain events such as predator encounters can occur often enough to make context-specific rules a way to navigate these situations (Budaev et al., 2019). This frequent exposure to events could translate into the development of simple fixed strategies, where an individual reacts the same way every time a stimulus is presented but can also manifest as a set of relatively fixed heuristics, or rules of thumb.

2.3 Heuristics

Numerous species are able to behave in ways that are consistent with the potential use of heuristics, also known colloquially as “rules of thumb,” for decision-making. A heuristic is a simple, default rule that an animal may follow to make movement decisions. The term *heuristics* is used across various disciplines, but the definition I will use is from Joyce (2021) where heuristics are “inflexible decision-making rules that have a simplified or generalized response” (Joyce 2021, p. 10).

But why employ decision-making rules instead of trying to find the best solution to every problem? The short answer is energy. There is an inherent cognitive energetic cost to making any decision, especially when one must stop in order to acquire all the information needed to puzzle out the best solution for every situation. So, it makes sense that especially for scenarios that occur frequently (e.g., foraging, encountering a predator, etc.), over time an organism could develop some decision-making shortcuts, or heuristics. This does not mean that heuristics always provide the best solution or shortest path, in fact it is part of many definitions in literature that heuristics are not meant to be perfect (Gigerenzer & Gaissmaier, 2011; Janetos & Cole, 1981; Romanycia & Pelletier, 1985). Rather, heuristics function as a tradeoff between accuracy and effort, with a long-term gain in energy saved during these decisions, at the cost of not always having the best solution (Gigerenzer & Gaissmaier, 2011). The identification of heuristics can be beneficial in research, as heuristics can aid in the construction of behavioural models (Delgado, 2017). The use of heuristics can also be beneficial to organisms, as they can improve outcomes for a multitude of organisms, both in foraging and in other areas of decision-making (Oberhauser et al., 2020; Sayers & Menzel, 2012; Todd & Gigerenzer, 2000; C. G. Wilson et al., 2021).

Humans employ a wide variety of heuristics. In a recent review of 214 empirical studies involving heuristics in decision making, 19 types of heuristics employed by humans were identified (Blumenthal-Barby, 2016). The next most robust body of heuristic use literature centers around non-human primates (Andrews, 1988; Cramer & Gallistel, 1997; Erhart & Overdorff, 2008; Hopkins, 2016; MacDonald & Wilkie, 1990; E. W. Menzel, 1973; Teichroeb & Smeltzer, 2018; Trapanese et al., 2019; Valero & Byrne, 2007). It is from this body of work that I draw the route choice heuristics that I will attempt to identify in my chosen population, namely the *nearest neighbor, straight line, convex hull, shortest path and sweep heuristic,* defined and elaborated on in the table below (Table 1).

Heuristic	**Definition**	**Reference**
Nearest neighbor	Movement between platforms is based on choosing the next closest site, though the total route may not be the shortest.	Adapted from Joyce et al., 2021; Teichroeb & Smeltzer, 2018
Straight line	Foraging occurs in a straight line and the individual only turning when it reaches the end of the line.	Adapted from Joyce et al., 2021; Bailenson et al., 2000
Convex hull	Perimeter platforms are visited consecutively, with the inner platforms being visited in order of proximity to the array edge.	Adapted from Joyce et al., 2021
Shortest path[a]	Platforms are visited in order that reflects the shortest possible total travel distance.	Adapted from Joyce et al., 2021; Teichroeb & Smeltzer, 2018
Sweep heuristic	Routes are selected to reduce isolation of platforms.	Adapted from Joyce et al., 2021

Table 1: Heuristics and definitions to be used in this study

[a] The shortest path itself is not a heuristic *per se*; it represents an optimal outcome or goal rather than a procedural rule that can be followed (Teichroeb & Smeltzer, 2018).

2.3.1 Individual and social factors that can affect foraging behaviour

2.3.1.1 Age

The development of foraging strategies is essential for juveniles to be able to identify suitable habitats and exploit them for their long-term fitness (Grecian et al., 2018; Carter et al., 2020). Inexperience is one of the drivers of inequalities in foraging abilities that may result in young animals being competitively excluded from better foraging habitats by adults (Grecian et al., 2018). Behaviours learned from parents or other experienced individuals early in life, can allow for better foraging outcomes for individuals. This ability to apply learned behaviour from conspecifics is the central ideal behind the *exploration-refinement foraging hypothesis*, which stipulates that individuals progress from more exploratory random movements to more optimal movements strategies with age and experience (Votier et al., 2017). This behavioural refinement, with increased foraging effectiveness with age, has been seen in bumblebees (Osborne et al., 2013), seabirds (Frankish et al., 2020; Franks & Thorogood, 2018), terrestrial birds (Schuppli et al., 2012) and marine mammals (Grecian et al., 2018; McConnell et al., 2002). Squirrels are also known to learn foraging behaviours from conspecifics (Galef & Giraldeau, 2001), however their propensity to refine their foraging route choices over time has not been investigated.

2.3.1.2 Predation & Sex

In mammalian species, maternal investment in offspring includes pregnancy and lactation as way of providing nutrition to newborns (Bales, 2017). In 95-97% of species, parental care is provided exclusively by the females (Bales, 2017). Thus, mammalian females can have greater energy requirements than males, which can have impacts on how both sexes forage and acquire energy. These differing energy demands can lead to distinct strategies for resource distribution. The socio-ecological model proposed by Wrangham (1980) and developed by Sterck et al. (1997) and others, suggests that females will spatially distribute according to food availability while males will distribute themselves to maximize mating opportunities with females (Wrangham, 1980). According to this model females, motivated by their reproductive energetic requirements, might be expected to forage more quickly and efficiently than males.

However, the *predation risk hypothesis*, (developed under the term *reproductive strategy hypothesis*, by Main et al., 1996, retitled *predation risk hypothesis* by Ruckstuhl & Neuhaus, 2000) focuses on differences in individuals' actions to maximize lifetime reproductive success (Wearmouth & Sims, 2008). It assumes that females and their offspring are most vulnerable to predation pressures and have behavioural adaptations designed to minimize this risk. Notably, Wearmouth & Sims (2008) suggest that females will select foraging patches that reduce predation risk, even at the cost of foraging in sub-optimal conditions. Moreover, they also suggest that male foraging habitat selection is based on resource availability and that, not constrained by parental care, males are able to select high quality foraging patches even under riskier conditions. This means that even if females can have an inherently higher energetic demand but choose to forage in sub-optimal patches, they should employ strategies to maximize their foraging activities. According to the predation risk hypothesis, males would be expected to forage more often than females in the presence of predators and females would be expected to forage in sub optimal patches, and thus have foraging behaviour adaptations to overcome this. This could include both more frequent use of heuristics in general, or more consistent use of specific heuristics compared to their male counterparts.

2.3.1.3 Size

Size-dependent foraging–predation risk tradeoffs are often attributed to the *asset protection principal* (Clark, 1994). This principle posits that larger individuals will be more risk averse than their smaller conspecifics due to increased accumulated fitness "assets" and diminished energetic return for a foraging event with increasing body size (Naman et al., 2019). This means that larger individuals will be less likely to forage in the presence of a predator. This separation may be a method that allows smaller individuals to forage in more resource rich patches, when they would otherwise be outcompeted by larger individuals. However, as small individuals are more vulnerable to predation pressures, I expect them to modify their foraging behaviour to compensate for this risk (Newman et al., 1988). This could include foraging faster than their larger counterparts, for example.

2.3.1.4 Presence of conspecifics

The presence of conspecifics is known to have an impact on individual foraging behaviours. The *Information Center Hypothesis* posits that in some highly social species, the presence and aggregation of conspecifics can improve foraging outcomes for individuals by increasing the amount of information available to individuals (Cheng et al., 2020; Fernández-Juricic et al., 2005; Ward & Zahavi, 1973). Moreover, in many squirrel species foraging behaviours can be modified by the presence of conspecifics, such as altering the location of caches (Leaver et al., 2017). However, in many squirrel species, such as the eastern gray squirrel, *S.carolinensis* , individuals compete against each other for resources as opposed to working together to forage (Gorman & Roth, 1989; Hopewell et al., 2008). However, as many populations can have overlapping home ranges, eastern gray squirrels are expected to compete by exploitation instead of interference (Beltran & Meyer, 2013; J. L. Koprowski, 1996). Hopewell et al., (2008) describe eastern gray squirrels as modifying foraging behaviour in a context dependant manner. Individuals can either reduce the amount of food stored (opting to consume more often) or increase number of cached items (opting to cache more) in the presence of conspecifics (Hopewell et al., 2008).

2.4 Study Species

2.4.1 What is a squirrel?

The eastern gray squirrel (*S. carolinensis*) is a tree squirrel indigenous to and inhabiting most of North America. They have been transported across the globe; introductions of eastern gray squirrels have occurred at least 84 times in 8 countries on four continents, with a successful establishment of this species in at least 84% of these cases (J. Koprowski et al., 2016). While outside of their native range they are considered highly invasive with important impacts to local biomes. Here in Quebec, eastern gray squirrels are a keystone species, critical to the maintenance of forest landscapes via seed dispersal and seed predation (J. Koprowski et al., 2016; Steele et al., 2005).

Most eastern gray squirrels are gray in color (as the name suggests), but other phenotypes including brown, melanistic and albino can be found in nature (Ferron & Laplante, 2013; J. Koprowski et al., 2016) (Figure 1). In the wild, these diurnal squirrels inhabit dense forests, preferring areas with mature hardwood and mast producing trees (Parker et al., 2014). However, they have adapted to urban settings, and can be found in urban parks and cities. In the winter, squirrels live in dens constructed in hollowed trunks of trees, and in the summer, they build leaf nests in trees called "dreys" (Abu Baker et al., 2015). Eastern gray squirrels are omnivores, consuming a diverse and adaptable diet ranging from most plant tissues (i.e., berries, seeds, leaves, and bark) to animal matter (i.e., bones, small birds, eggs, small mammals, and vertebrate tissues including conspecifics) (Abu Baker et al., 2015; Hartney et al., 2003; J. L. Koprowski, 1996; Korschgen, 1981; Young, 2013). Foraging is a vital part of a squirrel's existence. In Maryland, a study estimated that eastern gray squirrels spend 80% of their daily activity budget on varied foraging activities (van der Merwe et al., 2007). Their natural diets vary with season and with presence of predators such as coyotes, foxes, owls, domestic cats, and dogs (J. Koprowski, 1994; D. E. Wilson & Reeder, 2005). Whenever food is plentiful, and especially during autumn, these squirrels are known to hide or "cache" their food for future consumption. This behaviour is called "scatter hoarding" and helps ensure survival through the winter. Scatter hoarding involves caching individual food items to be retrieved for future use. These squirrels do not hibernate in the winter, relying entirely on long-term spatial memory to recover foods cached up to several months prior (Delgado, 2017; Preston & Jacobs, 2009; Sundaram et al., 2017).

Figure 1: Examples of possible coat variation present in *S. carolinensis* populations in North America (Photo sources: Airwolfhound, 2017; BirdPhotos.com, 2010; Sackton, 2016; Trimming, 2017))

2.4.2 Squirrel social systems

A linear sex-based hierarchy has been described for many squirrel species (including eastern gray squirrels), where males dominate females with rank increasing with age (Delgado, 2017; Koprowski et al., 2016). Eastern gray squirrels, unlike fox squirrels, are not considered to be a territorial species, and they share their home ranges with other squirrel species (Hartney et al., 2003; J. Koprowski et al., 2016; Tounzen et al., 2012). However, some territorial behaviour has been observed with territory marking (scent marking or bark stripping), or as seasonal intraspecific male to male aggression (Allen & Aspey, 1986; Johnston, 2013; Youngblood, 1979). There have also been reports of maternal females defending home ranges against unrelated individuals and creating strong female kinship groups within a home range. Also, females will aggressively defend nest sites during the breeding season from unrelated squirrels (Delgado, 2017; J. Koprowski et al., 2016; Tounzen et al., 2012). Eastern gray squirrel mating systems are believed to be polygynous or promiscuous. Females are in oestrous for less than one day, and as many as 34 males can be drawn to a single oestrous female (J. Koprowski et al., 2016).

There is a high level of sociality present in this species, with the formation of small close-knit kinship groups, comprised almost exclusively of mothers and their female offspring with aggressive exclusion of unrelated individuals. Natal philopatry of females contributes to population recruitment, confirmed with microsatellite genetic analysis (J. Koprowski et al., 2016). Co-nesting occurs within these female groups, with shared care of juveniles until the babies are weaned at ~3 months of age (Delgado, 2017). However, while most squirrel interactions suggest that there is significant tolerance of conspecifics, there are many aggressive interactions noted especially surrounding food, as squirrels may perceive conspecifics as competitors around select food sources (Delgado, 2017; Leaver et al., 2007). In the winter, single sex groupings can be found of unrelated adults, both male and female, and these groups are thought to help individuals with thermoregulation during cold winter months (J. L. Koprowski, 1996)

2.5 Urban wildlife and behaviour

Eastern gray squirrels thrive in urban environments alongside humans. Having to modify behaviours to meet new and rapidly changing pressures, urban squirrels present some different behaviours from their wild, non-urban dwelling counterparts. The term “urban wildlife syndrome” was coined by Warren in 2006 to describe a set of frequently described characteristics of various wildlife species undergoing *synurbanization*, the process of becoming urbanized (Warren et al., 2006; Parker & Nilon, 2008). These traits include increased population density, increased intraspecific aggression and a reduced fear of humans and have been described in urban populations of gray squirrels (and many other species as well, including blackbirds, *Turdus merula,* raccoons, *Procyon lotor*, and northern water snakes, *Nerodia sipedon*) (Parker & Nilon 2008).

2.6 Studies on squirrel behaviour

Work with squirrel behaviour has explored decision making with regards to several types of movement in squirrels, such as dispersal in Siberian flying squirrels (*Pteromys volans*) (Selonen & Hanski, 2010), gap crossing by red squirrels (*Sciurus vulgaris*) (Bakker & Van Vuren, 2004), and natal dispersal in red squirrels (Hämäläinen et al., 2018). Foraging behaviours and cognition have been explored in fox squirrels (*Sciurus niger*), and to a lesser extent eastern gray squirrels (*Sciurus carolinensis*). These two species are sympatric throughout most of North America and share very similar morphology and behaviours (J. Koprowski & Steele, 2001). Of all the foraging behaviours, caching behaviours have been best studied and most explored in recent literature. Preston and Jacobs (2009) conducted three experiments on a group of fox squirrels (*S. niger)* investigating the influence of nut species, presence of nutshell and weight, on the decision of the individual to cache the item or consume it. Caching is an important foraging behaviour that contributes to the survival of an individual by storing food usually out of sight of conspecifics (Preston & Jacobs, 2009; Smith & Reichman, 1984; Stephens et al., 2008; Wall, 1990). Preston and Jacobs (2009) developed a detailed schematic of a possible decision-making process for when *S. niger* encounters a nut, incorporating both nut characteristics, familiarity with the item type, and squirrel physical condition (i.e., hungry or not), and including visual behaviours such as paw manipulation or head flicks. All these were found to be important components of the decision-making process for this species, with regards to nut selection.

In his PhD dissertation, Delgado (2017) explored cache decision and cognition in fox squirrels. He described some possible heuristics used by this species, specifically for where they chose to bury food items. Delgado (2017) identified key variables in the cache decision process: distance and direction traveled, locations of cache areas of different nut species, and density of caches. He also identified three specific heuristics employed by the individuals: matching the distance traveled before caching to the value of the food item (traveling further for more valuable food items), systematically covering a caching area (applying a hierarchical organization method to their cache sites that improves recall of cache locations), and matching cache density to minimize pilferage risk by other individuals (increasing caching activity of high value items in the presence of conspecifics).

2.7 Conclusion

In this Chapter, I explored the foraging behaviour of urban squirrels, examining the multifaceted impact of urbanization and anthropogenic activities on wildlife through a review of the literature. Urbanization, characterized by habitat fragmentation and the creation of novel ecological niches, presents challenges to local wildlife. In particular, the proliferation of urban trash provides both opportunities and challenges for urban-dwelling animals, influencing their foraging strategies and overall behaviour. Behavioural plasticity emerges as a critical trait, enabling wildlife to adjust behaviours and adapt to the dynamic conditions of urban environments. Squirrels exhibit considerable flexibility in their foraging behaviour, adapting to the availability of anthropogenic food sources through social learning and individual innovation.

In conclusion, the interplay between urbanization, wildlife foraging behaviour, and behavioural plasticity is complex and dynamic. There is a need for continued research to deepen our understanding of these interactions and inform conservation efforts and urban planning strategies. By examining the adaptive strategies employed by urban wildlife, valuable insights are gained into managing urban ecosystems to foster coexistence between human development and wildlife conservation. The importance of maintaining resilient and diverse urban ecosystems in the face of ongoing anthropogenic change is emphasized, advocating for a balanced approach to urbanization and wildlife conservation.

Chapter 3: Foraging Strategies and Route Selection Among Urban Squirrels in Montreal, Canada

3.1 Introduction

The focus of my field research was to investigate the foraging behaviour and route choice decision-making behaviours of eastern gray squirrels (*Sciurus carolinensis*) and compare them to those of Japanese macaques (*Macaca fuscata).* By examining how these two species run a foraging array, I aim to understand the heuristics and strategies they employ in navigating foraging arrays and how urban environments might influence these behaviours. This research contributes to our broader understanding of wildlife behaviour and cognitive processes in different species, particularly in the context of increasing anthropogenic pressures.

Eastern gray squirrels and Japanese macaques share several key ecological and behavioural traits that make them suitable for comparative analysis in this study. Both species are arboreal, which influences their foraging strategies and spatial navigation (Higurashi et al., 2018; J. Koprowski et al., 2016). An arboreal lifestyle necessitates climbing, which in some cases can drive evolutionary adaptations in musculoskeletal anatomy, for example enhancing grip to prevent falls from trees (Böhmer et al., 2018). In some species, these adaptations can eventually extend to using their hands for more than just climbing (Patel et al., 2015). For example, Japanese macaques and eastern gray squirrels both use their hands for various foraging tasks, in addition to their climbing activities (Dhananjaya et al., 2022; Makowska & Kramer, 2007). Additionally, both species are omnivores, adapting their diets based on the availability of food resources, which is particularly relevant in the dynamic environments of urban landscapes and areas of increasing anthropogenic pressure (He et al., 2021; Parker et al., 2014). They inhabit forested areas and live in regions with distinct seasonal variations, necessitating adaptations in their foraging behaviour to cope with periods of resource scarcity (Hill, 1997; J. Koprowski et al., 2016; Kurihara et al., 2020). Moreover, both species have been increasingly found in areas impacted by human development, with squirrels often inhabiting urban centers directly, while macaques are more commonly found on the periphery of human settlements (Cooper et al., 2008; Mochizuki & Murakami, 2011). Finally, both species have demonstrated problem-solving abilities in the context of foraging, a crucial similarity that underpins the hypothesis that they would exhibit comparable foraging strategies in the experimental array (Chow et al., 2021; Joyce et al., 2023).

Despite these similarities, Eastern gray squirrels and Japanese macaques also exhibit differences in their foraging behaviours and ecological adaptations. One of the most notable differences is in their food storage strategies: squirrels engage in scatter hoarding, where they store food in various locations for long-term use, relying heavily on spatial memory to retrieve these caches (Hopewell et al., 2008; Leaver et al., 2007). In contrast, Japanese macaques have specialized cheek pouches that allow them to store food temporarily for later consumption, which is a more immediate form of food management (Chatani, 2003). Additionally, macaques possess opposable thumbs, which not only facilitate more precise manipulation of objects but also enable potential tool use, a behaviour documented in some macaque populations (Higurashi et al., 2018; Huffman & Quiatt, 1986; Leca et al., 2011). Another critical difference lies in their social structures: squirrels are solitary foragers, whereas macaques forage in groups, a factor that influences their potential use of heuristics and spatial memory during foraging (Jayne et al., 2015; Kazahari & Agetsuma, 2008; Leaver et al., 2007; Sugiura et al., 2011). Squirrels, for example, must independently manage their foraging decisions and predator avoidance, which may lead to a different allocation of memory resources compared to macaques, who can rely on social learning and group dynamics to enhance foraging efficiency (Clark & Dukas, 1994; Garg et al., 2022; Jayne et al., 2015; Leaver et al., 2007, 2017; C. R. Menzel, 1991; Trapanese et al., 2019).

This chapter focuses on two primary research questions:

1) How do eastern gray squirrels navigate a foraging array in an urban environment?
2) How does their foraging behaviour compare to that of Japanese macaques on a similar foraging array?

My first research question aims to explore the strategies squirrels use to optimize their foraging efficiency. I hypothesized that they would minimize energy expenditure while running the array. I predicted that squirrels would run the array in a similar manner to Japanese macaques, employing foraging behaviours that reduce the energy needed to forage, such as visiting all the platforms on the field consecutively and collecting all available food items from the array before leaving. Additionally, I predicted that squirrels would avoid revisiting emptied platforms, and would select routes that correspond to a heuristic more often than expected by chance.

For my second research question, I hypothesized that macaques would run the array more efficiently than squirrels, utilizing strategies that would minimize energy expenditure. I predicted that Japanese macaques would cover shorter distances, run faster, and select routes consistent with heuristics more often than squirrels. Furthermore, I expected Japanese macaques exhibit less variability in route sequences than squirrels (see Table 2 for a summary).

Research Question	**Hypothesis**	**Prediction(s)**
1. How do squirrels navigate a foraging array in an urban environment?	1. Squirrels will minimize energy expenditure during their runs on the array	1.1 Squirrels will run the array in a similar manner to macaques (e.g., visiting all the platforms, collecting all food items from the field)
		1.2 Squirrels will avoid revisiting platforms
		1.3 Squirrels will select routes that correspond to a heuristic more often than expected by chance

2. How does the foraging of eastern gray squirrels compare to that of Japanese macaques on a foraging array?	2. Japanese macaques will run the array more efficiently than eastern gray squirrels	2.1 Japanese macaques will run shorter distances than squirrels
		2.2 Japanese macaques will run the array with greater speed that squirrels
		2.3 Japanese macaques will select routes consistent with heuristics more often than squirrels
		2.4 Japanese macaques will select unique route sequences less frequently than squirrels

Table 2: Overview of research questions, hypotheses, and predictions for this thesis

Comparing the foraging behaviours of Eastern gray squirrels and Japanese macaques offers valuable ecological insights, particularly in understanding how solitary versus social foragers adapt to urban environments. The solitary nature of squirrel foraging necessitates a reliance on individual cognitive processes, including spatial memory and decision-making, to navigate and exploit food resources efficiently (Leaver et al., 2007). This is reflected in the prediction that squirrels, while capable of applying heuristics, may do so less consistently and with more variability compared to macaques. On the other hand, the group foraging behaviour of macaques allows for the sharing of information and social learning, which can enhance the application of heuristics and lead to more consistent and efficient foraging patterns (Trapanese et al., 2019).

The predictions made in this study are grounded in these ecological and behavioural differences. For instance, the expectation that macaques will run shorter distances and select routes consistent with heuristics more often than squirrels is based on their spatial memory and the benefits of social foraging (Sugiura et al., 2011). Conversely, the prediction that squirrels will avoid revisiting platforms is linked to their reliance on spatial memory for scatter hoarding, which necessitates efficient use of foraging time and energy (Hopewell et al., 2008; Leaver et al., 2017). However, the solitary nature of squirrel foraging might also result in greater variability in their route selection, as they must independently balance the demands of resource acquisition with predator avoidance (Hopewell et al., 2008). Overall, this comparison provides a deeper understanding of how different species utilize cognitive strategies in response to the challenges posed by urban environments, with broader implications for conservation and wildlife management in increasingly urbanized landscapes.

3.2 Methods

3.2.1 Study Site and Subjects

I conducted my research at Mont Royal Park (45°30'07.5"N 73°35'45.5"W) (Figure 2). The study subjects were individual squirrels in a population of eastern gray squirrels present in the park. The 200-hectare Mont Royal Park is part of a larger 1000-hectare site consisting of three summits, and has been declared a heritage site by the Government of Quebec (Les Amis de la Montagne, n.d., *Actors and Stakeholders*). My study site was near Lac au Castors portion of the park. The area has anecdotally been known to harbor many squirrels and has a strong human presence that attracts squirrels who feed on discarded human food items. Gray squirrels share this park with many other animals, including 20 species of mammals (including direct competitors chipmunks and red squirrels), as well as many predatory bird species (including several owl and hawk species) (Les Amis de la Montagne, n.d., *Nature on Mount Royal*).

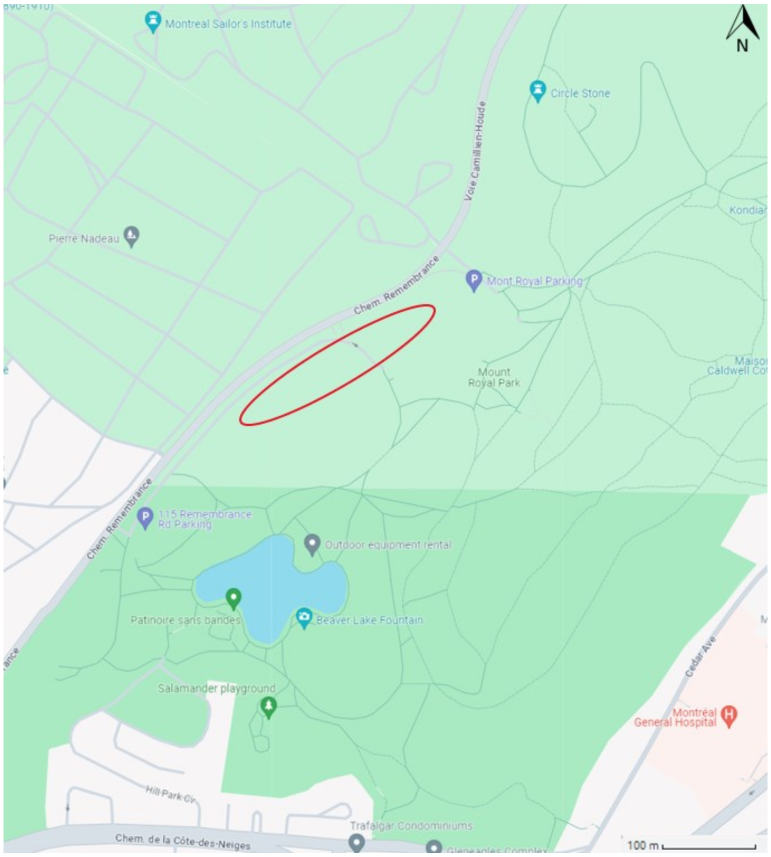


Figure 2: Map of Mont Royal Park study site, with the specific location of the foraging trials outlined in red (Google Maps, 2022).

3.2.1.1 Field data collection: Experimental foraging array

In this study, I used an *in situ* experimental foraging array to collect foraging movement choice data on individual squirrels at Mount Royal Park. The array configuration and video protocol were adapted from Joyce (2021), utilizing a technique developed by Teichroeb and colleagues to study decision making in primates (Teichroeb & Smeltzer, 2018). The array is a multi-destination foraging experiment, consisting of six feeding platforms arranged in a Z shape (Figure 3).

Originally, I used array dimensions identical to the array utilized by Teichroeb and Smeltzer (2018), however after several trials, I made some modifications. The primary issue I encountered with the array configuration was that after initial trials, squirrels were not completing the array, as they would wander off part way through running the array, either to investigate elsewhere or to cache their food item. At best, a squirrel would visit one or two platforms before returning to the forest edge. I thought that reducing the array size would allow the squirrels to locate food items with more ease, and minimize the number of interrupted or incomplete trials. To optimize the array for the squirrels, I shrunk the dimensions of the array to 25% the size of the original array. My justification for this resizing relied on two arguments. First, I was inspired by the rational employed by Kumpan et al. (2022) for their experiments. Kumpan et al. (2022) designed a multi-destination foraging array experiment involving different sized primate species and adjusted the size of the array according to the different species' size. They modified their arrays such that the shortest distance between two platforms was approximately twice the body length of the subject species (Kumpan et al,. 2022). Second, I thought the final dimensions of the array should be comparable to those employed on similar-sized rodents, such as laboratory rats, who have similar body size to eastern gray squirrels and have been used in similar types of experiments in laboratory settings (Blaser & Ginchansky, 2012; De Cothu et al, 2022; Jackson et al., 2020). I therefore scaled down the array to 25% of the original (Figure 3)

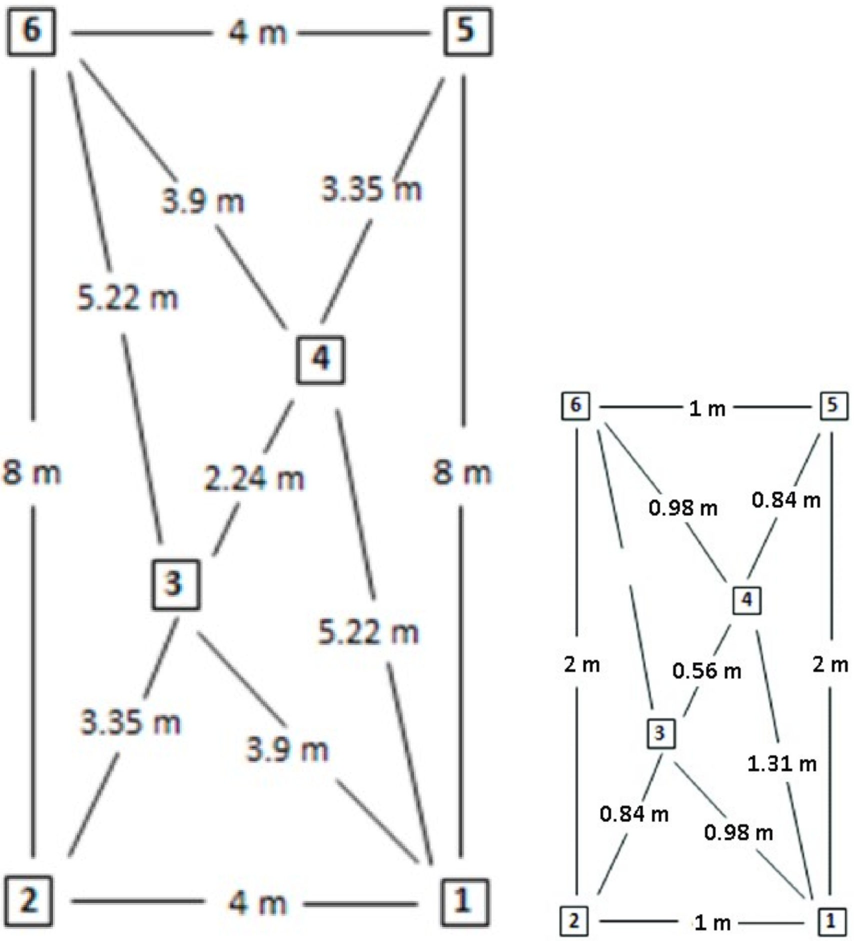


Figure 3: A diagram illustrating original and modified dimensions of Z-shape array used in the experiment (adapted from Teichroeb & Smeltzer, 2018)

As the array had to be taken down and reset for each field day (instead of permanent wooden platforms affixed to the ground like in the original primate arrays), six Styrofoam bowls (15cm diameter) were placed at ground level, secured with metal tent poles through the middle to ensure they could not be moved by the wind or by squirrels. I positioned the platforms using a precut template made from a stiff plastic tarp to ensure consistent placement every time the array was set up (Figure 4). The orientation of the array was rotated relative to the line of the forest edge, utilizing 6 different positions, each position rotated 30 degrees. To control for potential bias in the choice of entry point in the array, the array position was determined using a non-repeating random number generator.

When there were no squirrels visible within 20m of the array, I baited each platform with a single food item. During my initial field time, I found that using whole or partial nut pieces created the opportunity for squirrels to take the food item and cache it offsite, thus interrupting their trial of the array and creating an incomplete trial. To combat this, I mixed equal parts organic peanut butter with ground almonds and manually shaped them into small 1-2mm balls that I called “squirrel boba”. This seemed to mitigate caching behaviours, as the resulting food item was firm enough to hold but too soft to cache without it spreading on their paws.

Figure 4: Array setup in the field, a) Initial array setup with tarp template. and b) Fully assembled and operational array.

3.2.2 Data collection

The field experiment was run from August 2022 to November 2022, for a total of 25 days. I collected foraging behavioural data using video and directly with a behavioural custom-programed website application created by Ivan Miloslavov for this purpose. I set up 4 GoPro Hero7 4k video cameras, one clipped into a nearby tree branch as an overview, one backup aerial view from one of a variety of positions, and two at opposing ends of the array at ground level. The cameras were connected using a wireless remote and when an individual squirrel approached the array within a 5m radius, I began recording from all four cameras.

Using the website application, I recorded a description of each squirrel that visited the array including its color and any distinguishing features (e.g., bent or short tail, eye color, patchy coat). Despite my best efforts to identify individuals based on defining traits such as rare coat color or unique physical traits such as presence of scars, alopecia, differences in tail bushiness or skull shape (shorter versus longer snout), I was unable to identify individuals or sex in the field or from footage collected.

I recorded the order of visited platforms, the moment when a food item was eaten, presence of conspecifics within 5m of the field or also participating in the array, as well as any conspecific interactions. While I was prepared to record the presence of predators and presence of allospecific competitors on the field, none showed up during my trials. I also quantified human presence near the study site during trials, as well as distance of each platform from the tree line. Human presence was quantified by the total number of humans visible, measured every half an hour. I found that unlike macaques who were found to run the array consecutively mostly without interruption (Joyce et al. 2023), some squirrels would take a food item and leave the study site to cache the item and then return to the platforms. Considering this caching behaviour, I modified my food item (as detailed earlier) and recorded when an animal left the array to cache food (with a food item in their paws, mouth or cheek pouches) and when they returned to the array. If they did not return after 5 minutes, I ended the sample. I also found that, unlike the macaques, squirrels would continue to run the array after consuming all the food items, often doubling back on previously visited platforms, so I recorded entire platform visitation sequence and waited for squirrels to leave the array before ending the sample.

3.2.3 Data Analysis

3.2.3.1 Squirrel and monkey movement trials

I collected a total of 68 trials on squirrels using the array. All analyses were carried out in R 4.3.3 (R Core Team, 2022). The route sequences (order in which platforms were visited by the individual squirrels) were recorded at the time of experiment and confirmed later with video footage when possible. Time spent running the array (duration) was taken from timestamps in the field and confirmed with video footage, when possible, as well. The total distance the squirrel covered in the array (distance) was calculated post hoc by adding distances between platforms travelled. Due to technical difficulties in the field, clear video footage was unavailable for 15 trials. The squirrels did not always visit every platform, and I excluded trials where the squirrels visited three platforms or fewer, considering these as incomplete. All instances of caching also resulted in an incomplete trial, so were removed from final samples. This left me with 62 complete array trials.

I compared my data on squirrel movement choices to those collected by Megan Joyce for her MSc research on free-ranging Japanese macaques (*Macaca fuscata)* in 2019 at the Awajishima Monkey Center in Japan (Joyce et al., 2023; Joyce, 2021). Japanese macaque foraging array data from Joyce (2021) was adapted for comparison for this thesis. The movements of the macaques were much more consistent compared to the squirrel trials. Monkeys ran the foraging array, visiting all 6 platforms each time, and usually did so without revisiting any platforms, whereas I found that squirrels did not always visit all platforms, and frequently revisited platforms where they had already removed food. To enable a more meaningful comparison between the two species, I had to create subsets of my original data, adjusted to be more comparable to the Japanese macaque data. Details of these subset are described below.

Monkeys ran the array in a very straightforward manner, with almost every run being composed of a sequence of 6 unique platform visits. Squirrels did not demonstrate this same consistency. There were only two trials where a squirrel visited all six platforms, without revisiting any platforms first, however there were 28 trials where a squirrel visited 5 platforms consecutively without revisiting (SData5). I therefore had to adapt the experimental approach to accommodate the squirrel foraging patterns. Collaborating with my supervisor Sarah Turner, and Megan Joyce, we devised a novel strategy to address this challenge. Instead of relying on a single, classic six-platform array configuration as employed in prior studies, we developed six conceptual, 5 platform "quasi-arrays" by systematically “removing” one platform from the original array setup (Figure 5). Subsequently, we analyzed these quasi-arrays to manually identify routes corresponding to different heuristic patterns, including nearest neighbor (NN), and sweep heuristic (SW) patterns (Joyce et al. 2023). The shortest path outcome (SP) was determined by generating a list of every possible sequence for each of the 5-point “quasi-arrays” and identifying the shortest distance path(s). We were unable to generate routes corresponding to other heuristics, such as convex hull and straight line, on the quasi arrays. Therefore, these heuristics were not assessed. I used a Chi-square test to compare the frequency with which routes were consistent with potential use of heuristics between monkeys and squirrels.

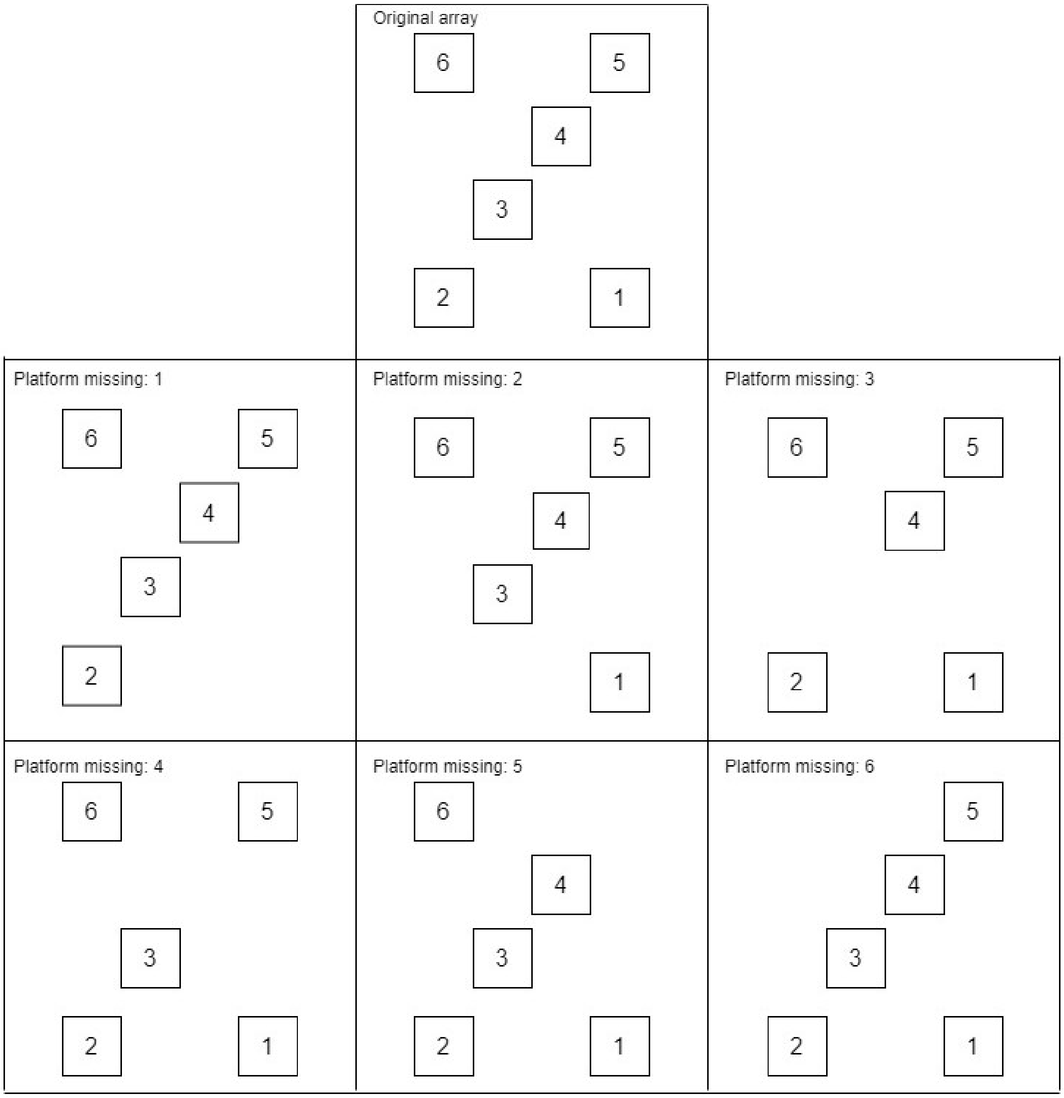


Figure 5: All permutations of 5-point foraging arrays (quasi arrays)

I classified the squirrel trials into separate groups, based on if the data was on the original 6 platform array, or modified for 5 platform arrays, then subdivided based on other traits, such as platform revisits, potential heuristic use, and trials with timestamps associated (Table 4). I also extracted grouped the macaque trials into same categories as for the squirrel data (Table 4)

	Trial	Description	Squirrel	Monkey	Dataset name *
6 platform array	Complete array run including revisits	All 6 platforms were visited	n=62	n=155	Data1
	Complete array run without revisits	All 6 platforms were visited consecutively without revisits or caching	n=2	n=155	Data2
	Runs with durations	Trials that had times associated with the data	n=62	n=139	Data3
5 platform arrays	Potential heuristic use	Selected a route corresponding to a known heuristic (e.g., shortest path, nearest neighbor or sweep heuristic)	n=20	n=98	Data4
	Complete array run without revisit	All 5 platforms were visited consecutively without revisits or caching	n=28	n=155	Data5

*Primate data are labeled with a "P" prefix (e.g., PData1, PData2, etc.), while squirrel data are labeled with an "S" prefix (e.g., SData1, SData2, etc.).

Table 3: Summary of data groupings for this thesis

The variables assessed in this study were chosen to be able to capture key aspects of foraging behaviour both Eastern gray squirrels and Japanese macaques. These variables include distance traveled, time spent on the array, heuristic use, revisit frequency, run sequence, and speed. The variables and their definitions are summarized in Table 4, and additional visualizations of the data can be found in Appendix A.

Variable	Definition
Distance	The total length traversed by the subject on the array, measured in meters (m).
Duration	The total time spent by the subject on the array, measured in seconds (s).
Heuristic use	Indicates whether the route sequence followed by the subject corresponds to a known heuristic such as Nearest Neighbor (NN), Shortest Path (SP), or Sweep (SW).
Revisit	Instances where the subject visits a platform that has already been visited during the trial.
Run sequence	The specific order in which the subject visits the platforms during the trial.
Speed	The rate of movement of the subject calculated as the trial distance divided by the duration, measured in meters per second (m/s).

Table 4:Definition of variables used in this study

3.2.3.2 Statistical analyses: trial duration, distance, and speed

When data did not meet the requirements for parametric tests, I attempted log, square root, and rank transformations to achieve normal distribution of residuals. I then tested for normalcy with a Shapiro-Wilk test and examining histograms and QQ plots. Most data did not meet the assumptions for normalcy, so I used non-parametric analyses for most variables: chi-square and Mann-Whitney U test. Only speed of trials met the requirements for parametric statistics when log transformed (monkeys W = 0.9892, p-value = 0.3558; squirrels W = 0.96835, p-value = 0.1888) and was therefore analyzed using F- test and equal variance t test.

To control for size differences between squirrels and Japanese macaques, I indexed the duration for each trial where all 6 platforms were visited using a scale from 0-1, with 0 representing the slowest recorded run for that species, and 1 indicated the fastest (SData3, MData3).

For the trial distance, I adjusted the distance tested to compensate for the difference in array size between monkeys and squirrels. I adjusted the squirrel data by multiplying the distance by four, as the array was scaled down by a factor of 0.25 from the original primate designed one. I then ran Wilcoxon rank-sum test and Cohen's d test for effect size.

Trial speed was extrapolated from trial duration and distance (SData3, MData3). As I was unable to modify the duration on the array for the monkeys to conform to a 5-platform array configuration, I compared trial speed for the two species on the full 6 platform array, using squirrel data where the entire array was emptied, and monkey data that had time associated with them. Once log transformed, the data met the criterion for normal distribution (Shapiro Wilks p-value >0.05), so I employed an F test to compare variance of log speeds checking for homogeneity of variances (F = 1.1183, p-value = 0.6622). As there was no significant difference in variances, I then ran a two-sample t-test to compare mean log speeds of the two species. Platform visit sequences were also compared between species. This included assessing both the presence or absence of platform revisiting behaviour, as well as general sequence order comparisons. I conducted Pearson's Chi-squared test with Yates' continuity correction to compare the frequency of platform revisiting behaviour between squirrels and monkeys. I then examined the proportions of trials with repeats and without repeats within each species.

3.3 Results

3.3.1 Just squirrel data

The average time spent by squirrels on the array across all 62 runs was 145 seconds (SData1). However, when focusing on a subset of runs where squirrels visited the first 5 unique platforms in a sequence, the average time increased significantly to 368s (SData5). Squirrels exhibited a variety of foraging behaviours on the array, rarely adhering to a straightforward pattern of emptying the platforms in a sequence. Surprisingly, not every trial concluded with an emptied array, as only 82% of the runs resulted in this outcome, indicating that squirrels occasionally left food untouched on the field (SData1). On average, it took squirrels approximately 8.2 platform visits to deplete the array, although in some cases, there were up to 14 visits required before the array was emptied. Even after depleting the array, squirrels did not consistently cease their foraging activity; the total sequence length ranged from 7 to 19 platform visits, with an average of 13 platforms visited per trial (Figure 6). Squirrels visited an average of 5 extra platforms if they emptied the array during their runs.

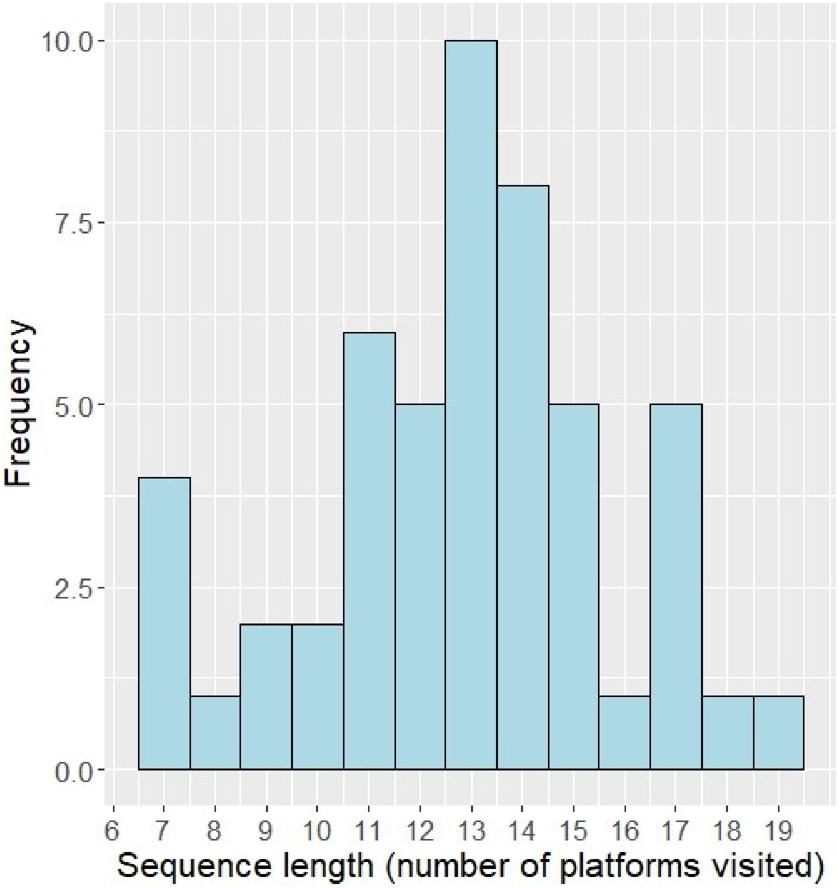


Figure 6: Frequency of total squirrel route sequence lengths (SData1)

3.3.2 Interspecific comparisons

3.3.2.1 Interspecific trial durations

I used descriptive statistics to summarize and visualize the durations on the 6-platform array for both monkeys and squirrels (SData3, MData3). Squirrels had a wider range of trial durations than the monkeys did; Monkey trial durations ranged from 16s to 184s, while for squirrels, the range was 35s to 632s. I conducted Shapiro-Wilk normality tests to assess the distribution of the standardized run durations. The trial duration was not normally distributed for either species (p-value<0.05), so I used a Mann- Whitney U test. The results of the Mann-Whitney U test (p-value<0.001) indicate a significant difference in trial duration between the two species.

3.3.2.2 Interspecific trial distance comparison

Given that the data for the 5-point array did not meet the requirements for parametric testing, as confirmed by the Shapiro-Wilk test results (p-value < 0.05), I used data visualization and non-parametric tests for statistical analysis (SData5, MData5). The results of the Wilcoxon rank-sum test revealed no significant difference in run distances between the two species (p-value > 0.05).

Furthermore, the effect size was negligible (Cohen's d, d= was 0.1146, 95% confidence interval = -0.2908 to 0.5199).

However, for the total distance run on the 6 platform arrays (MData1, SData1), adjusted for species size, Mann-Whitney U test/Wilcox rank sum showed a significant difference between the two groups (p-value < 0.001), and Cohen's d quantifying the effect size as large (d=4.068566, 95% CI = 3.562996 4.574137), with squirrels trials longer than those of the monkeys (Figure 7). Looking at the median of run distances shows squirrels were covering more than double the relative distance on the array compared to monkeys (44.6m for squirrels and 20.19m for monkeys).

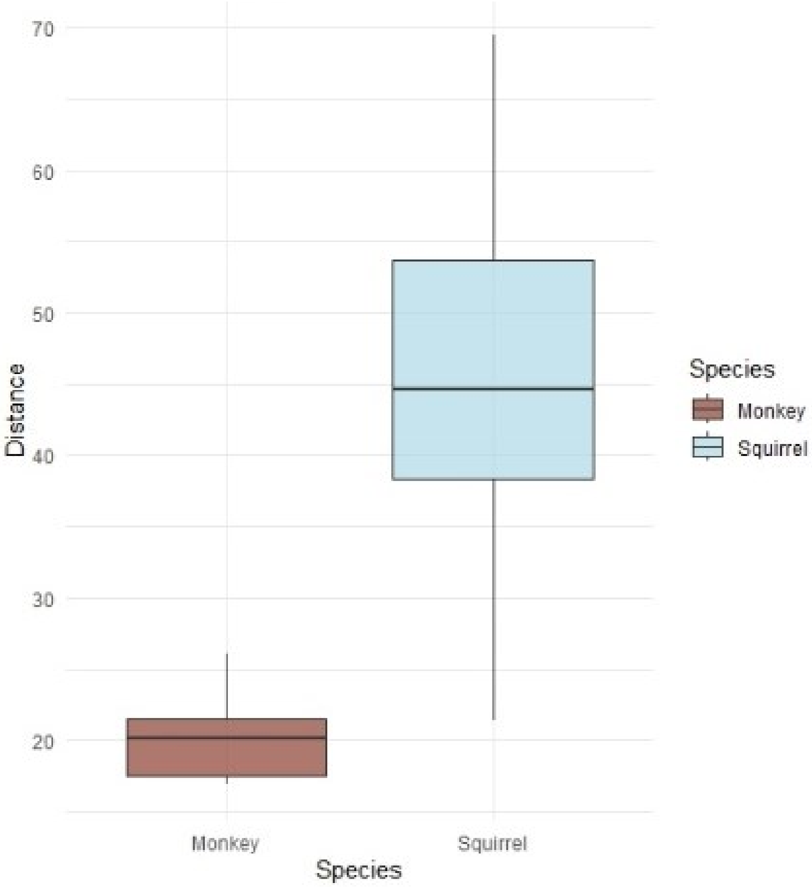


Figure 7: Comparison of total run distances (m) between monkeys and squirrels on the 6-platform array (SData1, MData1) Distance adjusted for body size, see section 3.2.1.1. This boxplot illustrates the median values for squirrel and monkey trial distances (thick lines inside the boxes). The top and bottom lines of the boxes represent the inter-quartile range (25th and 75th percentiles). The whiskers show the maximum and minimum values of the samples.

3.3.2.3 Interspecific speed comparison

The analysis began with log-transforming the speed data for both monkeys and squirrels (SData13, MData3) to stabilize variance and meet normality assumptions. The log transformed data for both species passed Shapiro-Wilk test criterion for normal distribution (monkeys W = 0.9892, p-value = 0.3558; squirrels W = 0.96835, p-value = 0.1888). The Shapiro-Wilk test confirmed that the residuals from the linear model fit were also normally distributed (W = 0.99251, p-value = 0.4398), validating the assumptions for subsequent t-tests. The F-test indicated no significant difference in variances between the log speeds of the two species (F = 1.1183, p-value = 0.6622), supporting the use of the equal variance t-test. The two-sample t-test assuming equal variances revealed a significant difference in mean log speeds between the two species (t = 17.83, df = 188, p-value < 0.001). The mean log speed for monkeys was 3.688981, while for squirrels, it was 2.107932. Visualizations generated showed a visible difference in trial speed between species (Figure 8).

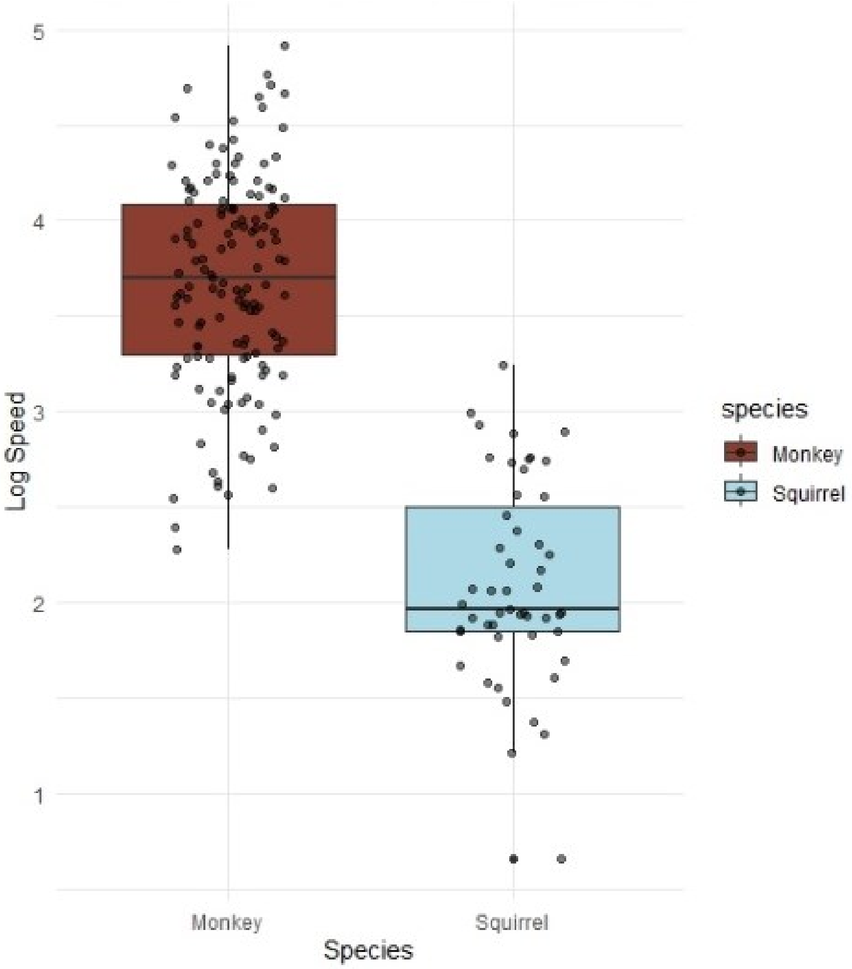


Figure 8: Log transformed trial speeds for monkeys and squirrels on 6-platform arrays (MData3, SData3). This boxplot illustrates the median values for the log of squirrel and monkey trial times (thick lines inside the boxes). The top and bottom lines of the boxes represent the inter-quartile range (25th and 75th percentiles). Additionally, jitter dots are overlaid on the plot to show

individual data, providing a clear visual representation of the data points and their spread within the distribution.

3.3.2.4 Interspecific platform sequences and potential use of heuristics comparison

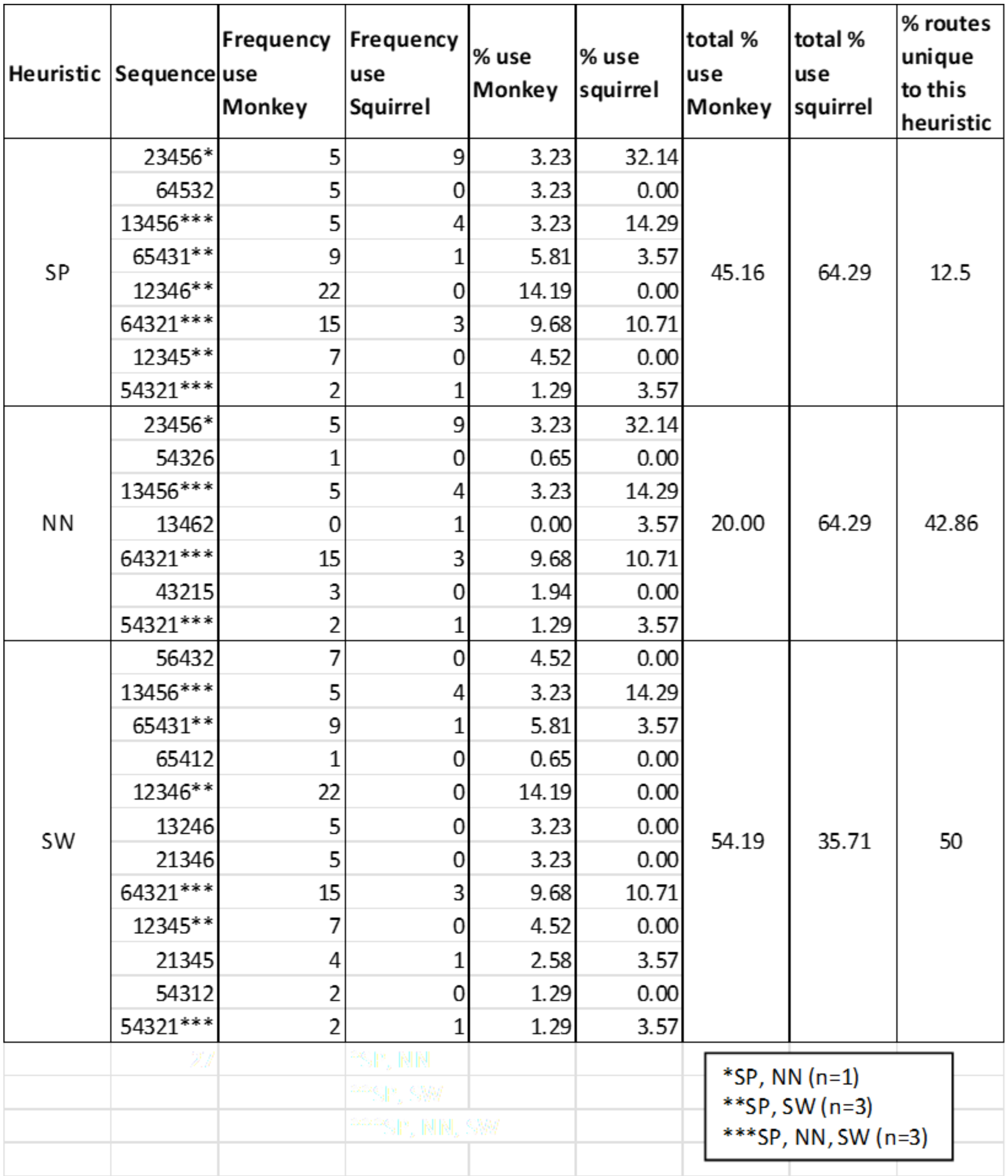
Comparing the trials between monkeys and squirrels revealed differences in foraging patterns. Monkeys demonstrated a higher degree of consistency in navigating the entire 6-platform array compared to squirrels. While squirrels rarely completed trials that encompassed all 6 platforms in a non-repeating sequence (SData2, n=2), they displayed a notable tendency to run the first 5 platforms uniquely much more frequently (MData2, n=28). Upon further comparison of 5-sequence runs between the two species (SData5, MData5), distinct trends emerged regarding platform preferences. For squirrels, platform #1 was consistently the most missed within the 6-platform array, whereas for monkeys, platform #5 emerged as the most frequently missed. Intriguingly, both species demonstrated a consistent visitation pattern for platform #4 within their first 5-platform sequence, suggesting some strategic importance in their foraging behaviour.

Revisiting platforms on the array was also investigated between the two species (SData1, MData1). Statistical analysis revealed a highly significant difference in revisiting behaviour between squirrels and monkeys, as evidenced by Pearson's Chi-squared test ($\chi^2 = 166.98$, p-value $< 2.2e-16$). This result indicates a substantial disparity in the tendency of the two species to revisit platforms. Specifically, monkeys exhibited 96.13% non-repeats and 3.87% revisits, while squirrels showed 6.45% non-repeats and 93.55% revisits. These proportions highlight the fact that squirrels revisit platforms significantly more often than monkeys.

In contrast, a Chi-squared test ($\chi^2 = 0.38461$, p-value $= 0.5351$) for heuristic use between the two species indicated no significant difference (SData4, MData4). This suggests that the frequency with which squirrels and monkeys employ heuristics in their foraging behaviour is statistically similar. 63.23% of monkey trials were consistent with heuristic use, compared to 71.43% of squirrel trials. There was a significant overlap between sequences and heuristics, with many paths corresponding to more than one heuristic. Across both species, 17 of all the selected route sequences were identified as corresponding to one or more heuristics on the quasi-arrays (Table 5). Of these 17 sequences, 10 (58.82%) were associated with a single heuristic, while the remaining sequences corresponded to two or all three heuristics (Table 6). Squirrels used routes associated with both the SP and NN heuristics equally, each accounting for 64.29% of their selected routes. In contrast, the heuristic most frequently favored by monkeys was the SW heuristic, which accounted for 54.19% of their selected routes.

Route	Heuristic	% use monkey	% use squirrel
23456	NN, SP	3.23	32.14
54326	NN	0.65	0.00
56432	SW	4.52	0.00
64532	SP	3.23	0.00
13456	NN,SP,SW	3.23	14.29
65431	SP, SW	5.81	3.57
65412	SW	0.65	0.00
12346	SP, SW	14.19	0.00
13246	SW	3.23	0.00
13462	NN	0.00	3.57
21346	SW	3.23	0.00
64321	NN,SP,SW	9.68	10.71
12345	SP, SW	4.52	0.00
21345	SW	2.58	3.57
43215	NN	1.94	0.00
54312	SW	1.29	0.00
54321	NN,SP,SW	1.29	3.57

Table 5: Summary of the 17 selected sequences corresponding heuristic(s) on the quasi-array setups. This table details each sequence's association with specific heuristic(s) and includes the percentage of occurrences for each sequence in monkey and squirrel trials



Heuristic	Sequence	Frequency use Monkey	Frequency use Squirrel	% use Monkey	% use squirrel	total % use Monkey	total % use squirrel	% routes unique to this heuristic
SP	23456*	5	9	3.23	32.14	45.16	64.29	12.5
	64532	5	0	3.23	0.00			
	13456***	5	4	3.23	14.29			
	65431**	9	1	5.81	3.57			
	12346**	22	0	14.19	0.00			
	64321***	15	3	9.68	10.71			
	12345**	7	0	4.52	0.00			
	54321***	2	1	1.29	3.57			
NN	23456*	5	9	3.23	32.14	20.00	64.29	42.86
	54326	1	0	0.65	0.00			
	13456***	5	4	3.23	14.29			
	13462	0	1	0.00	3.57			
	64321***	15	3	9.68	10.71			
	43215	3	0	1.94	0.00			
	54321***	2	1	1.29	3.57			
SW	56432	7	0	4.52	0.00	54.19	35.71	50
	13456***	5	4	3.23	14.29			
	65431**	9	1	5.81	3.57			
	65412	1	0	0.65	0.00			
	12346**	22	0	14.19	0.00			
	13246	5	0	3.23	0.00			
	21346	5	0	3.23	0.00			
	64321***	15	3	9.68	10.71			
	12345**	7	0	4.52	0.00			
	21345	4	1	2.58	3.57			
	54312	2	0	1.29	0.00			
	54321***	2	1	1.29	3.57			

*SP, NN (n=1)
**SP, SW (n=3)
***SP, NN, SW (n=3)

Table 6: Summary of routes selected by Awajishima monkeys and Montreal squirrels, that correspond to heuristics for the 5-platform quasi-arrays. Includes route (sequence of platforms visited), which corresponds to potential heuristic(s), frequency and overall percentage of each route selected from total runs.

I conducted statistical tests to compare the proportions of unique sequences selected by monkeys and squirrels, accounting for their respective total trials on a 5-platform array (SData5, MData5). The Chi-square test for proportions yielded a test statistic of $\chi 2$= 3.6403, with df=1 and a p-value of 0.0564, suggesting weak evidence against the null hypothesis of equal proportions. This indicates that there may not be a significant difference in the proportions of sequences selected between monkeys (26.45%) and squirrels (46.43%). In contrast, Fisher's exact test provided a p-value of 0.04271, leading to the rejection of the null hypothesis. This indicates a statistically significant association between animal type and sequence selection, suggesting that the odds of selecting certain sequences differ between monkeys and squirrels, with monkeys potentially selecting unique sequences less frequently than squirrels. The 95% confidence interval for the odds ratio (0.1686, 1.0408) further supports these findings, although it includes 1, indicating some uncertainty in the magnitude of the effect. A summary table of findings for the outcomes of research questions is included below with outcome column added (Table 5)

Research Question	**Hypothesis**	**Prediction(s)**	**Result(s)**
1. How do squirrels navigate a foraging array in an urban environment?	1. Squirrels will minimize energy expenditure during their runs on the array	1.1 Squirrels will run the array in a similar manner to macaques (e.g., visiting all the platforms, collecting all food items from the field)	Squirrels exhibited foraging behaviours that differed from macaques, including sometimes not visiting all the platforms and leaving food items on the field.
		1.2 Squirrels will avoid revisiting platforms	Squirrels revisited platforms on nearly every trial, 93.55% of the time. (SData1)
		1.3 Squirrels will select routes that correspond to a heuristic more often than expected by chance	Squirrels selected routes corresponding to one (or more) heuristic in 71% of trials (SData4)
2. How does the foraging of eastern gray squirrels compare to that of Japanese macaques on a foraging array?	2. Japanese macaques will run the array more efficiently than eastern gray squirrels	2.1 Japanese macaques will run shorter distances than squirrels	Macaques ran the array with significantly shorter distances than squirrels, due in part to squirrel tendency to revisit platforms (mean distance was 44.6m for squirrels and 20.19m for monkeys, adjusted for body size).
		2.2 Japanese macaques will run the array with greater speed that squirrels	Macaques ran the array significantly faster than squirrels (MData3, SData3)
		2.3 Japanese macaques will select routes consistent with heuristics more often than squirrels	The two species selected heuristics at statistically similar rates (71.43% and 63.23%, respectively) (MData4, SData4)

		2.4 Japanese macaques will select unique route sequences less frequently than squirrels	Macaques selected unique route sequences at approximately the same rate as squirrels (26.45% and 46.43% respectively)

Table 7: Overview of research questions, hypothesis, predictions and summary of associated results for this thesis

3.4 Discussion

In this study, my aim was to investigate the foraging behaviour and animal decision-making (ADM) behaviours in urban squirrels and compare them to those of Japanese macaque monkeys. We sought to understand the potential differences in run distances, revisiting behaviours, heuristic use, and running durations between these species to inform understanding about the tradeoffs animals make in foraging, their uses of space, and potential differences between species capacity to forage efficiently and solve foraging route choice problems.

3.4.1 Route trial time, distance, speed

The analysis of Eastern gray squirrels' (*Sciurus carolinensis*) foraging behaviour on the experimental array revealed significant insights into their foraging in urban environments. The data indicated that squirrels predominantly selected routes that minimized travel distance or were consistent with a foraging heuristic, supporting the hypothesis of energy-efficient foraging. However, their higher-than-expected rate of revisiting previously visited platforms suggested less precise spatial memory and route planning, possibly due to the dynamic nature of urban food sources. On one hand, their relatively low foraging speed, coupled with repeated platform visits, might reflect a cautious and thorough approach to foraging in novel environments, potentially an adaptive strategy to avoid threats and ensure no food items were left behind stemming in part from a history of being solitary foragers. On the other hand, unexpectedly, many array runs concluded with left food on the field, suggesting further complexity in their foraging behaviour.

It was interesting to see the differences between how monkeys and squirrels ran the array, both 6-platform and 5-platform configurations. My results suggest and highlight some differences in how these species go about finding food. When looking at 5-array configurations, I found no significant differences in run distances between the species (MData5, SData5), however this changed when looking at entire foraging events on the 6-platform arrays (MData1, SData1). Overall, squirrels spent significantly more time during the entirety of each foraging event than monkeys, and covered almost twice the distance relative to body size, of their primate counterparts. Monkeys exhibited a much narrower range of trial speed, suggesting a more consistent performance during foraging events, with times likely clustering more closely to a maximum foraging speed. Speed proved to be a very interesting metric to look into considering the significant difference in run distances (MData3, SData3). Monkeys demonstrated significantly faster average speeds than squirrels, indicating a more direct and possibly more focused approach to completing the array trials.

3.4.2 Foraging behaviour: revisiting and heuristics

3.4.2.1 Revisiting behaviour

Revisiting platforms emerged as a significant behavioural difference between Japanese macaques and eastern gray squirrels during foraging trials on the array. While macaques virtually never revisited a platform, with only 3.87% of platforms revisited (MData1), squirrels almost always did, revisiting at least one platform in 93.55% of trials (SData1). This consistent behavioural difference in foraging activities raises questions about the underlying mechanisms and adaptive strategies driving these behaviours.

One potential explanation lies in potential differences cognitive abilities and memory functions. Japanese macaques are known to possess advanced spatial memory and problem-solving skills, enabling them to remember which platforms they have already visited and to avoid revisiting empty ones (Joyce et al., 2023; Trapanese et al., 2019). In contrast, while squirrels possess excellent memory for caching and retrieving stored food items, their memory might be more tuned to hiding items rather than seeking them out (Jacobs & Liman., 1991; Delgado et al., 2017; Koprowski et al., 2017; Leaver et al., 2007). This difference in memory prioritization and specialization could lead to more frequent revisits by squirrels as they double-check for overlooked food items.

Foraging strategies and ecological adaptations could also play a crucial role. In natural habitats, squirrels often encounter poorer quality or less abundant food sources, necessitating prolonged foraging efforts to gather sufficient resources (Jokimaki et al., 2017; Wist & Dausmann, 2024). This might lead to a higher tolerance for revisiting platforms to maximize food intake, a behaviour that could improve foraging outcomes in other contexts, however, is less efficient in the context of the experiment. Additionally, the high density of squirrels in urban settings might drive them to attempt ensure no food is left behind, as leaving food could attract competitors, so it might be that they are making a tradeoff, worth the increased risk of foraging longer in a given patch to ensure that the patch is empty before moving to another area (Dantzer et al., 2012; Dobbs et al., 2007).

The design of the foraging array itself may also contribute to these behavioural differences. Originally designed for primate experiments, the array might be more intuitive for macaques to navigate. Because they are taller and have a broader field of vision compared to squirrels, they may be able to survey more of the array at a glance, unobstructed by minor landscape features. This enhanced visibility could reduce their need to revisit platforms, as they can easily determine if a platform is empty. This design bias could inadvertently make it more challenging for squirrels, who might not find the array as easy to navigate and thus revisit platforms more often. This stark contrast in revisiting behaviours underscores the distinct foraging strategies and environmental adaptations of the two species, highlighting the complexity of their foraging behaviours and the influence of ecological contexts.

3.4.2.2 Heuristics

Potential use of heuristics during foraging events was assessed on the 5-platform or quasi-arrays setup. The majority of trials and routes selected by both Japanese macaques and Eastern gray squirrels corresponded to potential heuristics, even though these heuristics were in the minority of the overall potential route sequences. Specifically, while 36.56% of all route sequences selected by monkeys corresponded to one or more heuristics, 63.23% of their trials involved possible heuristic use (table 5). For squirrels, these numbers were 53.85% and 71.43%, respectively. Interestingly, a Chi-square test for heuristic use ($\chi^2 = 0.38461$, p-value = 0.5351) indicated no significant difference between squirrels and monkeys. This finding aligns with those in the existing literature on primates, who are known to utilize routes corresponding to heuristics when foraging (Joyce et al., 2023; Sayers & Menzel, 2012; Teichroeb, 2015; Teichroeb & Smeltzer, 2018). Squirrels are also known to behave as though they are employing heuristics in the context of caching food items (Delgado, 2017; Preston & Jacobs, 2009). However, it is also possible that their potential use of heuristics extends beyond caching to include acquiring and searching for food items (Leaver et al., 2017).

When examining the specific possible heuristics employed by each species, I found that squirrels used routes associated with both the Shortest Path (SP) and Nearest Neighbor (NN) heuristic equally, with each accounting for 64.29% of their selected routes. This suggests that squirrels might be relying on a combination of proximity-based decision-making (NN) and overall efficiency (SP) when navigating the array, reflecting their need to balance energy conservation with effective foraging. In contrast, Japanese macaques most frequently favored the Sweep (SW) heuristic, which accounted for 54.19% of their selected routes. The preference for the SW heuristic by macaques may indicate a strategy that prioritizes systematic coverage of the array to ensure that no food items are missed, possibly reflecting their social foraging behaviour and the need to maximize resource acquisition within a competitive group setting.

Heuristic use leverages memory to make quick judgments, a fundamental cognitive ability (Schwikert et al., 2014). The fact that both squirrels and monkeys exhibit similar rates of potential heuristic use is intriguing and may stem from shared characteristics in their social systems and environmental interactions. Both species exhibit complex social systems with vertical behavioural transmission from parents to offspring (Mateo, 2014). This close contact with conspecifics facilitates the transmission of foraging skills and social strategies, likely enhancing foraging efficiency within their populations (Galef & Giraldeau, 2001; Harel et al., 2017; Miller et al., 2014). Additionally, the ecological and environmental contexts in which both species operate could contribute to their similar potential heuristic use. Both Japanese macaques and eastern gray squirrels are arboreal mammals that forage both in trees and on the ground, and both use their hands to forage (Dhananjaya et al., 2022; Makowska & Kramer, 2007; Tamura, 2020). These shared environmental interactions might lead to convergent foraging strategies, including potential heuristic use. The differences in specific potential heuristic use likely reflect the different foraging contexts of these two species. As solitary foragers, squirrels may be seeking to optimize their individual energy expenditure by getting individual food items in the most effective way possible. On the other hand, macaques' foraging strategies could reflect their social foraging dynamics, where trying to minimize isolation of individual food pieces could reduce the risk of another group member taking it. These findings underscore the influence of social structure on foraging behaviour and highlight the flexible cognitive strategies these species employ as a response to the unique challenges of their environments.

On the other hand, the experimental design might not have been sensitive enough to capture species-specific differences in potential heuristic use (Casler, 2015; Karp & Fry, 2021; Uher & Visalberghi, 2016) . This may because squirrels and Japanese macaques, as inherently different species, possess distinct cognitive and sensory processing mechanisms. Comparative studies between rodents and non-human primates reveal that primates have a more complex cortical structure, including a well-developed prefrontal cortex and greater neural diversity, which are associated with advanced cognitive functions and problem-solving abilities (Belmonte et al., 2015; Matzel & Sauce, 2017; Zhang et al., 2023). In contrast, rodents have less specialized brain structures and may possess more limited cognitive capabilities in certain problem solving situations (Zhang et al., 2023). These differences suggest that primates, including Japanese macaques, may utilize more sophisticated or distinct heuristics and strategies in navigating tasks compared to squirrels, which have different sensory and cognitive adaptations. Since the array was originally designed with primates in mind, it may not be tailored to accurately assess squirrel foraging behaviours, and the potential heuristics use in this species.

In summary, the similarity in potential heuristic use between Japanese macaques and eastern gray squirrels during foraging events highlights interesting parallels in their cognitive abilities and ecological adaptations. This finding underscores the importance of considering both species' social systems and environmental contexts when examining their foraging behaviours. The lack of significant difference in heuristic use could reflect a common adaptation to increasing anthropogenic pressure or a shared evolutionary strategy. Squirrels' tendency to revisit platforms and cover greater distances suggests a strategy that balances exploration and efficiency. In contrast, monkeys' faster speeds and more consistent performance may reflect a different cognitive strategy optimized for task completion speed. Further research might explore the nuances of heuristic use in more varied experimental designs to better understand the specific strategies employed by each species.

Chapter 4: Trash Foraging: A Review of Behavioural Implications for Urban Wildlife

4.1 Introduction

The impacts of human activities on the environment have soared dramatically, leading to significant human-induced environmental changes and unsustainable practices (Otto, 2018). Modern humans have become a dominant force of nature, exerting a global impact that rivals natural environmental and geological processes (S. L. Lewis & Maslin, 2015; Mackay, 2015; Walters et al., 2023). Global urbanization, the increased concentration of urban settlements, is an important driver and acerating aspect of these changes (Elmqvist et al., 2021; US EPA, 2015; Vlahov, 2002). The increasing urbanization processes pose challenges to wildlife. Rapid destruction of natural habitats, driven by activities such as land clearing for agriculture and to construct and expand cities, alongside long-term and gradual ecosystem degradation due to edge effects, invasive species, and pollution among other factors, creates a complex set of stressors for wildlife (McDonnell & Hahs, 2015). These disturbances, coupled with documented instances of biodiversity loss and local extinctions within urban areas, highlight the impact of urbanization on natural ecosystems (Hahs et al., 2009; Thompson & Jones, 1999).

Hand in hand with the increasing human global population is the increase in food production, a phenomenon that has implications for both human sustenance and ecological dynamics (Cumming et al., 2014). Every year a staggering 1.3 billion tonnes of food produced for human consumption end up as waste globally; a major challenge in our quest to sustainably feed the growing human population (Gustavsson et al., 2011; Newsome & Van Eeden, 2017). This widespread waste of food, in addition to ethical and economic dimensions, has far-reaching ecological repercussions. Large quantities of discarded food, including fruit, vegetables, grain crops, and even animal carcasses, have become readily accessible to wildlife as sources of food (Newsome & Van Eeden, 2017). The consequences of this accessible food waste are multifaceted, ranging from alterations in wildlife ecology and behaviour to cascading effects on entire ecosystems (Newsome & Van Eeden, 2017; Plaza & Lambertucci, 2017).

As landscapes change, so does the behaviours of urban wildlife. Learning and behavioural plasticity – the ability to make behavioural adjustments – become critical for survival in these highly modified environments (Ritzel & Gallo, 2020). The urban environment, with its unique suite of stressors, such as noise, light, vibrations, and pollution, becomes a proving ground for wildlife adaptability (Arcangeli et al., 2022; Lowry et al., 2013). Urbanization is a global phenomenon, with up to 50% of the Earth's land surface modified by human activities, and nearly 1% dedicated to cities (Fehlmann et al., 2021). This shift has created transition zones between natural/sustainably stewarded lands and built-up/extensively human-modified spaces, increasing contact between humans and wildlife (Estrada et al. 2017; Estrada et al. 2022). Consequently, wildlife species living within or close to human-modified landscapes experience dramatic changes in resource availability, especially concerning food (Fehlmann et al., 2021; Hunter, 2007).

However, amid the challenges posed by urbanization, certain wildlife species thrive in urban environments. Access to reliable food sources, sometimes in the form of human-generated waste, can play a pivotal role in positively influencing the body condition of urban wildlife (Murray et al., 2019). The success of these species, often labeled as urban "adapters" or "exploiters," challenges the prevailing notion of inevitable biodiversity loss in urbanized areas (McKinney, 2006). The diversity of response strategies to habitat modifications is striking; while some species exhibit resilience and proliferation within urban settings, others, termed "urban avoiders" or "urbanophobes," actively retreat from encroaching urban sprawl (Bateman & Fleming, 2012). This variability underscores the dynamic nature of how different species cope with the challenges posed by urbanization. Thus, urban areas, serving as ecological filters, tend to favor species able to adapt to or behave plastically in human-modified environments, while excluding those incompatible with human activities (McDonnell & Hahs, 2015).

Urban animals and wildlife have garnered increased attention over the last decade, reflecting a growing recognition of the impact of expanding urban centers on biodiversity and the behaviour and ecology of many species (Blair, 2004; Goddard et al., 2010; A. J. Hansen et al., 2005; Lepczyk et al., 2017; Shochat et al., 2010). Extensive research has been devoted to unraveling the intricate ways in which urbanization shapes and transforms the behaviour of animals. Investigations into the impacts of urban life have particularly explored the consequences of pervasive factors like light and noise pollution (Rodrigo-Comino et al., 2023; Shannon et al., 2016). Light pollution, emanating from artificial sources in urban areas, has been shown to disrupt natural behavioural patterns in numerous species, affecting their circadian rhythms, navigation, and communication (for reviews see: Gaston et al., 2013; Rodrigo-Comino et al., 2023). Similarly, noise pollution, a ubiquitous feature of urban landscapes, has been associated with altered foraging behaviours, communication difficulties, and heightened stress levels in various wildlife populations (for review see: Shannon et al., 2016). Another prominent focus of research revolves around the effects of urban infrastructure, especially roads, on the movement across landscapes (Cole et al., 2023; Soanes et al., 2024) and migratory patterns of diverse species. Roads bisecting natural habitats can act as formidable barriers, impeding traditional migration routes and leading to fragmented populations (Holderegger & Di Giulio, 2010). The disruption of migratory routes and patterns of animal movement across landscapes is also a concern, potentially impacting breeding success, genetic diversity, and the overall resilience of wildlife populations in urbanized regions (García-Berro et al., 2023; Wereszczuk et al., 2017).

While much research has explored how urban life induces changes in behaviour at a broad level—examining factors such as light and noise pollution and disruptions to migratory patterns—there remains a conspicuous gap in the exploration of the intricate interactions between urban animals and their food sources. Studies on this topic primarily concentrate on the direct physical and health consequences, diet composition alterations, and human-animal interactions, often overlooking or only briefly mentioning behavioural aspects associated with the use of novel anthropogenic food sources (Cox & Gaston, 2018; Fehlmann et al., 2021; Newsome & Van Eeden, 2017; Oro et al., 2013; Plaza & Lambertucci, 2017; Ritzel & Gallo, 2020). The dynamic relationship between urban fauna and the food resources provided by human activities has received limited attention, and specifically the behavioural aspects of wildlife responses to these novel dietary opportunities remain understudied (but see, Plaza & Lambertucci, 2017 for some examples). In response to this gap in knowledge, in this chapter, I aim to provide a comprehensive analysis of existing literature, focusing on the relationship between urban animal behaviours and these novel, human origin food sources. I will investigate how urban animals modify their behaviours in response to the challenges and opportunities presented by urban food sources. I first go over which species forage on waste and trash, and the types of effects this foraging can have on these species. I will then explore how these species learn how to forage on waste, and unpack the behaviours related to the exploitation of this novel food source.

4.2 Methods

I conducted a systematic search of the scientific peer-reviewed literature (including relevant graduate theses) using Google Scholar, Web of Knowledge, Academic Search Complete, and Scopus. The inclusion criteria were established to ensure relevance and quality: 1) articles had to explicitly mention at least one vertebrate animal species or populations in urban settings; 2) and had to articles published in English or those that had been well-translated; and 3) needed to relate to behaviour and foraging on garbage. I employed searches on a comprehensive set of terms and their variations to capture a wide array of relevant literature. Variations included, but were not limited to, terms related to behaviour, foraging, urban environments, and waste. I searched the literature using the following terms and Boolean operators:

Behav*
AND (Forag* OR Feed* OR Scavang*)
AND (Urban* OR City OR Town* OR Metro* OR Cities OR Suburb* OR Residential*)
AND (Trash OR Waste OR Human Byproduct* OR Refuse OR Plastic* OR Landfill* OR Dump* OR Garbage*)

The initial search generated 1,640 results from the specified databases. Duplicate entries were removed to ensure the uniqueness of each source, leaving 1489. I then conducted a preliminary review of the titles, eliminating those deemed irrelevant, which reduced the number of papers to 438. Next, I examined the abstracts of these 438 papers, applying the inclusion criteria to assess their relevance. Relevant articles were organized in Zotero. Each selected article was read and highlighted, with tags applied to indicate content related to trash and behaviour and separating review papers from primary research articles. For each paper, I created a summary note detailing key findings. I then employed an iterative process, in which I extracted additional relevant articles from the references and conducted a thorough review of their bibliographies. Based on the relevance of titles and abstracts, these newly identified articles were also added to Zotero. This process resulted in the extraction of 124 new articles. In total, 243 articles were cataloged in Zotero. Of these, 177 were deemed most relevant to the selection criterion, and were sent to Sarah Turner for further evaluation against the inclusion criteria.

During the review process, I observed that papers on nonhuman primates appeared to be underrepresented in my searches. Consequently, I created a secondary set of search terms and Boolean operators specifically to search for primate-related papers. This adjustment ensured a comprehensive inclusion of relevant literature on primate behaviour in urban and waste foraging contexts. I applied the same process detailed above to documents extracted during the review:

Primate*
AND (Forag* OR Feed* OR Scavang*) ((OR REPLACE WITH BEHAV*))
AND (Urban* OR City OR Town* OR Metro* OR Cities OR Suburb* OR Residential*)
AND (Trash OR Waste OR Human Byproduct* OR Refuse OR Plastic* OR Landfill* OR Dump* OR Garbage*)

The nonhuman primate-related searches added 27 publications to my review, for a final total of 52 reviewed in this chapter. During the initial literature search, I began with broad search terms related to urban trash, waste, and wildlife behaviour. As I reviewed the initial results, I made note of interesting and relevant terms that frequently appeared in the literature, including synonyms for trash and waste, as well as various ways to refer to urban areas. These observations led to iterative refinements of the search parameters. For example, I expanded the search to include alternative terms like “human byproducts” or “refuse”, and “suburb” which helped capture a wider range of relevant studies. By initially being flexible with and adjusting the search parameters based on the emerging terminology, I ensured a comprehensive capture of relevant literature while homing in on studies that specifically addressed the relationship between urban trash and wildlife behaviour.

The process of winnowing down the number of articles I included was driven by a focus on the direct relationship between urban trash and wildlife behaviour. Initially, I collected many papers that broadly addressed the impact of trash on wildlife. However, not all these studies were relevant to the specific focus of this review. The key criterion for inclusion was the paper’s emphasis on behavioural outcomes associated with trash consumption or exposure. For instance, studies that merely noted a species that occasionally consumed trash without detailing the behavioural implications were excluded. Similarly, papers that discussed the physical repercussions of eating trash, without linking these to behaviour or behavioural changes, were also excluded. The papers that remained were those where a direct or inferred relationship between trash and a specific foraging behaviour or behavioural shift could be identified. This process of critical review and selection significantly reduced the number of papers to those most relevant to the research questions.

As I read through the final selected papers, I focused on identifying the main behavioural impacts of trash on wildlife. I made notes on the specific behaviours or behavioural shifts observed in relation to trash exposure. I then categorized these behaviours into broader themes based on commonalities observed across studies. For example, behaviours such as altered foraging strategies, increased kleptoparasitism, and changes in social dynamics were grouped together. The goal was to streamline these observations into coherent categories that reflected the most significant impacts of urban trash on wildlife behaviour. This thematic analysis allowed for a structured synthesis of the literature, highlighting and narrating key patterns and trends in how urban trash influences wildlife behaviour across different species and environments.

4.2.1 What is trash?

For the purpose of this thesis, trash, waste, refuse and garbage refers to any discarded material that is not naturally occurring within the environment but has been introduced by human activities. This includes a wide range of items that wildlife might encounter in urban settings including organic waste, inorganic waste, and other debris. Interestingly, the papers selected for the review used a variety of words to refer to trash, and I compiled a summary table of all the terminology employed by these papers, which can be found in Appendix B (Table 10).

4.3 Who is foraging on trash?

Understanding what types of animals are more likely to exploit and thrive in anthropogenic modified landscapes is crucial for biodiversity conservation, human-wildlife conflict mitigation and informed urban planning (Fehlmann et al., 2021; González-Crespo et al., 2023). Which species are found in and successfully exploit anthropogenic modified landscapes varies depending on their geographic location and biomes, but there are certain linking and common threads between species that inhabit and can be expected to survive and thrive in urban settings (Fehlmann et al., 2021; Kark et al., 2007). Foraging on trash in urban environments is exhibited by a variety of animals, but certain factors such as social standing (Harel et al., 2017; Struller et al., 2022), life history traits (Elliott et al., 2006), and individual traits (Toscano et al., 2016) impact this. Understanding the demographics of animals exploiting these resources is crucial for having a clearer understanding of ecosystems and to inform conservation efforts and wildlife management to mitigate human-wildlife conflict.

4.3.1 Generalists and specialists

Trash foraging has been largely observed among omnivores and generalist species (e.g., raccoons, *Procyon lotor,* Prange et al., 2003*,* and house crows, *Corvus splendens*, Kumar & Ojha, 2022), as well as certain carnivores (e.g., black bears, *Ursus americanus*, Bateman & Fleming, 2012; red foxes, *Vulpes vulpes*. and domestic cats, *Felis silvestris catus,* Castañeda et al., 2019; coyotes, *Canis latrans*, bobcats, *Lynx rufus*, McTigue & DeGregorio, 2023) engaging in this behaviour (Ritzel & Gallo, 2020). The degree of dietary specialization and niche overlap with human altered environments are useful predictors for success in exploitation of novel food sources, such as those found in urban landscapes (Fehlmann et al., 2021). Generalist species have been observed to be more successful than specialists at adapting to introduced anthropogenic modified environments (Ducatez et al., 2015). It has been proposed that this may be due to generalists showing improved food processing innovation rates and neophilia, meaning they are more likely to show dietary flexibility, and incorporate new food types into their diet and can show increased behavioural plasticity associated with foraging, traits which are essential to thriving in novel habitats (Ducatez et al., 2015; Henke-von der Malsburg et al., 2020). Prominent examples include corvids (family Corvidae), who have been known to have flexibility in resource use and adaptability that allows them to settle in urban environments across the globe (Benmazouz et al., 2021). However, some specialist species can also thrive in urban landscapes and exploit new food sources, especially if human-modified landscapes closely mimic the species' fundamental niches. An often-cited example is that of birds of prey utilizing tall buildings that mimic cliff edges in their normal habitats (Francis & Chadwick, 2012; Moller, 2014).

4.3.2 Social standing

Social dynamics and dominance rank can play a pivotal role in trash foraging patterns. Individuals with lower social standing/rank may be compelled to forage on trash when excluded from higher quality food patches, while those in higher social standing might monopolize these resources (Dorning & Harris, 2017; Duclos et al., 2020; Marty et al., 2020; Pavez et al., 2019). An example of this is urban red foxes, *Vulpes vulpes*, in Bristol, UK, where dominant individuals would take advantage of human provisioned, predictable food patches, being the first to utilize these resources, whereas subordinates visited these patches later or undertook extra territorial movements to minimize conflict (Dorning & Harris, 2017). This social dimension adds a layer of complexity to the understanding of resource utilization in urban settings. Similarly, there was a famous case of high-ranking, bold male olive baboons (*Papio anubis*) foraging on garbage at a tourist resort and eating meat contaminated with tuberculosis. The baboons that ate the garbage contracted tuberculosis and died, while lower-ranking males and females survived(Sapolsky, 2002).

4.3.3 Life history

Trash foraging behaviours also vary at different life history stages. Some studies indicate that younger individuals, particularly among gulls and eagles, show a higher inclination towards foraging on trash (Turrin et al., 2015). Moreover, sex can impact tendency to forage on urban waste (Dorning & Harris, 2017). Females, especially those with increased energetic demands of rearing young are more likely to prioritize reliable, high energy food sources such as human provisioned sites (Dorning & Harris, 2017).

Additionally, sex, and dominance rank and kinship bonds emerged in the literature as influential factors affecting the likelihood and manner in which animals engaged in urban foraging (Belant et al., 1995; Duclos et al., 2020; Fehlmann et al., 2021; Mangalam & Singh, 2013; Ramos et al., 2009; Turrin et al., 2015). In baboons, *Papio hamadryas ursinus*, increased concentration of resources, such as in urban settings, caused changes in social interactions, such as increased intra-group competition for limited anthropogenic resources. This lead to increased conflicts, particularly among male adults, who sometimes forced out lower-ranking adults in an effort to monopolize food patches (Marshall et al., 2015; Mazué et al., 2023).

4.3.4 Individual traits

While broad species-level trends offer insights into preferences, plasticity in, and adaptations to urban habitats, individual differences play a crucial role in determining success within these environments (Toscano et al., 2016). The literature suggests that intraspecific, individual variation can sometimes wield greater ecosystem impacts than interspecies differences (Rudolf & Rasmussen, 2013; Toscano et al., 2016). Toscano et al. (2016) present a comprehensive review on the intersection of behavioural ecology and food webs, employing an individual-based approach to reveal how animal personality influences individual dietary specialization, foraging behaviours, and preferences. The authors delineated five mechanisms linking personality to individual foraging specialization, encompassing foraging activity, navigating the urban "landscape of fear" (defined as the spatial distribution of perceived risk by a given population or individuals (Bleicher, 2017)), social dynamics, spatial considerations (such as individual dispersal and home range size), and physiological drivers (such as baseline metabolic) (Toscano et al., 2016).

Personality, defined individual behavioural differences that are consistent over time (Réale et al., 2007), can be an important factor influencing an animal's ability to thrive in urban settings. Shyer individuals, often deemed less innovative and adaptable, may face challenges in such environments (Toscano et al., 2016). Paradoxically, the risk-averse nature of shy individuals could lead them to be forced to forage in novel, riskier urban settings, driven by bolder individuals exploiting more optimal habitats (Toscano et al., 2016). Bolder and more innovative individuals, exemplifying aspects of neophilia, may excel in navigating the challenges of anthropogenically modified environments, where plasticity is paramount for survival and the exploration of new foraging opportunities becomes imperative (Breck et al., 2019; Henke-von der Malsburg & Fichtel, 2018). Beyond personality traits, certain individuals within populations sometimes emerge as refuse specialists, distinctly preferring trash as a food source—a trait highlighted in recent studies (Plaza & Lambertucci, 2017; Turrin et al., 2015).

4.4 What are the effects of trash foraging?

The research on the ecological impact of rubbish dumps reveals a complex relationship between vertebrate species and their consumption of trash(Plaza & Lambertucci, 2017). An in-depth review by Plaza & Lambertucci (2017) explores these dynamics extensively, highlighting both the benefits and drawbacks of foraging at garbage dumps. They identify several positive outcomes, such as a strong correlation between body mass and body condition with organic waste consumption; specifically, individuals foraging at dump sites often exhibit greater body mass and better body condition. Furthermore, reproductive parameters, including higher breeding success and increased population growth, are frequently associated with the use of garbage dumps by various avian and mammalian species (e.g., white storks, *Ciconia Ciconia* and Black bears*, Ursus americanus*, Plaza & Lambertucci, 2017). However, these positive effects are accompanied by challenges and tradeoffs. Survival rates can vary widely depending on the species and specific context, and the surge in population abundance, particularly among birds, may have broader ecological implications, such as increased competition for resources, increased conflict with humans, and the potential for invasive species to disrupt ecosystems (Noreen & Sultan, 2021a). Additional concerns include the risk of pathogen transmission and exposure to toxins, which can lead to health problems across various species (e.g., river frogs, *Rana heckscheri*, Plaza & Lambertucci, 2017). Amphibians and birds, in particular, are at risk due to the ingestion of plastic and other foreign objects (Plaza & Lambertucci, 2017; Riley et al., 2014). For a more detailed analysis of wildlife contaminants, see Riley et al., (2014) for an extensive review on the subject.

Moreover, population level impacts can be identified for foraging at garbage dumps and trash. Dump-associated food resources alter movement patterns across landscapes, affect migration and contribute to resident population establishment, and modify existing species compositions (Plaza & Lambertucci, 2017). The presence of abundant, stable resources can lead to increased intraspecies and interspecies competition, modified species ranges, and help invasive species spread and persist in new territory (Noreen & Sultan, 2021b; Otto, 2018). Population level genetic changes have also been documented, with micro adaptations to urban foraging becoming prevalent in many species (Beliniak et al., 2022; Caspi et al., 2022; Donihue & Lambert, 2015; Murgui & Hedblom, 2017; Newsome & Van Eeden, 2017; Otto, 2018; Sol et al., 2013).

4.5 How do animals learn to forage on trash?

Cities impose intense novel pressures on individuals, resulting in high rates of behavioural change in city-dwelling animals. In this context, behavioural plasticity emerges as a vital trait for species and individuals entering urban landscapes (Caspi et al., 2022). Behavioural plasticity is defined as the ability to adjust behaviour in response to complex environmental conditions (Mery & Burns, 2010). As outlined by Caspi et al.(2022), behavioural plasticity in urban animals encompasses four scales: (1) contextual plasticity, which involves immediate behavioural responses to current environmental conditions; (2) learning, where past experiences induce adjustments in behaviour relative to specific tasks; (3) developmental plasticity, where early experiences affect behavioural tendencies; and (4) transgenerational plasticity, where parental experiences shape offspring phenotypes. All four scales of behavioural plasticity are crucial for coping with novel situations and thus impact selective pressures. This trait offers a mechanism for population persistence by providing time for founder populations to evolve and generate phenotypic variations subject to natural selection, and helps animals exploit new food sources (Caspi et al., 2022; Ducatez et al., 2015).

Adapting to rapidly changing urban environments necessitates being able to or learning how to exploit novel food sources (Dammhahn et al., 2020; Sol et al., 2013). Animals can diversify and expand their ecological niches by capitalizing on resources associated with human presence, such as using introduced species as food sources or unintentional feeding from human activities like trash disposal (Rose et al., 2023). The process of learning to exploit these resources often begins with individual trial and error, an energetically costly but crucial method for discovering locally adaptive behaviours (Sih et al., 2011). In gregarious species, social facilitation, defined as the effect the presence of a conspecifics on the performance and learning of tasks and behaviours (Zajonc, 1965) has been found to play a pivotal role in the learning process. The presence of conspecifics can reduce neophobia and encourage exploratory behaviour, thereby hastening the assimilation of new foraging strategies (Rose et al., 2023; Zajonc, 1965). Furthermore, the introduction of novel food items and foraging outcomes is expedited through social learning mechanisms(Miller et al., 2014) Social enhancement, where the presence of others enhances an individual's learning or performance, along with horizontal transmission (the spread of information or behaviour between individuals of the same generation), and vertical transmission (the transfer of information or behaviour from parents to offspring) are key ways individuals learn to forage on new food sources (Fehlmann et al., 2021). This cultural transmission not only aids in the widespread implementation of beneficial behaviours within populations but also mitigates the trial and error costs of individual discoveries error through kin benefits (Rose et al., 2023).

In summary, the interaction between urban environments and wildlife necessitates a multifaceted response from wildlife in terms of learning and adaptation. Behavioural plasticity, operating across various scales, enables individuals to cope with the challenges posed by novel urban pressures (Caspi et al., 2022). This plasticity is particularly crucial for foraging in urban environments, providing a mechanism for population persistence and time for adaptive evolutionary responses to changing conditions. Learning to exploit novel food sources becomes a central aspect of this plasticity, encompassing individual trial and error, social facilitation in gregarious species, and intricate social learning mechanisms such as enhancement, horizontal transmission, and vertical transmission (Fehlmann et al., 2021; Mateo, 2014). These processes collectively reflect the dynamic strategies observed in wildlife species, allowing many species to thrive amidst the dynamic landscapes of urbanization (Fehlmann et al., 2021).

4.6 Behaviour and trash foraging

When animals begin to exploit novel resources such as trash, waste, or refuse, they often undergo substantial changes to their foraging strategies and overall behaviour. The decision to utilize anthropogenic food sources necessitates the development of new foraging techniques and can lead to shifts in dietary preferences (Tauler-Ametller et al., 2017). This resource exploitation not only fosters the emergence of novel feeding behaviours but also influences a range of non-foraging behaviours. Key among these are changes in aggression levels (Flint et al., 2016), alterations in social structures (Struller et al., 2022), and modifications in group cohesion (Macdonald et al., 1999). The presence of consistent and abundant food supplies from urban waste can profoundly reshape foraging patterns (Spelt et al., 2021), affect competition dynamics (Lato et al., 2021), and modify social hierarchies (Dorning & Harris, 2017). These changes have far-reaching implications for the survival and reproductive success of species in urban environments (Tauler-Ametller et al., 2017). The diverse impacts of trash foraging on vertebrate species can be exemplified by several key species. They highlight the broad spectrum of behavioural adaptations driven by the exploitation of anthropogenic food sources. The following table provides select examples of some ways vertebrate species have modified their behaviours in response to the availability of urban waste (Table 8).

Species	Impact on behaviour	Reference
Gulls, multiple species of *Larus*, including *L. fuscus, L, argentatus, L. marinus*	Gulls exhibit novel behaviours such as kleptoparasitism and show increased spatial predictability, choosing to stay around dumps due to the consistent availability of food. They adapt their foraging schedules to human activities and trash patterns, learning specific days of the week and holidays for trash closures.	Eronen et al., 2021; Lato et al., 2021; Spelt et al., 2021
Hyenas, *Crocuta crocuta*	Hyenas develop novel social structures in urban settings, with cubs learning different skill sets compared to their wild counterparts. Their behaviour at garbage dumps is altered, showing less aggression in larger groups. Additionally, hyenas exhibit a shift in food preferences, favoring anthropogenic food over hunting, which results in reduced range and changes in space use dynamics.	Struller et al., 2022; Kolowski & Holekamp, 2008; Yirga et al., 2012
Macaque, *Macaca fascicularis*	Macaques demonstrate reduced movement and increased social tension and aggression as a result of trash foraging. They alter their use of vertical space to monitor human activities and change their activity budget. Additionally, their range use is modified due to the increased proximity to anthropogenic food sources.	Hasan et al., 2023; Ilham et al., 2017; Ilham et al., 2018; Sha & Hanya, 2013
Black bears, *Ursus americanus*	Black bears exhibit increased home range and more diurnal activity patterns due to trash foraging. Bears accessing trash in developed areas develop food-conditioned foraging behaviours, leading them to seek out human food sources rather than natural ones. This shift in food preference also extends to their young, as they teach their offspring to forage on anthropogenic sources.	Lewis et al., 2015; Mazur & Seher., 2008
Coyotes *Canis latrans*	Coyotes exhibit changes in their activity patterns and larger home ranges. They are more nutritionally stressed and more likely to forage on trash when diseased or relegated to lower-quality habitats. Additionally, their social status can be affected by the availability and quality of trash resources.	Murray & St.Clair., 2017; Murray et al., 2015

Table 8: Examples the impacts of trash foraging on behaviour in select species from the final selected papers.

4.6.1 Kleptoparasitism

Kleptoparasitism refers to the theft of a resource or food item already procured by another individual (Morand-Ferron et al., 2007). This form of resource acquisition is a form of interference competition (Hamilton, 2002; Iyengar, 2008), direct, or contest competition (Beauchamp, 2014). It is also referred to in the literature as "piracy," or "aggressive scrounging" (Beauchamp, 2014; Noreen & Sultan, 2021b). Research on kleptoparasitism has predominantly focused on wild populations or populations living in rural environments, revealing it as a facultative behavioural strategy that can change in response to ecological conditions (Spencer et al., 2017). Previous studies suggest that the frequency of kleptoparasitic behaviour varies with host and resource concentrations, being more prevalent during resource scarcity (Hamilton, 2002; Turrin et al., 2015). Increased resource competition, resulting from heightened competition and diminished resource quantity, has been associated with elevated rates of kleptoparasitism (Spencer et al., 2017).

However, this foraging strategy has been increasingly observed in urban settings, particularly when animals forage on waste and other anthropogenically provided food sources (Noreen & Sultan, 2021b; Richard et al., 2022). A comparative study by Spencer et al. (2017) examining kleptoparasitic behaviour in rural and urban gulls, *Laridae spp*., revealed a higher occurrence of kleptoparasitism in urban areas compared to other habitats. The study suggests that kleptoparasitism might serve as a behavioural mechanism for gulls when exploring and invading novel urban spaces. This strategy appears energy-efficient, leveraging existing knowledge within local populations to locate edible food sources while avoiding the costs associated with direct foraging. Kleptoparasitism is not only utilized in urban settings but has become a dominant foraging strategy, as evidenced by a study on urban kites, *Milvus migrans govinda*, foraging at garbage dumps in Kolkata, India (Mazumdar et al., 2016). Here, half of the identified foraging strategies were forms of kleptoparasitism, occurring at significantly higher rates compared to alternative foraging methods. The authors proposed that the prevalence of kleptoparasitism at garbage dumps was a result of increased cost-benefit efficiency in these locations, indicating its potential adaptive benefits as a specific foraging strategy in urban waste settings (Mazumdar et al., 2016).

Kleptoparasitism can therefore be a behavioural strategy to improve foraging efficiency in urban settings (Mazumdar et al., 2016). However, in response to the growing prevalence of this behaviour, individuals that might be victims of this foraging strategy have developed specific behavioural adjustments to mitigate the risk of being parasitized. Observed strategies include temporal and spatial segregation, as well as changes in food item selection.

Temporal segregation, or partitioning, can arise as a direct response to the challenges of kleptoparasitism and as way to minimize competition (Baglione & Canestrari, 2009; Bennie et al., 2014; Polidori et al., 2009). By foraging at different and sometimes less optimal times of day, individuals can effectively reduce competition from other species, thereby reducing the likelihood of kleptoparasitic encounters. Spatial segregation, another potentially adaptive strategy, helps to lower the risk of kleptoparasitism (Austin et al., 2021; Krell et al., 2003; Polidori et al., 2009). An example of spatial segregation could be individuals choosing suboptimal food patches, attracting fewer competitors and reducing the risk of food theft. By choosing areas with lower food density or quality, animals may tradeoff a loss in access to some food resources against a benefit of reduced competition for the food resources they do access (Kumar & Ojha, 2022). In addition to temporal and spatial behavioural modifications, individuals have also been found to pick specific food items over others, apparently in order to limit the risk of kleptoparasitism (Suraci & Dill, 2011). This can include choosing less desirable food items that are less likely to attract potential thieves (Mazumdar et al., 2019). Moreover, individuals may opt for food items that require shorter handling times, as longer handling times are associated with a higher risk of kleptoparasitism (Mazumdar et al., 2019). Overall, these examples of behavioural plasticity highlight a nuanced response to the increasing prevalence of kleptoparasitism in trash foraging settings, illustrating the dynamic interaction between foragers and potential exploiters in these ecological niches.

4.6.2 Changes in foraging method preferences

Urban food sources, such as landfills and waste sites, have been found to have strong influences the foraging behaviours, foraging techniques, methods, and preferences of various animal species (Benmazouz et al., 2021; C. P. Hansen et al., 2020; Kumar & Ojha, 2022; Mazumdar et al., 2016). These anthropogenic environments create unique adaptive pressures that can drive changes in foraging strategies, often favoring behaviours that optimize resource acquisition in competitive and altered landscapes. For example, in the case of black kites, *Milvus migrans govinda*, urban waste sites have been shown to impact their foraging method (Mazumdar et al., 2016). Described as non-visual tactile foragers, when foraging in the wild, they tend to walk and pick food out of the substrate (Sharma & Soni, 2017). However, despite the higher energetic cost of flight compared to walking, black kites predominantly engage in flight-based foraging behaviours at garbage dumps (Mazumdar et al., 2016). This is likely because flying allows them greater maneuverability and the ability to cover larger areas quickly, which is crucial in competitive environments like garbage dumps. Moreover, gliding and soaring flights, which are energetically less costly than flapping, enable kites to efficiently search for food over wide areas. Kites will still collect food while standing on the ground as they do in the wild, but this strategy is typically adopted only under specific conditions in urban settings, such as when competition from other scavengers, like house crows *(Corvus splendens*) is low, and food availability is visibly high (Kumar & Ojha, 2022). Although ground foraging is the least preferred strategy due to the diminished maneuverability and higher risk of mobbing by other birds, it results in the highest success rate once the kite commits to it (Mazumdar et al., 2016). This suggests that black kites only resort to ground foraging when they are confident of acquiring food, highlighting their behavioural plasticity in response to urban environments.

Many nonhuman primates have also been found to exhibit changes in foraging methods and techniques, in response to the pressures of urbanization (Altmann & Muruthi, 1988; El Alami et al., 2012; Gutierres et al., 2023; Hasan et al., 2023; Ilham et al., 2017; Mangalam & Singh, 2013). The need to extract packaged foods and explore novel objects in urban settings is thought to have accentuated the use of hands over mouths in some groups of primates. A study by Dhananjaya et al., (2022) investigated hand and mouth use during food acquisition in urban vervet monkeys, *Chlorocebus pygerythrus*, under experimental conditions. The results showed that this urban primate exhibited a higher preference for hand use when manipulating food items in urban settings compared to their counterparts in non-urban environments. This shift towards manual handling is likely due to the design of most urban objects, which are optimized for human manipulation, necessitating a similar behaviour for nonhuman primates, to access the food sources.

Overall, the impact of urban food sources and waste sites on foraging behaviours highlights the behavioural plasticity animals employ to navigate and exploit these human-altered environments. The ability to modify foraging methods, whether through increased reliance on flight in birds or enhanced manual dexterity in vervet monkeys, underscores the dynamic relationship between wildlife and urbanization. These behavioural modifications not only facilitate survival in urban landscapes but also offer insights into the broader ecological impacts of human activities on wildlife.

4.6.3 Changes in foraging time

Urban environments, with their irregular human activity patterns and resource availability, can drive modification of foraging behaviours in various species. Many animals have shown remarkable behavioural flexibility, adjusting their foraging times and methods to align with human schedules and activities (Ciucci et al., 1997; Hasan et al., 2023; Ilham et al., 2017; Spelt et al., 2021). These potentially adaptative strategies not only includes shifting foraging strategies but also modifying their circadian rhythms to better exploit anthropogenic resources.

A study by Spelt et al., (2021) highlighted how urban gulls, *Larus fuscus*, adjust their foraging schedules, apparently based on human activity patterns. Gulls were observed to synchronize their foraging with school breaks and the opening times of waste centers, times that differed from their natural circadian rhythms and foraging patterns. During school breaks, gulls flock to the vicinity, capitalizing on the food discarded by students. Conversely, on weekends, when schools are closed and no new waste is deposited, their presence diminishes. Similar foraging patterns were observed at waste centers, with gulls adjusting their presence based on the days of the week, recognizing that fresh waste was deposited during weekdays but not on Sundays. This memory-based behavioural plasticity with gulls exhibiting reduced activity at waste dumps on Sundays, highlights their ability to learn and remember specific timing. This cognitive sophistication allows them to thrive in urban environments by maximizing their food intake during peak food availability times. Such behavioural flexibility underscores the gulls' capacity to adapt to both regular and irregular human schedules, optimizing their foraging efficiency in the urban landscape.

Other studies also support the idea that animals can modify their foraging behaviours in response to human activity patterns. Animals have been found to apparently use visual cues such as the presence of certain species, human workers, or tourists at trash bins, and modify their schedules accordingly (García-Arroyo et al., 2023; Ilham et al., 2017, 2018; Noreen & Sultan, 2021b). Some species can even alter their natural activity patterns in response to predictable human food provision (e.g., raccoons, *Procyon lotor* Bozek et al., 2007). Such modifications can include going against their circadian rhythm, such as shifting between nocturnal and diurnal activity based on food availability (Widdows & Downs, 2015).

In summary, urban environments can create novel contexts, pressures and opportunities, necessitating a high degree of behavioural plasticity among animals, leading to modifications in their foraging times and methods. By modifying behaviour in response to human schedules and learning to predict resource availability, species (e.g., gulls and vervets) can optimize their foraging efficiency and thrive in these altered landscapes. This plasticity highlights the profound impact of human activities on wildlife behaviours and the intricate ways in which animals adjust to the rhythms of urban life.

4.6.4 Changes in energy budgets

Urban and waste foraging has potential impacts on the energy/activity budgets of urban species compared to their wild counterparts, primarily due to the increased quantity, density, and predictability of food sources (Coogan et al., 2018; Ilham et al., 2018). Human-derived food is often rich in energy and also predictably available in time and space (Fehlmann et al., 2021). The altered population dynamics and species composition in urban areas can also reduce actual and perceived predation risk. With fewer predators, foraging animals in urban settings do not face the same predation pressures, allowing them to spend less time engaging in vigilance and other antipredator behaviours. This reduced predation, combined with the reliable food supply in urban areas, enables animals to allocate more time to other activities. This shift in energy allocation can lead to increased resting and sedentary behaviours, and can positively impact survival and reproductive success, and contributing to higher population densities and potential genetic divergence (Sol et al., 2013).

Research has shown that access to anthropogenic food sources often results in shifts in energy budgets among individuals, including the adoption of lower-energy foraging strategies, reduced movement, increased resting time, and smaller home ranges. These behavioural changes represent a departure from those observed in wild counterparts (Altmann & Muruthi, 1988; El Alami et al., 2012; Gutierres et al., 2023; Ilham et al., 2018; Thatcher et al., 2019). However, the impact of anthropogenic food on foraging behaviours can vary between species. In some instances, food items of perceived higher value, originating from human sources, can reduce the reliance on natural foods and act as strong attractants, prompting individuals to travel greater distances from other resources, such as shelter, to access these high-value items (Sha & Hanya, 2013). Consequently, foraging on trash can also lead species to exhibit increased locomotion and reduced resting time in pursuit of concentrated food sources (Ramos et al., 2009).

Conversely, when anthropogenic food becomes less available, species must adapt their energy budgets to the scarcity of these resources. A study by Mazué et al., (2023) explored how chacma baboons, *Papio hamadryas ursinus,* modify their foraging strategies in response to changes in food availability within a peri-urban environment. The findings indicated that, in the absence of anthropogenic food, baboons significantly increased their foraging efforts in natural environments due to the higher time investment required to obtain natural foods. In this case, the reintroduction of trash items led to a swift return to urban foraging, highlighting the baboons' dependence on these predictable and accessible food sources (Mazué et al., 2023).

In summary, urban waste foraging leads to substantial changes in the energy budgets of urban species compared to their wild counterparts. The predictability and richness of anthropogenic food sources allow urban animals to acquire energy more efficiently, resulting in altered foraging behaviours, activity levels, and overall energy allocation.

4.6.5 Changes in social behaviour

The social dynamics of trash foraging introduce a shift in social behaviour, interactions and dynamics of vertebrate species (Fehlmann et al., 2021). The literature presents a spectrum of aggression changes—some species exhibit increased aggression (e.g., *Macaca fascicularis,* Hasan et al., 2023), while others display decreased aggression in both intra- and interspecies interactions (e.g., *Crocuta crocuta,* Widdows & Downs, 2015); (Burger & Gochfeld, 1983; Dhawale et al., 2020; Mazumdar et al., 2016; Novaes & Cintra, 2015; Pavlova & Wronski, 2020; Ramos et al., 2009; Rimbach et al., 2023; Widdows & Downs, 2015; Zelenskaya, 2021). Urban waste, being a consistent and abundant food source, can attract and sustain a larger number of individuals than wild resources do (Lato et al., 2021; Widdows & Downs, 2015). This can lead to increased competition for resources which can in turn increase aggressive response by individuals (Pavlova & Wronski, 2020). However certain species, like genets, *Genetta tigrina*, typically considered solitary foragers, have been found to exhibit a surprising tolerance for conspecifics at waste disposal sites in urban settings, suggesting that the quality and quantity of available food outweighs the potential costs and risks associated with aggressive displays (Widdows & Downs, 2015).

The introduction of urban waste as a food source not only influences aggression dynamics but also reshapes social structures (Struller et al., 2022). Urban hyenas, *Crocuta Crocuta*, for instance, demonstrate markedly different social behaviours compared to their wild counterparts, often forming a singular “super clan” around waste dumps and experiencing a modification, or even loss, of group cohesion in these settings (Struller et al., 2022). Notably, this loss of cohesion appears confined to the feeding site, as post-feeding events still witness some level of group coherence in dens, demonstrating a remarkable social and behavioural plasticity that facilitates their use of urban environments (Struller et al., 2022). In an experiment modifying access to anthropogenic food sources, Mazué et al., (2023) were able to observe changes in social structure in chacma baboons as a response to food availability. The removal of access to anthropogenic food resulted in heightened competition, increased conflicts, and a decline in group cohesion within the group. Overall, the implications of urban foraging opportunities on group cohesion and fusion-fission dynamics in gregarious and group-living species represent a significant area for future study to comprehend long-term impacts (Fehlmann et al., 2021).

4.7 Conclusions

The multifaceted relationship between urbanization and wildlife behaviour has emerged as a critical area of study, reflecting the profound impact of human activities on natural ecosystems. In this literature review, I have explored the various dimensions of how urban trash and waste influence the foraging behaviour of wildlife, focusing particularly on behavioural plasticity. Through a comprehensive analysis of existing literature, several key themes have emerged. These include modifications in foraging behaviour, such as kleptoparasitism, changes in foraging method preferences, shifts in foraging windows, alterations in energy budgets, and changes in social behaviour. Together, these findings shed light on the dynamic interactions between wild animals and human-modified environments. The increase in food production and the consequent rise in food waste have introduced new and abundant food sources for urban wildlife, such as landfills, dumps and household waste (Noreen & Sultan, 2021a; Struller et al., 2022; Turrin et al., 2015). This review has highlighted the dual nature of these anthropogenic food resources, which offer both opportunities and challenges to wildlife. On one hand, access to human-generated waste can enhance the body condition and reproductive success of some individuals and species, exemplified by urban "adapters" or "exploiters," like racoons, *Procyon lotor* (Prange et al., 2004) kites, *Milvus migrans Govinda* (Mazumdar et al., 2016), and gulls, *Larus fuscus*, (Spelt et al., 2021), that thrive in these modified environments. On the other hand, the consumption of waste is associated with health risks, including pathogen transmission and exposure to toxins, which can adversely affect wildlife individuals and populations, as was illustrated with the olive baboon example.

The review has explored the types of animals that forage on trash, emphasizing the role of generalist species (e.g., *Larus michahellis, Sciurus carolinensis,* and *Vulpes vulpes*), which possess dietary flexibility and behavioural plasticity, in exploiting urban food resources. These species often exhibit higher food-related innovation rates, allowing them to incorporate novel food items into their diets more readily than specialists(Macdonald et al., 1999; Ramos et al., 2009; Rimbach et al., 2023). Furthermore, social dynamics, life history traits, and individual characteristics have been shown to influence foraging behaviour (Grecian et al., 2018; Naman et al., 2019; Wearmouth & Sims, 2008). Lower social standing individuals, for instance, may be compelled to forage on trash when excluded from higher quality food patches, while individuals with at life history stages, such as reproductive females with increased energetic demands, may disproportionately prioritize reliable high-energy food sources.

Behavioural plasticity has emerged as a crucial trait for wild animals navigating urban environments (Caspi et al., 2022). The ability to adjust behaviour in response to changing conditions, learn from past experiences, and transmit knowledge across generations is vital for coping with and thriving in the novel pressures imposed by urban landscapes. The literature I have reviewed here has underscored the importance of social learning mechanisms, such as social facilitation and cultural transmission, in facilitating the assimilation of new foraging strategies among gregarious species (Fehlmann et al., 2021; Rose et al., 2023; Sih et al., 2011). These mechanisms not only enhance the efficiency of learning but also mitigate the costs associated with individual trial and error (Sih et al., 2011).

Trash foraging affects not only individual health and behaviour but also population dynamics and community structures (Sapolsky, 2002; Struller et al., 2022). The presence of stable food resources in the form of waste can alter movement patterns, disrupt migratory routes, and lead to the establishment of resident populations in urban areas (Ciucci et al., 1997; Cozzi et al., 2016). Additionally, these resources can facilitate the spread of invasive species and contribute to genetic changes within populations, reflecting the broader evolutionary impacts of urbanization (Caspi et al., 2022; Newsome & Van Eeden, 2017; Otto, 2018; Sol et al., 2013).

In conclusion, the interplay between urban trash, wildlife foraging behaviour, and behavioural plasticity represents a complex and dynamic field of study. This review has highlighted the need for continued research to deepen our understanding of these interactions and inform conservation efforts and urban planning strategies. By comprehensively examining the existing literature, this review contributes to an understanding of how urbanization shapes wildlife behaviour, offering insights into the implications of behaviours employed by wildlife in response to human-modified environments. The findings underscore the importance of fostering coexistence between humans and wild animals, between urban development and wildlife conservation, to ensure that urban ecosystems remain resilient and diverse in the face of ongoing anthropogenic change.

Chapter 5: Thesis Conclusions

The intricate relationship between urbanization and wildlife behaviour has emerged as a critical area of study, reflecting the impact of human activities on natural ecosystems. In this thesis, I have presented results from my in-situ foraging experiments conducted on wild squirrels in Montreal, compared these data to those collected in a similar project on Japanese macaques by Megan Joyce (Joyce et al., 2023; Joyce, 2021). I then conducted a literature review of the literature, exploring the various dimensions of how urban trash and waste influence the foraging behaviour of wildlife, focusing particularly on behavioural plasticity and flexibility. Through a comprehensive analysis of existing literature, I identified several key themes (e.g., behavioural modifications including kleptoparasitism, changes in foraging methods, energy budgets, and social behaviour) to elucidate on the dynamic interactions between wildlife and human-modified environments.

Behavioural plasticity has emerged as a crucial trait for wildlife navigating urban environments. The ability to adjust behaviour in response to changing conditions, learn from past experiences, and transmit knowledge across generations is vital for coping with the novel pressures imposed by urban landscapes (Caspi et al., 2022). This review has underscored the importance of social learning mechanisms, such as social facilitation and cultural transmission, in facilitating the assimilation of new foraging strategies among gregarious species. These mechanisms not only enhance the efficiency of learning but also mitigate the costs associated with individual trial and error (Fehlmann et al., 2021; Sih et al., 2011).

The ecological implications of trash foraging are profound, affecting not only individual health and behaviour but also population dynamics and community structures. The presence of stable food resources in the form of waste can alter movement patterns, disrupt migratory routes, and lead to the establishment of resident populations in urban areas. Additionally, these resources can facilitate the spread of invasive species and contribute to genetic changes within populations, reflecting the broader evolutionary impacts of urbanization.

My experimental findings, those from Joyce (2021) and the comparative analysis of these two datasets also contributes to this understanding by providing a detailed comparison of the foraging strategies and route selection between urban squirrels (*Sciurus carolinensis*) and Japanese macaques (*Macaca fuscata*). I found significant differences in run times and distances on a 5-platform array. Monkeys demonstrated more consistent foraging behaviour on the experimental array, often completing the array without repeating visits to platforms. In contrast, squirrels frequently revisited platforms, resulting in longer run distances overall.

In conclusion, the interplay between urban trash, wildlife foraging behaviour, individual route choice when foraging, and behavioural plasticity represents a complex and dynamic field of study. In this thesis, I have highlighted the need for continued research to improve human-wildlife co-existence, deepen our understanding of these interactions and inform conservation efforts and urban planning strategies. By examining the existing literature and integrating our experimental findings, my hope is that this thesis can contribute to a understanding of how urbanization shapes wildlife behaviour.

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Appendix A: Supplementary Tables and Figures

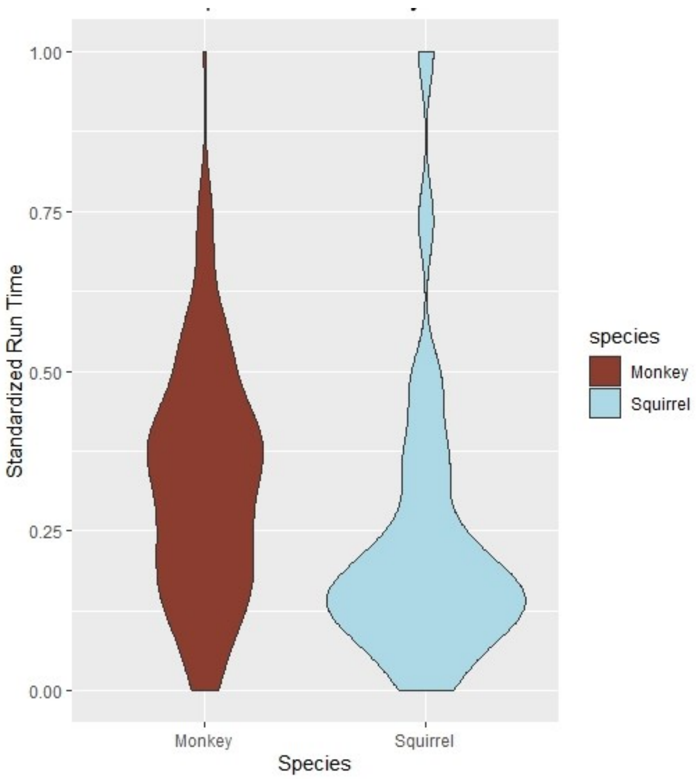


Figure 9: Standardized run duration for squirrels and monkeys on the 6-platform arrays (MData1, SData1). This violin plot displays the distribution of standardized trial duration for both squirrels and monkeys. Each "violin" represents the density of data points, with the width of the violin indicating the data distribution at different speed values.

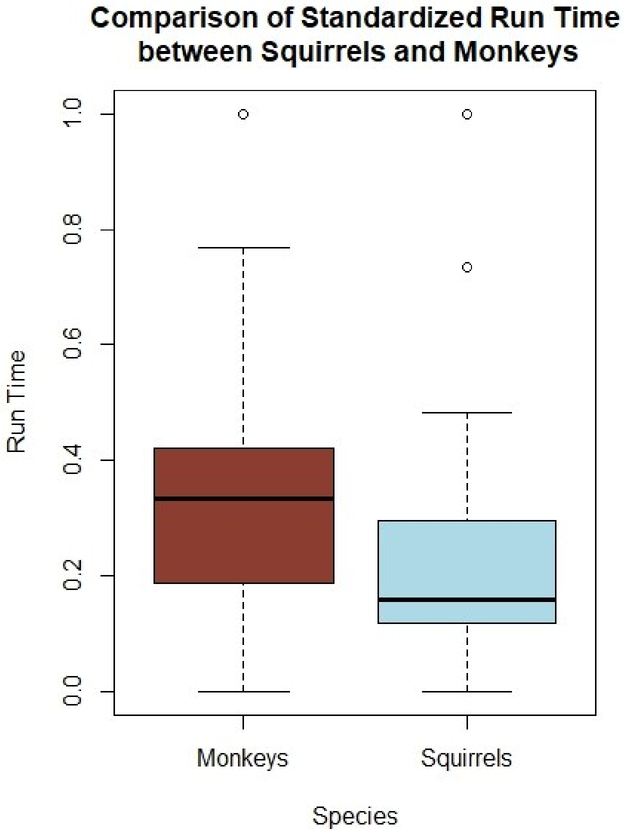


Figure 10: Comparison of squirrel and monkey trial duration on the 6 platform array. This boxplot illustrates the median values for squirrel and monkey trial speed (thick lines inside the boxes). The top and bottom lines of the boxes represent the inter-quartile (25th and 75th percentiles). The dashed-line whiskers and open circles (outliers) show the maximum and minimum values of the samples.

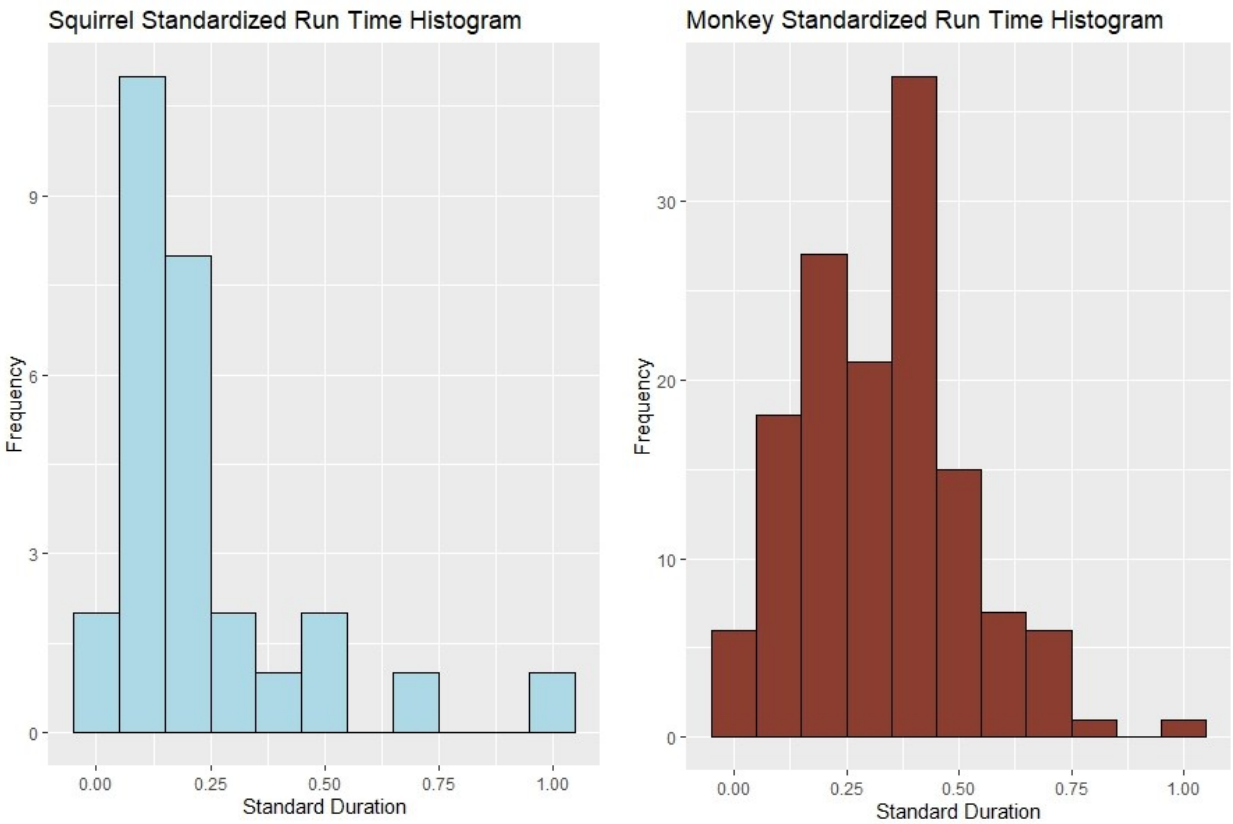


Figure 11: Standardized trial duration for squirrels and monkeys on the 6-platform array (SData3, MData3). a) Histogram of standardized run times for squirrels; and b) Histogram of standardized run times for monkeys.

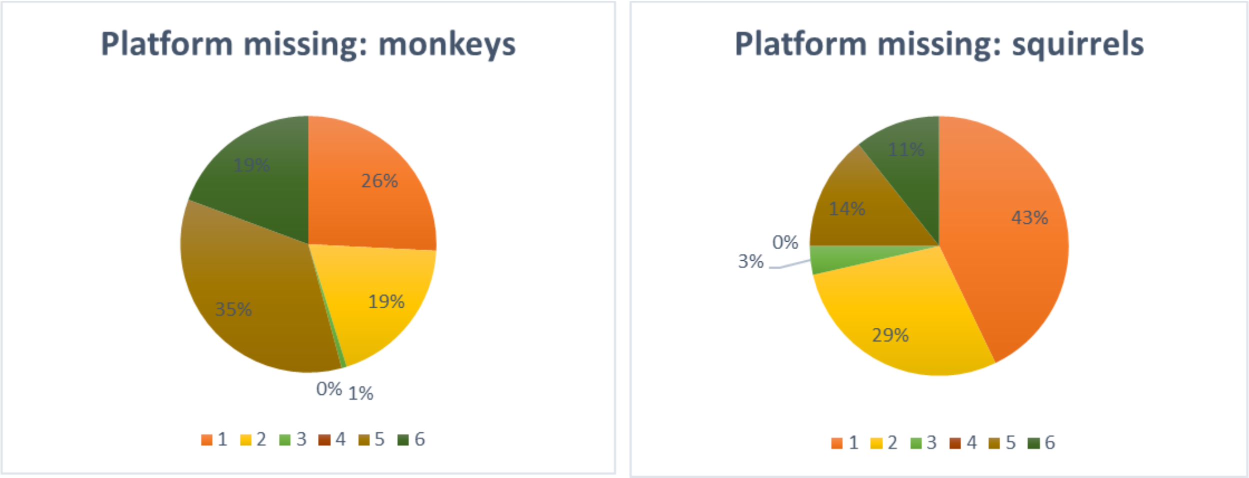


Figure 12: Platform removal during array sequence modification. (a) and (b) Pie charts showing the distribution of platforms number removed when transforming 6-platform array runs into 5-platform array (quasi arrays) for monkeys and squirrels, respectively (SData5, MData5).

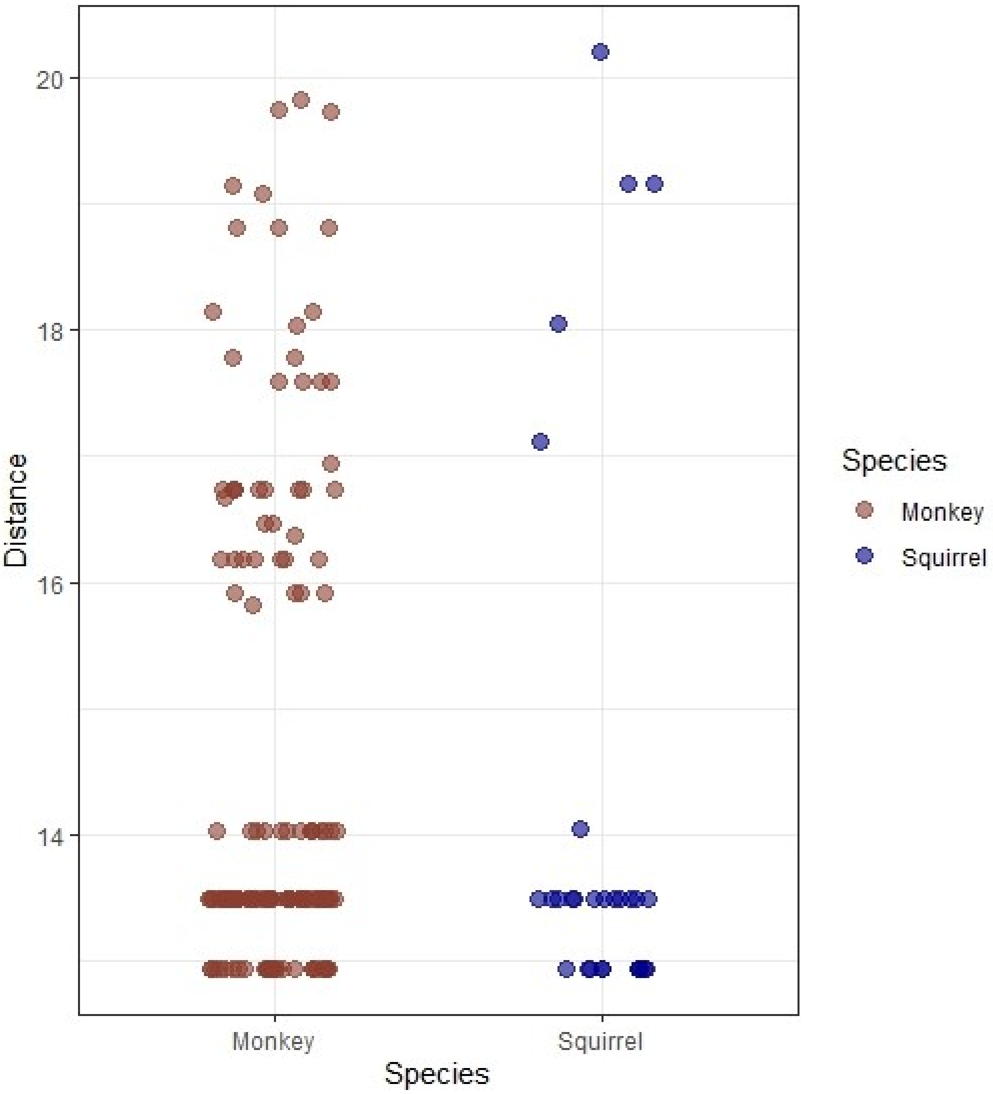


Figure 13: Comparison of total relative run distances for monkeys and squirrels on 6-platform array, (distance adjusted for body size) (MData1, SData1).

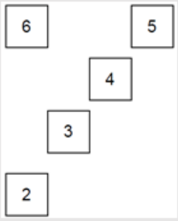
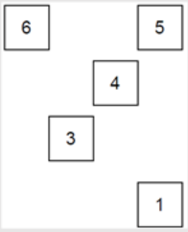
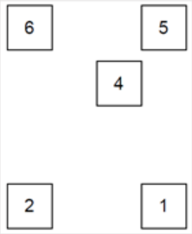
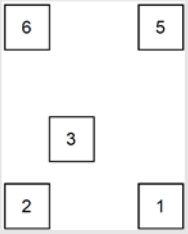
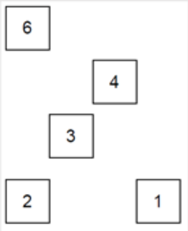
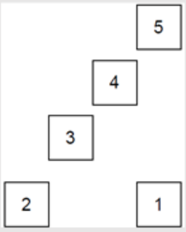
	Routes corresponding to heuristic		
Platform missing	Nearest Neighbor (NN)	Shortest path (SP)	Sweep Heutistic (SW)
1 	23456	23456	23465
	34562	65432	56432
	43265		
	54326		
2 	13456	13456	13456
	34561	65431	65431
	43156		
	54316		
	64315		
3 	12456	21456	12465
	21456	65412	56421
	45621		65412
	54621		
	64512		
4 	65321	56321	65321
	56321	12365	21356
	32156		12365
	23156		
	13265		
5 	13462	12346	12346
	23461	64321	21346
	34621		64321
	43216		
	64321		
6 	13452	12345	12345
	23451	54321	21345
	34512		54312
	43215		54321
	54321		

Table 9: Summary of all 5-platform array configurations, and all possible routes corresponding to nearest neighbor, shortest path and sweep heuristic.

Appendix B: Supplementary Tables for Literature Review

Term used to refer to trash/waste	Variants on the term	References
Garbage	Garbage dumps, garbage tips, garbage bins, organic garbage	Altmann & Muruthi, 1988; Bozek et al., 2007; Burger & Michael., 1983; Cozzi et al., 2016; Dhananjaya et al., 2022; Elliiott et al., 2006; Eronen et al., 2021; Flint et al., 2016; Gutierres et al., 2023; Houston et al., 2007; Ilham et al., 2017; Ilham et al., 2018; Kumar & Ojha, 2022; Lewis et al., 2015; Marty et al., 2020; Mazué et al., 2023; Mazumdar et al., 2016; Noreen & Sultan, 2021; Pavez et al., 2019; Plaza & Lambertucci, 2018; Prange et al., 2003; Ramos et al., 2009; Rimbach et al., 2023; Sazima, 2007; Tortosa et al., 2002; Zelenskaya, 2021; Zhao et al., 2022
Waste	Food waste, organic waste, mixed waste, meat waste, solid waste	Elliiott et al., 2006; Eronen et al., 2021; Flint et al., 2016; Struller et al., 2022; Gautrelet et al., 2023; Giacomo & Guerrieri., 2008; Kumar & Ojha, 2022; Macdonald et al., 1999; Mazué et al., 2023; Murray & St.Clair., 2017; Murray et al., 2015; Noreen & Sultan, 2021; Pavez et al., 2019; Plaza & Lambertucci, 2018; Ramos et al., 2009; Rimbach et al., 2023; Sha & Hanya, 2013; Spelt et al., 2021; Tortosa et al., 2002; Turrin et al., 2015; Widdows & Downs, 2015; Yirga et al., 2012; Zelenskaya, 2021; Zhao et al., 2022
Refuse	Food refuse, packed refuse, refuse dumps, human refuse	Altmann & Muruthi, 1988; Bozek et al., 2007; Duclos et al., 2020; Elliiott et al., 2006; Flint et al., 2016; Giacomo & Guerrieri., 2008; Kolowski & Holekamp, 2008; Kumar & Ojha, 2022; Lato et al., 2021; Macdonald et al., 1999; Mazumdar et al., 2019; Noreen & Sultan, 2021; Prange et al., 2003; Ramos et al., 2009; Sazima, 2007; Sha & Hanya, 2013; Tortosa et al., 2002; Turrin et al., 2015; Widdows & Downs, 2015; Yirga et al., 2012
Human	Human food, human-provided food, human trash,	Altmann & Muruthi, 1988; Cozzi et al., 2016; El Alami et al., 2012; Hasan et al., 2023; Kolowski & Holekamp, 2008; Marty et al., 2020; Mazur & Seher., 2008; Zelenskaya, 2021

	human related food sources	
Anthropogenic	Anthropogenic food, anthropogenic food sources, anthropogenic fruit, anthropogenic waste and debris,	Duclos et al., 2020; Gutierres et al., 2023; Hansen et al., 2020; Lewis et al., 2015; Murray & St.Clair., 2017; Tauler-Ameltller et al., 2017; Yirga et al., 2012
Food	Packaged food, processed food, urban food, unintentional food sources	Dhananjaya et al., 2022; Eronen et al., 2021; Lato et al., 2021
Other terms	Rubbish, landfills, carcasses, trash bins, street litter, leftovers, compost, junk, grubby, offal, bone waste transfer stations, trash, remains, discards, organic material, pollution, indigestible material	Ciucci et al., 1997; Duclos et al., 2020; Elliiott et al., 2006; Struller et al., 2022; García-Arroyo et al., 2023; Giacomo & Guerrieri., 2008; Hansen et al., 2020; Houston et al., 2007; Kumar & Ojha, 2022; Mangalam & Singh, 2013; Mazué et al., 2023; Mazumdar et al., 2016; Mazumdar et al., 2019; Mazur & Seher., 2008; Murray et al., 2015; Noreen & Sultan, 2021; Pavez et al., 2019, Plaza & Lambertucci, 2018; Ramos et al., 2009; Rimbach et al., 2023; Shlepr et al., 2021; Tauler-Ameltller et al., 2017; Turrin et al., 2015; Widdows & Downs, 2015; Zhao et al., 2022

Table 10: Terminology used to refer anthropogenic sources of trash and garbage in papers selected for the literature review.