The influence of anthropogenic food on bird behaviour and community structure in urban environments

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i. Declaration

I, Miqkayla Stofberg, hereby declare that this thesis was carries out in accordance with the regulations of the University of Cape Town; that the work upon which this dissertation is based is my original work (except where expressly indicated otherwise); and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university.

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ii. Abstract

Anthropogenic food sources have been recognized as an important trophic input in urban systems, and a major driver of the colonization of urban areas. Among various taxonomic groups, birds have exhibited a remarkable adaptation to incorporate anthropogenic food into their diets. This may have profound impacts on almost every aspect of their ecology, with the potential to trigger cascading effects on the functionality of urban ecosystems. Despite the clear significance of these dietary shifts, they have only recently begun to receive attention. To address this knowledge gap, this thesis aims to investigate the impacts of anthropogenic food on avian populations thriving in urban environments. By examining its influence on the selection of avian ecological traits, diversity, behaviour, physiology, and morphology of urban birds, I aim to gain a comprehensive understanding of their adaptation to this novel ecological niche.

Species vary widely in their ability to exploit these novel foods; therefore, it sees evident that anthropogenic food is likely to favour some species over others. In Chapter 2, I employed a trait-based approach to investigate the utilization of anthropogenic food by avian species. I review the global literature of studies quantifying the diet of urban-inhabiting bird species. The results showed a diverse range of bird species exploiting anthropogenic food sources, with varying degrees of utilization, ranging from 0% to 93% of their diets across species. There was no evidence of a phylogenetic relationship between species and the level of exploitation. Instead, the percentage of anthropogenic food in the diet of birds differed with dietary guild. Scavengers, generalists, and species with aquatic diets exhibited a greater propensity to consume anthropogenic food in substantial quantities when compared to dietary specialists, such as insectivores and carnivores. I also observed a notable disparity in the utilization of anthropogenic food between hemispheres, with birds in the Northern Hemisphere demonstrating a considerably higher consumption of anthropogenic food compared to their Southern Hemisphere counterparts. This likely mirrors the prevalence of bird feeding practices that are more established and prominent in the Northern Hemisphere, particularly in European cities, where residents are deeply motivated by their desire to enhance bird survival during the harsh winter months. My research underscores the significance of preserving natural resources for specialist species while also managing and controlling the availability of anthropogenic resources to mitigate the dominance of particular species in urban ecosystems.

The spatial distribution of food resources may vary substantially in urban environments and be directly responsible for the patterns of diversity observed in urban environments. For example, within urban areas there is considerable evidence that species diversity and abundance correlate

positively with socioeconomic status, a pattern termed the ‘luxury effect’. The potential influence of anthropogenic food abundance on the luxury effect has not yet been investigated. In Chapter 3, again using a trait-based approach and citizen science data, I explored the reporting rates of species in relation to household income within urbanised areas across South Africa. Carnivores, generalists, granivores and aquatic species exhibited the most pronounced rise in their likelihood of occurrence with increasing income. I also found evidence that the luxury effect was steeper for species endemic to South Africa and for species which were locally threatened. In contrast, species with differing nesting location, clutch size, body mass, residency and territoriality responded similarly to income. My results support to the idea that avian functional diversity in urban environments may be influenced by differences in the availability of both natural and human-provided food in urban areas and may have far-reaching implications for the delivery of ecosystem services and disservices to urban residents.

Under adverse natural food conditions, the abundance of anthropogenic food can compensate for natural food scarcity, thereby improving survival. The most notable evidence for this comes from the effects of supplementary feeding during winter in cities in the Northern Hemisphere. The potential for anthropogenic food in urban areas to buffer the potential costs associated with foraging under elevated temperatures however have been less considered. In Chapter 4, I explore the impacts of air temperature on the foraging behaviour and body mass of an urban-dwelling passerine, the Red-winged starling, *Onychognathus morio* at a university campus, where anthropogenic food abundance fluctuates over short timescales, with food being more abundant on weekdays and less abundant on weekends. I hypothesized that abundant anthropogenic food on weekdays could mitigate the negative effects of elevated temperatures on behaviour and mass change. More specifically, I predicted that the onset of evaporative heat dissipation (i.e., panting) would occur earlier with greater access to water resources from anthropogenic food sources (e.g., fruit). With regards to behaviour, I predicted that foraging effort would decline more rapidly with elevated temperature as birds can avoid prolonged activity and heat exposure under unfavourable temperature conditions. As a consequence of higher anthropogenic food availability on weekdays, I also predicted that starlings would be able to maintain food consumption rates with under elevated temperature conditions and that diurnal body mass changes would be less pronounced. I found that individuals increased panting with temperature while foraging effort declined. Despite reduced foraging, starlings were able to maintain food intake rate and body mass with rising temperatures irrespective of the short-term food fluctuations. This suggests that both natural and anthropogenic food sources in this urban environment were abundant enough to buffer individuals from the effects of elevated temperature.

Anthropogenic food may lack the essential nutrients typically provided by more balanced natural diets and could have detrimental effects on health and fitness. While bird species extensively exploit anthropogenic food, there has been limited exploration of the physiological implications associated with such consumption. In Chapter 5, using a food supplementary food experiment, I investigated the effects of a "processed" and "unprocessed" diet on the (1) behaviour (foraging effort, food consumption, provisioning, perching and preening) and (2) body mass change of adult Red-winged starlings and on the (3) relative plasma fatty acid (FA) percentages and (4) morphology (body mass, head, wing, tarsus and tail length) of their nestlings. My results showed no difference in adult behaviour and body mass with treatment. Instead, the blood plasma of nestlings assigned to a processed diet were significantly higher in saturated FAs and lower in ω-6 polyunsaturated FAs, while treatment had no effect on nestling morphology. These findings provide limited support for the idea that anthropogenic food benefits adults or poses detriments to the growth and development of their nestlings. They may indicate that urban species display physiological flexibility, allowing them to withstand substantial changes in morphology despite distinct variations in the physiological effects of anthropogenic food.

This thesis significantly advances our understanding of urban avian species' interactions with anthropogenic food resources. It highlights the central role of anthropogenic sustenance in shaping urban ecosystems, driven by species-specific tolerance levels. The research sheds light on why certain species, like generalists, scavengers, granivores, and aquatic species, thrive in urban environments while others face challenges. These insights have broad implications, emphasizing the need to regulate food access and cater to dietary specialists. The study also explores the positive and negative effects of processed anthropogenic food, with potential species-specific variations. These findings are vital for urban management, especially amid increasing urbanization and climate change challenges.

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Pictured: The process of patiently habituating one of the very first Red-winged starlings (female, ID: pink, metal, red, orange (PMRO)) to hop onto a scale in return for a reward (raisin).

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CHAPTER 1

General introduction

1.1. The ecological importance of food resources

A fundamental component of animal ecology is understanding how environmental factors determine species' abundance, survival and reproduction (Krebs, 1985; Andrewartha, 2012). This has become increasingly important as global biodiversity loss has accelerated over recent decades, exacerbated by ongoing anthropogenic drivers (Turvey & Crees., 2019). Thus, understanding how anthropogenic factors affect species' fitness is important for the conservation and management or urban fauna.

Although various factors such as climate, habitat, predation and disease can affect species persistence (Power, 1992; Sinclair & Krebs, 2002), one of the most important limiting resources for animal populations is food availability (Lack, 1954; Newton, 1998; Martin, 1987; Ostfeld & Keesing, 2000). Food abundance generally sets the limit on the number of individuals that can persist in a given environment (Newton, 1980; Lack, 1954), thereby controlling breeding success, population size and community structure (Kitaysky, et al., 2007; Martin, 1987; Lack, 1954; Ostfeld & Keesing, 2000). Species-energy relationship theories suggest that environments with more food resources promote the coexistence of dietary specialists (Vázquez & Stevens, 2004) and support a greater number of species (Karr, 1976; Wright, 1993; Wright, 1983; Srivastava & Lawton, 1998). The correlation between food availability and species abundance is well illustrated by seasonal fluctuations in species biomass, which either align with periods of peak food resource availability or become more pronounced following such periods (Shimadzu, et al., 2013; Southwood, et al., 2004; Karr, 1976; Toft, 1980).

1.2. Anthropogenic food in urban environments

Food resource abundance can undergo significant alterations in urban areas, with a higher prevalence of anthropogenic food sources and a reduction in natural food sources. Anthropogenic food has been recognized as an important trophic input in urban systems (Jones & Reynolds, 2008; Jones, 2011; Oro, et al., 2013; Penick, et al., 2015) to the extent that it is considered a key driver of the colonization of urban areas by certain animal species (Shochat, 2004; Anderies, et al., 2007; Marzluff, et al., 2001). Thus, despite the many challenges associated with urban living, the abundance of anthropogenic food may allow some species to persist even thrive in such modified environments (Shanahan, et al., 2014; Chace & Walsh, 2006). Large quantities of anthropogenic food are added into urban systems each year, provided either intentionally, for example through wild-life feeding (Jones & Reynolds, 2008; Chace & Walsh, 2006; Warren, et al., 2006) or unintentionally, such as food from garbage bins or landfills (Lowry, et al., 2012; Oro, et al., 2013; Tryjanowski, et al., 2015; Shochat, 2004). Anthropogenic food is typically more abundant, easily accessible and more predictable in time and space compared to natural food sources (Shochat, et al., 2004; Shochat, et al., 2006; Anderies, et al., 2007). Hence, it could potentially alleviate the effects of natural food shortage in urban environments (Jokimäki, et al., 2002; Mackenzie, et al., 2014; Robb, et al., 2008).

Due to its high abundance, a wide range of taxa have shifted their diets to incorporate more anthropogenic food (McKinney, 2002). For example, the exploitation of anthropogenic food has played a crucial role in enabling certain primates to thrive in urban environment (Frédéric, et al., 2022; Maibeche, et al., 2015). Many carnivores such as red foxes (*Vulpes vulpes*), coyotes and racoons have achieved higher population densities in urban areas likely driven by the exploitation of anthropogenic food (Bateman & Fleming, 2012). Wild boars (*Sus scrofa*) in urban environments also take advantage of anthropogenic food when natural food sources are limited (Stillfried, et al., 2017). Even pavement ants (*Tetramorium immigrans*) in urban environments have isotope signatures which indicate the consumption of junk food (Penick, et al., 2015).

In the case of bird species, the proliferation of anthropogenic food resources stands out as a significant driver behind the observed increase in avian biomass within urban environments (Fuller, et al., 2008; Evans, et al., 2009). Birds provide a good model group for investigating the impacts of anthropogenic food consumption on wild animals. This is because they are among the most frequent consumers of anthropogenic food resources (O'Leary & Jones, 2006; Carmona, et al., 2021; García-Arroyo, et al., 2023) and they often reach high densities where access to anthropogenic food is most abundant (Buijs & Van Wijnen, 2001; Bernat-Ponce, et al., 2022). In some cases, they rely heavily upon these resources, with anthropogenic food comprising a substantial portion of their diets (Robb, et al., 2008; Stofberg, et al., 2019; Belant, et al., 1998). Birds therefore constitute a useful model for understanding the effects of anthropogenic food consumption.

1.3. Population and community-level responses to anthropogenic food

Consuming anthropogenic food may impact almost every aspect of species' ecology (Amrhein, 2013), however the consequences of this dietary shifts have only recently been considered. For example, the ability of some species to persist or even thrive in urban environments (Møller, et al., 2012; Marzluff, 2001) has largely been attributed to the exploitation of anthropogenic food (Rodewald, 2012; Sol, et al., 2014; Marzluff, 2001). These subsidized populations are often larger and more aggregated than their conspecifics in rural environments. For example, several gull and ibis species utilize landfills and as a consequence occupy urban environments in high densities (Martin, et al., 2011; Clergeau & Yesou, 2006; Hatch, 1996; Belant, et al., 1998). Similarly, a recent study has shown that the number of restaurants in a city correlated positively with the abundance of several Columbidae species (Brown, et al., 2022). Therefore, anthropogenic food also has the potential to influence bird assemblages in urban communities by shifting abundances in favour of selected species (Fuller, et al., 2008; Chamberlain, et al., 2005; Galbraith, et al., 2015; Shochat, et al., 2004).

The exploitation of anthropogenic food can also influence population size (Oro, et al., 2013; Evans, et al., 2009). Studies indicate that anthropogenic food may contribute to larger population sizes by diminishing the risk of starvation and enhancing overall survival rates (Jansson, et al., 1981; Brittingham & Temple, 1986; Batten, 1978). Alternatively, it can increase population sizes through bolstering reproductive output through the provision of extra nutrients and energy required for successful breeding (Anderies, et al., 2007; Evans & Gawlik, 2020; Oro, et al., 2013). For example, access to anthropogenic food has been associated with the improved winter survival of Eurasian blackbirds (*Turdus merula*) (Batten, 1978) and with the earlier onset of breeding and fledging success observed in many corvid species (Webb, et al., 2004; O'Leary & Jones, 2006; Schoech, et al., 2004).

1.4. Behavioural and fitness responses of anthropogenic food consumption

Anthropogenic food consumption can also impact positively on populations densities through its effect on behaviour. More specifically, a possible consequence of predictable anthropogenic food is the tendency of some individuals to meet their daily energy and nutrient requirements with relatively reduced space use (Almaraz & Oro, 2011; Marzluff, 2001) and less time allocated to foraging (Rolando, et al., 2003; Lowry, et al., 2012; Józkowicz & Gorska-Klek, 1996). This has been observed in suburban Florida Scrub-Jays, which, with access to anthropogenic food, demonstrated improved foraging efficiency, reduced foraging time and increased perching compared to their wildland counterparts (Fleischer Jr, et al., 2003). Even during the breeding season when nutrient and energy requirements are heightened (Williams, 2012) access to anthropogenic food may enable breeders to spend a relatively small proportion of their off-nest time foraging (Lill & Geraldene, 2016). In some instances, access to year-round anthropogenic food has even allowed some birds to shift from being wholly migratory to maintaining resident populations close to anthropogenic food sources (Gilbert, et al., 2016).

Devoting less time to foraging could also improve aspects of fitness by other behavioural mechanisms such as allowing individuals to allocate excess time to provisioning their young, engaging in anti-parasite behaviour (e.g., grooming or preening), or increasing vigilance or defence against predators (Fleischer Jr, et al., 2003; Goldenberg, et al., 2016; Bollinger, et al., 1990; Murray, et al., 2018; Lowry, et al., 2012). From a physiological perspective, reduced activity should result in a net energy gain for individuals thereby improving aspects of fitness (i.e., improved body mass or body condition) and survival, potentially leading to improved breeding performance (Almaraz & Oro, 2011). While numerous studies have documented behavioural disparities between urban-dwelling birds and their rural counterparts, there has been limited exploration into the underlying mechanisms that might be responsible for these differences (Magle, et al., 2012).

1.5. Anthropogenic food quality

Central to surviving in urban environments is the need to meet nutritional requirements. Abundant anthropogenic foods may alleviate the effects of natural food scarcity (Pravosudov & Grubb, 1997; Cuthill, et al., 2000) however, the quality of anthropogenic food may be drastically altered. Anthropogenic food is typically higher in calories, carbohydrates (Bateman & Fleming, 2012; Ottoni, et al., 2009), and fat (Townsend, et al., 2019; Bateman & Fleming, 2012; Ottoni, et al., 2009) and lower in protein (Murray, et al., 2015; Heiss, et al., 2009) compared to natural food. The abundance and reliability of anthropogenic food resources can boost individual fitness and survival by enabling the accumulation of surplus energy reserves, potentially leading to improved breeding performance (Lyons, et al., 2017; Wilcoxen, et al., 2015; Auman, et al., 2008). For example, studies have shown that consumption of anthropogenic food may elevate plasma cholesterol and improve body condition (Townsend, et al., 2019; Ishigame, et al., 2006; Gavett & Wakeley, 1986) which could lead to an earlier onset of breeding and higher breeding performance.

Alternatively, anthropogenic food may lack the essential nutritional requirements typically provided by natural diets and could lead to reduced health and fitness (Annett, & Pierotti, 1999; Pierotti &

Annett., 1991; Basile, et al., 2021; Battin, 2004). The 'junk-food hypothesis' suggests that substituting high-quality food items with low quality alternatives may lead to nutritional imbalances and subsequent declines in fitness and survival (Alverson, 1992). So far, the junk-food hypothesis has only been tested for marine mammals and seabirds and has been demonstrated for natural changes in diet quality (Rosen & Trites, 2000; Litzow, et al., 2002; Jodice, et al., 2006) as well as for seabirds feeding on fisheries waste (Grémillet, et al., 2008). For example, experimental studies on marine birds have shown that nestlings raised on high-lipid prey experienced higher growth increments compared with nestlings raised on low-lipid prey of equal biomass (Romano, et al., 2006). Similarly, research on Cape gannets (*Morus capensis*) has shown that chicks fed with lower-calorie fisheries waste had lower growth rates and lower probability of survival compared to birds that provision predominantly higher-calorie live pelagic prey.

In drastically modified environments, traditional cues used to assess habitat quality (e.g., increased food abundance indicating good quality habitat) mislead individuals to choose attractive but low-quality habitats such as urban areas. These environments function as 'ecological traps', where the choice to settle within them leads to reduced fitness when compared to alternative, high-quality habitats. (Gates & Gysel, 1978; Dwernychuk & Boag, 1972; Schlaepfer, et al., 2002). Thus if increased consumption of lower-quality anthropogenic foods leads to nutritional imbalances, urban environments could act as an 'ecological trap', encouraging birds to settle in habitat where there is abundant anthropogenic food opportunities but of lower nutritional quality and result in reduced fitness (Robertson & Hutto, 2006; Schlaepfer, et al., 2002). The countless forms of anthropogenic food in urban environments and its potential to affect species both positively and negatively, make the consequences of anthropogenic food consumption on health and fitness difficult to predict.

1.6. Spatio-temporal variability of anthropogenic food abundance

Despite being more predictable and abundant than natural foods, the spatio-temporal availability of anthropogenic foods is altered by human activity. In urban environments, human activities have introduced new temporal cycles, such as our calendar week, which have resulted in more scheduled behaviour in some species. For example, anthropogenic food availability may fluctuate according to human weekday-weekend cycle in some urban areas, with higher activity and associated food abundance on weekdays relative to weekends (Risi, et al., 2021; Diniz, et al., 2021) or *vice-versa*. Accordingly, some species demonstrate the ability to adjust their daily foraging activity to closely match human time schedules in an attempt to maximize anthropogenic foraging opportunities

(Parra-Torres, et al., 2020; Diniz, et al., 2021). For example, the diet of Red-winged starlings (*Onychognathus morio*) strongly correlates with the weekly availability of anthropogenic food in urban environments, such that it comprises a greater anthropogenic food component on weekdays than on weekends (Risi, et al., 2021; Stofberg, et al., 2019; Catto, et al., 2021). Some species, particularly gulls, will even go as far as to fine-tune their daily foraging schedules to match specific times of greater human activity, such as during school break times and peak operating times of waste disposal facilities, in order to maximize foraging opportunities (Spelt, et al., 2021; Parra-Torres, et al., 2020). This kind of behavioural flexibility may be important to maximize anthropogenic food exploitation potentially enabling birds to thrive in urban environments, yet there is a lack of knowledge on how species have adapted to this new time schedule within urban environments. These short-term cyclic fluctuations in urban environments present an excellent opportunity to explore the effects of cyclic changes in anthropogenic food availability.

Spatially, urbanized habitats are also complex mosaics with altered resource structure and availability (Alberti, 2005). Human behaviour can determine much of the spatial distribution of food resources for urban wildlife (Collins, et al., 2000; Cannon, 1999; Chamberlain, et al., 2004; Lerman & Warren, 2011; Peris, 2003). For example, within urban areas there is considerable evidence that species diversity and abundance correlate positively with socioeconomic metrics such that wealthier neighbourhoods support disproportionately higher levels of species diversity and abundance than low-income areas (Chamberlain, et al., 2020; Hope, et al., 2003; Luck, et al., 2009; Martin, et al., 2004; Kinzig, et al., 2005). This pattern has been termed the 'luxury effect' (Hope, et al., 2003). One of the key drivers of the luxury effect is variation in the availability of private and public green space with socioeconomic status (Luck, et al., 2009; Hope, et al., 2003). Like the availability of green spaces, anthropogenic food (i.e., bird feeding practises), water features (i.e., irrigation, fountains, bird baths) may also vary substantially with socioeconomic status in urban environments (van Heezik & Hight, 2017; Tricam, 2020). The availability of these anthropogenically-derived food and water resources may be directly responsible for the patterns of diversity observed in urban environments. Understanding both natural and anthropogenic drivers of food abundance is crucial for conserving urban wildlife populations and their associated ecosystem services.

As urban areas continue to expand and encroach into natural habitat (United Nations, 2018), so too may species' encounters with anthropogenic food subsidies. Understanding the potential outcomes of species responses to anthropogenic food resources is thus essential for biodiversity conservation, especially given the important ecosystem services that birds provide in urban areas (Whelan, et al., 2008; Sekercioglu, et al., 2016).

1.7. Thesis aims and structure

To help fill the gaps in our knowledge related to the exploitation of anthropogenic food by birds in urban environments, this thesis aims to explore how anthropogenic food allows birds to thrive in urban environments. Firstly, I review the literature documenting the diet composition of birds inhabiting urban environments and explore the extent of anthropogenic food use across different foraging guilds (and amongst other ecological traits). Secondly, I explore the variation in the diversity and abundance of avian ecological traits across the socioeconomic gradient of urban areas in South Africa. More specifically, I explore whether improving socioeconomic conditions lead to increased diversity and abundance across all avian ecological traits or if birds with certain traits (e.g., generalists who benefit from greater natural and anthropogenic food opportunities) exhibit more pronounced increases compared to others. The chapters that follow explore the costs and benefits of anthropogenic food consumption by exploring its effects on behaviour, morphology, and physiology in an urban passerine. In terms of potential benefits, I explore whether access to anthropogenic food may buffer the potential trade-offs between foraging and heat dissipation behaviour (i.e., panting) and the associated costs on the ability to maintain body mass. In terms of costs, I explore the behavioural, physiological and morphological implications of anthropogenic food consumption on adult birds and their nestlings. Using a food supplementary experiment, I explore the effects of a highly processed diet. Through these last two chapters, I aim to obtain a more mechanistic understanding of how anthropogenic food use can influence a species' fitness within an urban context.

There is a strong conservation need to understand the ecological traits that allow species to adapt to urban environments (Oliveira, et al., 2017; Suárez-Castro, et al., 2022; Lakatos, et al., 2022; Sol, et al., 2020). Studies have found that urbanization tends to select dietary generalists, with larger brains and that produce larger clutch sizes (Bonier, et al., 2007; Kark, et al., 2007; Croci, et al., 2008; Callaghan, et al., 2019; Evans, et al., 2011). Urban environments offer a range of food sources including vegetation, trash, landfills, and birdfeeders (Chace & Walsh, 2006; Davies, et al., 2009; Thompson, et al., 2003). The ability to exploit these food sources is likely a key driver of succeeding in urban environments (Rodewald, 2012; Sol, et al., 2014; Marzluff, 2001; Kark, et al., 2007). However, it is clear that species vary widely in their ability to exploit anthropogenic food resources (Møller, 2009). This new resource may therefore species with certain dietary requirements and other ecological traits that enable them to thrive in urban environments, leading to their higher abundance. Understanding which ecological traits facilitate greater anthropogenic food exploitation may allow us to understand the trajectory of avian communities as urbanization continues to expand worldwide.

In Chapter 2, I conduct a comprehensive literature review of studies that have quantified the dietary patterns of bird species within urban habitats. I examine the extent to which various species rely on anthropogenic food sources in their diets and investigate potential correlations between specific ecological traits and the degree of anthropogenic food exploitation. The ecological traits I analyse include diet, distributional range size, body mass, territoriality, and brain size. The chosen traits were selected based on their availability in the literature and their association with greater urban tolerance as identified in previous studies (Bonier, et al., 2007; Kark, et al., 2007; Croci, et al., 2008; Callaghan, et al., 2019; Evans, et al., 2011). If the ability to exploit anthropogenic food significantly influences a species' ability to thrive in urban environments, I anticipate that the same traits linked to higher urban adaptability will also be correlated with a greater propensity for exploiting anthropogenic food sources. For example, generalist species displaying greater urban adaptability may have a larger proportion of anthropogenic food in their diets, compared to dietary specialists, such as carnivores, nectivores, frugivores and granivores.

The ‘luxury effect’ is a pattern of increased species diversity or abundance with improving socioeconomic conditions in urban areas. This pattern has been seen across multiple studies and taxonomic groups (Chamberlain, et al., 2020). A key driver of the luxury effect is variation in the availability of green space with socioeconomic status and associated natural food availability (Luck, et al., 2009; Hope, et al., 2003). Additionally, studies have found that residents from wealthier neighbourhoods are more likely to participate in bird feeding compared to those from lower income groups (Fuller, et al., 2008; Harrison, et al., 2010; van Heezik & Hight, 2017) suggesting that the availability of anthropogenic food sources for wildlife may also vary with socioeconomics. Birds in urban areas thus have access to a multitude of natural and anthropogenic food sources derived by human activities such as food provisions, rubbish bins, ornamental plants and nectar feeders (Fedriani, et al., 2001; Rodewald, 2012; Chace & Walsh, 2006; Thompson, et al., 2003). However, the potential influence of these food sources on variations in avian functional diversity in urban areas has received little investigation.

My hypothesis suggests that the availability of anthropogenic food sources may demonstrate a positive correlation with socioeconomic status and may favour particular species groups with specific ecological traits more prominently than others. To better substantiate this hypothesis**,** in

Chapter 3 I use citizen science data from the Southern African Bird Atlas 2 (SABAP2) to explore whether the luxury effect response differs depending on a species’ (1) dietary guild, (2) habitat type, (3) nest location (cavity, ground or elevated nests), (4) body mass, (5) clutch size, (6) level of territoriality (none, weak, strong), (7) migration status (resident, partial and full migrant), (8) endemism (endemic versus non-endemic), (9) residency (resident versus introduced) or (10) conservation status (threatened versus non-threatened). The chosen traits were selected based on their availability in the literature and their alignment with potential predictions. Hence, I investigate whether the species that increase with improving socioeconomic conditions in urban areas constitute a random subset of species or belong to specific functional groups. I anticipate that generalists, owing to their adaptable feeding habits, may show a substantial increase in both diversity and abundance with income. Understanding the fundamental drivers of diversity in urban environments and their variations across socioeconomic factors is essential, particularly in light of the diverse array of ecosystem services that birds offer within urban habitats.

Under adverse natural foraging conditions, supplementary food can increase population resilience through increased survival and reproduction. This is most commonly supported by studies investigating the effects of overwinter feeding on wild birds (Robb, et al., 2008; Jones & Reynolds, 2008). In winter, birds may face an energy imbalance due to reduced food availability, which is further exacerbated by the increased energy required for thermoregulation to stay warm and survive overnight (Bednekoff, et al., 1994). Supplementary food can compensate for the lack of natural food availability and alleviate the metabolic costs of thermoregulation thereby improving overwinter survival (Robb, et al., 2008; Jansson, et al., 1981; Brittingham & Temple, 1988; Cowie & Hinsley, 1988). For example, in the Northern Hemisphere studies have shown that anthropogenic food provisioning has improved the survival of wintering birds in urban areas (Källander, 1981; Grubb Jr & Cimprich, 1990; Jokimäki, et al., 1996).

High temperatures pose a mortality risk as they can result in heat stress that, if prolonged, exceeds an organism's ability to regulate body temperature within survivable limits (McKechnie, et al., 2012). Fatalities resulting from heat stress have indeed been documented in birds (McKechnie, et al., 2012; McKechnie, et al., 2021). To reduce the risk of exposure to elevated body temperatures birds can use evaporative heat dissipation (i.e., panting) (Dawson, 1982) or suppress physical activity during the hottest parts of the day (Ricklefs & Hainsworth, 1968; Silva, et al., 2015; Austin, 1976). However, these responses reduce foraging opportunities and can carry important costs for body condition, survival and reproduction (du Plessis, et al., 2012; Van de Ven, et al., 2019; Edwards, et al., 2015;

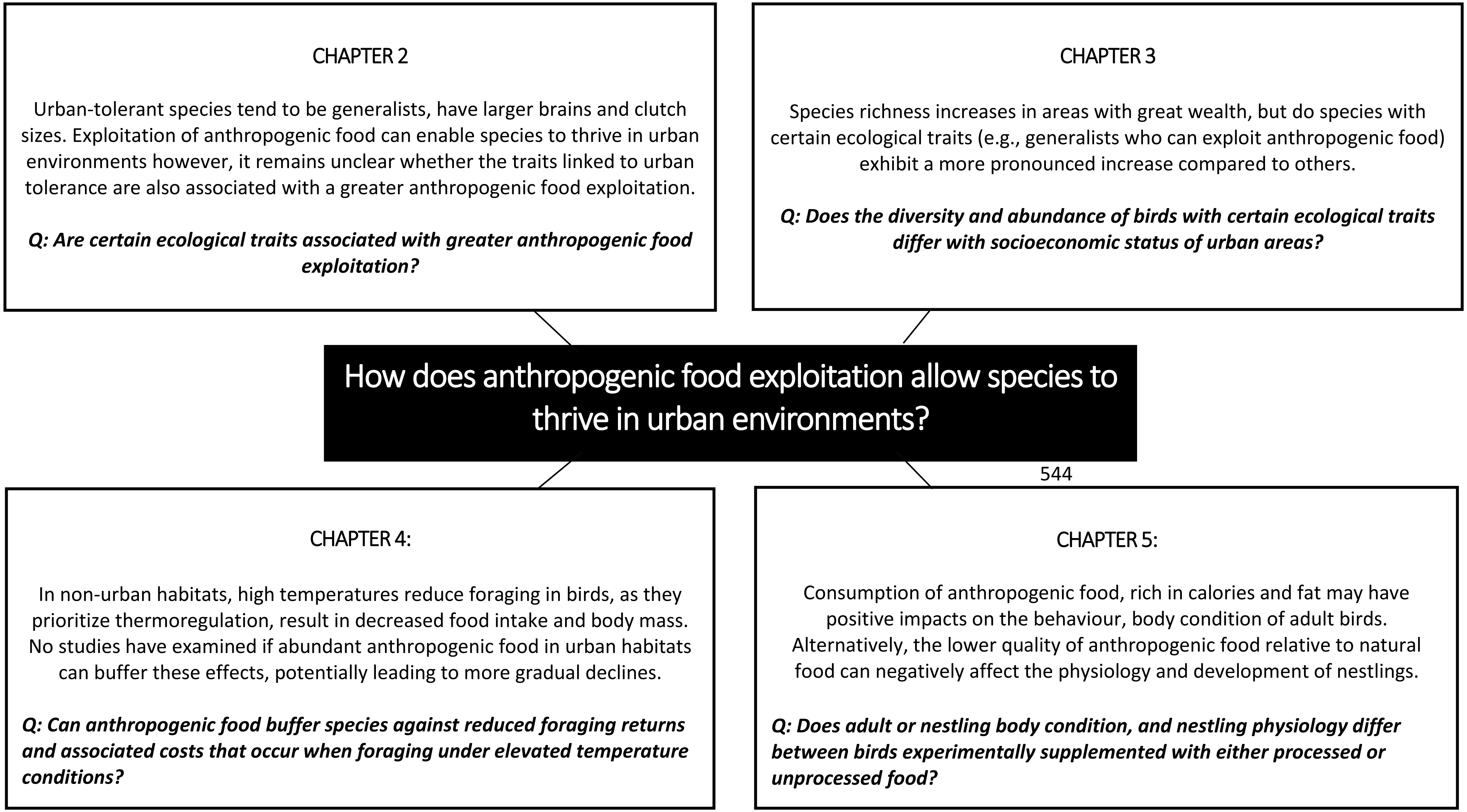
Van de Ven, et al., 2020). The costs associated with elevated temperatures may be exacerbated in urban environments due to the 'Urban Heat Island Effect' where ambient temperatures are substantially higher than natural environments (Oke, 1982; Voogt & Oke, 2003) Grimmond, 2007; Luber and Mcgeehin, 2008). However, anthropogenic food in urban environments could in theory buffer birds from the costs associated with reduced foraging under elevated temperatures. This idea, to the best of my knowledge, has not yet been explored.

Chapter 4 explores the impacts of elevated air temperature on the behaviour of an urban population of a passerine, the Red-winged starling, *Onychognathus morio* and whether anthropogenic food abundance could mitigate the potential of thermoregulation. Studies have shown that individuals with access to anthropogenic food sources have exhibited improved foraging efficiency (Saj *et al.,* 1999; Fleischer *et al.,* 2003) and higher body mass (Lyons, et al., 2017; Auman, et al., 2008; Stofberg, et al., 2019) compared to those without such access. I propose that higher anthropogenic food availability may help starlings regulate their food intake and better manage fluctuations in body mass. This could potentially reduce the usual rapid declines in food consumption and mass gain observed when foraging opportunities are reduced due to elevated temperatures. I therefore predict that the costs of thermoregulation, including reduced foraging activity leading to lower food consumption rates and reduced mass gain, would be less pronounced on days with greater anthropogenic food abundance on campus (i.e., weekdays during term time) compared to days with lower abundance (i.e., weekends, vacation).

The quality of anthropogenic food differs widely from natural food. Human diets have shifted dramatically over the past decades to include increasingly more processed foods, characterised by a high glycaemic index, carbohydrates, and saturated fats (Bonhommeau, et al., 2013; Drewnowski & Popkin, 1997; Jahren & Rebecca, 2008; Jew, et al., 2009) and have been shown to affect the physiology of some birds (Townsend, et al., 2019; Ishigame, et al., 2006; Gavett & Wakeley, 1986). The quality of food may be particularly important during the breeding season when the demand for food is high. While the quality of anthropogenic food may be adequate for adults, it may be nutritionally inadequate or detrimental for the growth and development of nestlings (Pierotti & Annett, 2001; Meillère, et al., 2015; Ricklefs, 1983). It has been suggested that anthropogenic food may be a major driver of lower nestling mass and fledging success of birds in urban environments (Chamberlain, et al., 2009; Seress, et al., 2012; Meillère, et al., 2015; Shawkey, et al., 2004). Despite the potentially negative influence of processed food, few studies have directly investigated the physiological consequences of consuming high levels of anthropogenic food, and whether this might differ between adult vs growing nestlings.

In Chapter 5, I conduct a supplementary feeding experiment in which I manipulate the quality of food available to pairs of Red-winged starlings (*Onychognathus morio*) breeding on a university campus in Cape Town, South Africa. More specifically, I hand-feed pairs with dependent nestlings with either processed or unprocessed food. I explore the effects of a processed and unprocessed diet on breeding adults' behaviour and diurnal body mass, and nestlings' fatty acid physiology and morphology. Fatty acids have three main functions in birds: (i) they form part of the structural components of cell membranes, (ii) serve as metabolic fuel and (iii) are involved in a wide range of physiological processes including oxidative stress balance, inflammation, and thermoregulation (Hazel, 1995; Pierce, et al., 2005; Ben-Hamo, et al., 2011; Hulbert & Abbott, 2012). Since previous research have indicated that anthropogenic food consumption benefits adult birds by improving their body condition but can have adverse effects on nestlings (Chamberlain, et al., 2009; Catto, et al., 2021; Auman, et al., 2008; Heiss, et al., 2009), I expected that processed food might be advantageous for adults but detrimental for the growth and physiology of their nestlings.

The thesis is presented as a series of chapters written as stand-alone manuscripts to facilitate publication. As such this has resulted in the use of the third person and the repetition of some information in the introduction and methods sections of these chapters.



CHAPTER 2

Urban-tolerant species tend to be generalists, have larger brains and clutch sizes. Exploitation of anthropogenic food can enable species to thrive in urban environments however, it remains unclear whether the traits linked to urban tolerance are also associated with a greater anthropogenic food exploitation.

Q: Are certain ecological traits associated with greater anthropogenic food exploitation?

CHAPTER 3

Species richness increases in areas with great wealth, but do species with certain ecological traits (e.g., generalists who can exploit anthropogenic food) exhibit a more pronounced increase compared to others.

Q: Does the diversity and abundance of birds with certain ecological traits differ with socioeconomic status of urban areas?

How does anthropogenic food exploitation allow species to thrive in urban environments?

CHAPTER 4:

In non-urban habitats, high temperatures reduce foraging in birds, as they prioritize thermoregulation, result in decreased food intake and body mass. No studies have examined if abundant anthropogenic food in urban habitats can buffer these effects, potentially leading to more gradual declines.

Q: Can anthropogenic food buffer species against reduced foraging returns and associated costs that occur when foraging under elevated temperature conditions?

CHAPTER 5:

Consumption of anthropogenic food, rich in calories and fat may have positive impacts on the behaviour, body condition of adult birds. Alternatively, the lower quality of anthropogenic food relative to natural food can negatively affect the physiology and development of nestlings.

Q: Does adult or nestling body condition, and nestling physiology differ between birds experimentally supplemented with either processed or unprocessed food?

Figure 1.1: Schematic representation of previous key findings that set the framework for this thesis and the resulting research questions.

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CHAPTER 2

A global review of anthropogenic food use by birds in urban areas: dietary guild and species distributional range is associated with propensity of use.

©Greg Morgan

Abstract

Avian species vary in their ability to adapt to urban environments. Some of this variability may be due to their ability to exploit anthropogenic food resources in this novel environment, yet we know little about the factors that may allow species to exploit such resources. In this study, I undertake a review of the global literature of studies which have quantified the percentage of anthropogenic food in the diet ('%AF') of urban-inhabiting bird species and extract these data therein. Using these extracted values, I then explore whether certain traits (e.g., dietary guild, geographic range size, body mass, territoriality, brain size) were associated with the propensity to exploit anthropogenic food. I found 155 studies which provided information on the %AF and extracted 424 total estimates from 132 species. Publications were biased towards the Northern Hemisphere and towards certain taxonomic groups, with gulls, ibises, owls, and kestrels featuring most often in the literature. Average %AF across species ranged from 0-93% and birds consumed a range of anthropogenic food types including human food, bird seed, and indigestible anthropogenic materials. The results showed no evidence of a phylogenetic signal for the %AF between species. Instead, %AF differed with dietary guild with scavengers, generalists and species with aquatic diets consuming anthropogenic food in greater quantities than other dietary specialists (i.e., carnivores and insectivores). This review highlights the widespread nature of anthropogenic food consumption across a wide range bird species globally and the importance of dietary guild as a potential key determinant of inhabiting urban environments alongside other traits. Additionally, these results also highlight the importance preserving natural resources for specialist species while also managing and controlling the availability of anthropogenic resources to mitigate the dominance of particular species in urban ecosystems.

2.1. Introduction

Urbanization is one of the most rapidly expanding land uses worldwide. Currently 55% of the world's population lives in cities and this is expected to increase to 68% by 2050 (United Nations, 2018). Urbanization drastically alters natural ecosystems in irreversible ways (McKinney, 2002; McKinney, 2006). The expansion of urban areas will therefore have profound consequences on biodiversity (Marzluff, 2001; McKinney, 2008; McKinney, 2006) and species living in urban environments must contend with multiple challenges such as loss of habitat, alteration of natural food sources, increased pollution, human disturbance and spread of parasites and pathogens (Sol, et al., 2013; Alirol, et al., 2011; Murray, et al., 2019).

Although many species are unable to adapt, and show reduced occupancy in urban environments, others successfully exploit urban environments, taking advantage of the opportunities they present (Marzluff & Neatherlin, 2006; Sol, et al., 2013). Some of these opportunities may include milder and more stable microclimates, fewer natural predators, and increased availability of nest sites (Mainwaring, 2015; Marzluff, et al., 2001; Eötvös, et al., 2018). One of the greatest of these opportunities is the availability of anthropogenic food resources, which has been recognized as an important trophic input in urban environments (Jones & Reynolds, 2008; Jones, 2011; Oro, et al., 2013; Penick, et al., 2015). Compared to natural food, anthropogenic food is typically more abundant, easily accessible, and more stable in its availability irrespective of weather and seasonal conditions (Marzluff, et al., 2001; Anderies, et al., 2007). Anthropogenic food is provided intentionally, in the form of bird feeding by the public (Jones & Reynolds, 2008) or unintentionally from food scraps, refuse and landfills (Auman, et al., 2008; Jones, 2011; Lowry, et al., 2013).

Many bird species living in urban areas have shifted their diets to incorporate anthropogenic food (Oro, et al., 2013; Plummer, et al., 2015). However, there is considerable variation in their anthropogenic food consumption: for some bird species living in urban areas it comprises the majority of their daily food consumption (Stofberg, et al., 2019) whereas others show little to no evidence of anthropogenic food exploitation (O'Leary & Jones, 2006; Mennechez & Clergeau, 2001). While a number of studies have investigated consumption of anthropogenic food within a single species or a few species within local regions, as yet no study has reviewed this literature to quantify how widespread anthropogenic food consumption by urban birds is, and whether certain ecological traits may be associated a propensity to exploit anthropogenic food.

In this study, I conduct a comprehensive literature review of existing studies that have investigated and quantified the diet of bird species within urban habitats and extract the percentage of anthropogenic food (hereafter '%AF') in the diet of the studied species. I whether there is any phylogenetic signal in anthropogenic food exploitation and whether certain traits are associated with greater anthropogenic food exploitation. For this I assess the following traits (1) dietary guild, (2) species geographic range size, (3) body mass, (4) territoriality and (5) brain mass. The chosen traits were selected based on their availability in the literature and their association with greater urban tolerance as identified in previous studies (Bonier, et al., 2007; Kark, et al., 2007; Croci, et al., 2008; Callaghan, et al., 2019; Evans, et al., 2011).

For each of these traits the following predictions were made: (1) Dietary guild – I expected generalists to incorporate a greater %AF in their diets compared to species from other dietary guilds. Generalists, as demonstrated by Bonier et al., (2007) have broader dietary requirements (Bonier, et al., 2007) this allows them to exploit a diverse range of food resources and could potentially lead to a greater exploitation of anthropogenic food items. (2) Species range – I predict that wide-ranging species may exhibit greater anthropogenic food exploitation compared to range-restricted species. This is mainly attributed to the increased tolerance of species with greater dispersal abilities, such as those with larger distribution range sizes, for urban environments (Neate-Clegg, et al., 2023; Møller, 2009) where anthropogenic food is most abundant. (3) Similar to body size, body mass is likely to play a significant role in determining dominance and subsequent access to resources (Forrester, 1991; Wojczulanis-Jakubas, et al., 2015; Miller, et al., 2017; Auman, et al., 2008). Hence, I expect that species with greater body mass are likely to outcompete smaller species, potentially leading to larger species incorporating a higher %AF into their diets. (4) Similarly, establishing territorial dominance over available resources to exclude others could lead to the monopolization of those resources ('competitive hypothesis') (Sol, et al., 2012). Alternatively, anthropogenic food resources may be concentrated in specific areas, which are often undefendable (Maher & Lott , 2000; Wilson, 2001). In these situations, species may engage in scramble competition, potentially resulting in similar %AF in their diets regardless of their territorial tendencies. (5) Research on brain size indicated that larger relative brain size is associated with increased urban tolerance (Sayol, et al., 2020). This heightened tolerance is likely a result of superior behavioural flexibility in novel environments, including urban settings (Sol, et al., 2005; Carrete & Tella, 2011). Therefore, I predict that this enhanced behavioural flexibility displayed by larger-brained species would enable them to adapt to the increased availability of anthropogenic food in urban areas, leading to a higher %AF in their diets.

2.2. Methods

2.2.1. Literature search

I searched for potentially relevant studies in *Web of Science* on the fourth of November 2021. I performed a title search using the terms (“urban diet”) and topic search using the search terms (“diet” OR “food” OR “foraging” OR “consumption” AND “urban bird” OR “urban passerine” OR “urban avian” OR “city bird”). Additionally, I performed a search in *Google Scholar* on the 23rd of November 2021 using the search terms ((“diet” OR “food consumption”) AND (“urban bird” OR “city bird”)). These searches found 373, 1383 and 820 studies respectively and they were combined to create a list of 2576 studies. Amongst these studies, I then removed any duplicates. Two additional relevant studies Fleischer et al. (2003) and Cowie & Hinsley (1988) were identified while reading Coogan et al. (2018), a study on my list. The final list contained 2414 unique studies.

To identify relevant studies my inclusion criterion was that a paper had to provide information on the composition of the diet of at least one bird species within an urban or sub-urban environment. The habitat types were determined by the papers themselves. To screen for relevant papers, I first read the title and if this indicated that the paper was relevant, I read the abstract. If the abstract further indicated that the paper could fit the inclusion criteria (i.e., to include the % of the diet that consisted of anthropogenic food), I then explored the study in more depth, aiming to extract the mean percentage of the diet consisting of anthropogenic food. Where the percentages were not explicitly stated but were presented in a plot, *graphreader.com* was used to extract the values from the plot. I also recorded the species, year of publication, study site location, timing of study (breeding/non-breeding period/both), age (adult/juvenile/nestling) and method for diet quantification when this information was provided. Where diet means were not provided in the study but may have been available based on the methods used, the author was contacted and if no response was received the study was excluded (Figure 2.1).

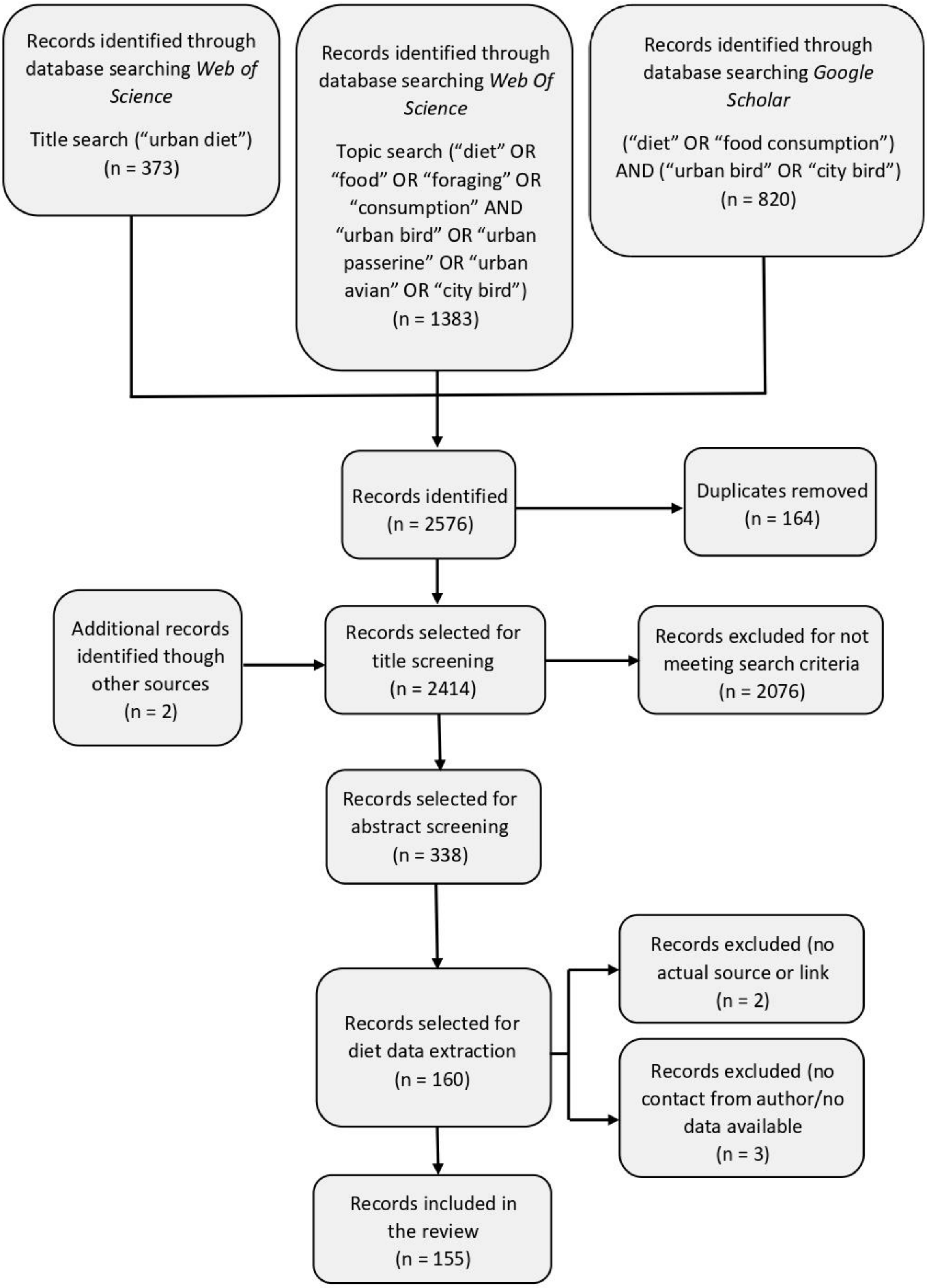


Figure 2.1: Flow diagram for the identification, screening, eligibility and inclusion of studies for publications in this review

2.2.2. Extraction of estimate for anthropogenic food

I was interested in investigating variation in the percentage of the diet consisting of anthropogenically-derived food of bird species residing in urban habitats. I therefore considered studies with study sites described within the papers themselves as urban, suburban, and peri-urban (including landscapes dominated by commercial, industrial, or residential habitats). For studies which provided data on multiple species I extracted the individual species level mean percentage. For experimental studies on birds in urban habitats, I only used the means reported for control groups and not those which were intentionally supplemented with anthropogenic food.

Where anthropogenic food exploitation was compared along a continuous gradient of urbanization and plotted in a linear regression, interpolation was employed to determine the estimate for three corresponding levels of urban cover; the maximum level recorded for the study, at 50% urban cover, and the minimum level of urban cover. When diet was compared for different fixed/discrete levels of urbanized habitats, I recorded the means at each level of urbanization. For studies which made comparisons between urban and non-urban populations, I only extracted the estimates of anthropogenic food consumption for the urban population. In this review, ‘anthropogenic food’ referred to food sources originating from human activities, including processed foods, fruits and provisioned food such as bird seed. However, studies providing the percentage of anthropogenic debris (plastic, rubber, cardboard etc.) in a species diet were also considered and were used as a proxy to indicate the %AF consumed. For studies which reported separate estimates for diet consumption within breeding status, or between sexes, and ages, I recorded each estimate, and treated these as multiple estimates within a species. Different studies used different techniques to quantity diet, and I recorded each approach used. Due to small sample sizes within the techniques used, I grouped pellet analysis with prey remains and regurgitates, and video footage with photographic records and direct observations. The remaining techniques used were stomach analysis, isotope analysis and faecal sampling. Therefore, the final dataset had five categories of diet quantification. I observed diversity in the units of measurement used to describe anthropogenic food consumption. This diversity encompassed metrics such as 95% credibility intervals, counts of food items, the frequency of occurrence of food items in the diet as well as the frequency of foraging on anthropogenic food sources during a period of observation. For my analysis, I standardized all estimates by converting them to a percentage scale relative to a total of 100.

2.2.3. Species functional traits

For each species for which I was able to extract data on the %AF within urban areas, I also obtained information on a number of traits. I obtained a complete list of species' (1) dietary guild classification for the species in my dataset from a global avian trait database compiled by Tobias & Pigot, (2019). The only adjustments made to the diet categories involved combining species with a diet classification of 'aquatic plants' and 'aquatic animals' into a single category termed 'aquatic'. Dietary guilds were classified into nine categories: generalists, aquatic, herbivores, granivores, frugivores, nectivores, insectivores, scavengers and carnivores.

I obtained a (2) range size (km^2) data from three global avian trait databases, namely Tobias & Pigot (2019), Tobias et al. (2022), and Wilman et al. (2014), all of which had a complete list of range size information for every species. Species-specific averages were calculated across all three databases.

I also obtained (3) body mass (gr) data from Tobias & Pigot (2019), Tobias et al. (2022) and Wilman et al. (2014). Both Tobias & Pigot (2019) and Tobias et al. (2022) contained a complete list of body mass data for all species, while Wilman had data for 114 species on my list of species. I calculated species-specific averages across all databases where body mass data for each species were available.

I obtained information on species' (4) level of territoriality ('*none*', '*weak*', '*strong*') for all species on my list from Tobias & Pigot (2019).

(5) Brain size (ml) was obtained from two databases, Sayol et al. (2020) and Fristoe & Botero (2019). Sayol et al. (2020) had brain size information for 54 species within my list, whereas Fristoe & Botero (2019) had brain size data for 124 of the species within the list. I calculated species-specific averages across the two databases where data were available from both sources (46 species), and in cases where the average could not be determined (86 species), I used the single brain size value provided by one of the databases. For the analysis '*corrected brain size'* was used which was the residuals generated from a linear model fitted with brain size as the response variable and body mass as the explanatory variable.

2.2.4. Statistical analysis

All analysis were performed in R 4.1.2 (R Development Core Team, 2021). A phylogeny of the species for which I had data was generated using the subset tool on the 'BirdTree' website (Jetz, et al., 2012, http://birdtree.org/). Jetz et al. (2012) generated a phylogenetic tree for nearly all bird species using Bayesian phylogenetic methods. I downloaded a sample of 10000 trees for the species in the dataset (i.e., those for which I had %AF consumption). The trees were based upon a composite of existing genetic data built upon a backbone tree from Hackett, et al. (2008). The 10000 trees were imported into R using the *ape* package (Paradis & Schliep, 2019) and then used to create a maximum clade credibility tree using the *phangorn* package (v.2.8.1) (Schliep, 2011).

Prior to the analysis I checked for collinearity among variables by plotting a covariance matrix using the package *ggcorrplot* (Kassambara, 2019) which showed no strong collinearity (maximum correlation coefficient <0.43; Figure S1.1).

I tested whether the %AF consumed showed evidence for a phylogenetic signal using a phylogenetic generalized least-squares multivariate regression (PGLS) from the *caper* package (Orme, et al., 2018). For this analysis, where a species had multiple estimates of anthropogenic food consumed, I calculated the average percentage for that species thus providing only a single measure of anthropogenic food per species. The PGLS model was fitted with the %AF in the diet as the response variable and dietary guild, range size, body mass, territoriality, and corrected brain size of each species as explanatory variables. The PGLS controls for any potential non-independence between clades due to shared ancestry of species, by explicitly incorporating the expected covariance among species into the model fit and generating a metric λ, Pagel's lambda (Pagel, 1999) which indicates whether the response variable shows evidence for a phylogenetic signal.

Following on from the PGLS, I continued to explore the relationship between the anthropogenic food consumption and the ecological traits, which incorporated the multiple estimates I obtained for many of the species. The proportions of the diet consisting of anthropogenic food and the remaining proportion out of one were combined using the *cbind* function in R and fitted as the response variables in a generalized mixed effects regression (GLMER) from the *lme4* package in R with a binomial error distribution. Dietary guild, range size, body mass, corrected brain size, territoriality and hemisphere were fitted as explanatory variables. Continuous explanatory variables were centred and scaled using z-score standardization, resulting in all variables having a mean of zero a standard deviation one, thus making variables more comparable. To account for overdispersion in the model I included an observation level random effect (Harrison, 2014). To control for variability across and within species and variability associated with different methods of diet quantification, species and method of quantification were fitted as random terms. To control model optimization, the *glmerControl* function was employed and the '*bobyqa*' optimizer was chosen.

Statistical significance was defined as P< 0.05. When significant differences between groups were found, I conducted pairwise comparisons using *emmeans* while implementing the Bonferroni correction to controls for the family-wise error rate.

2.3. Results

After reviewing the 2414 papers from the searches, a total of 155 publications met my inclusion criteria and were used in this review, from which 424 estimates of the % of the diet comprised of anthropogenic food were extracted from a total of 132 species, from 45 families. Papers were published from 1972 to 2021 and the number of studies showed a rapid growth during this period (Figure 2.2).

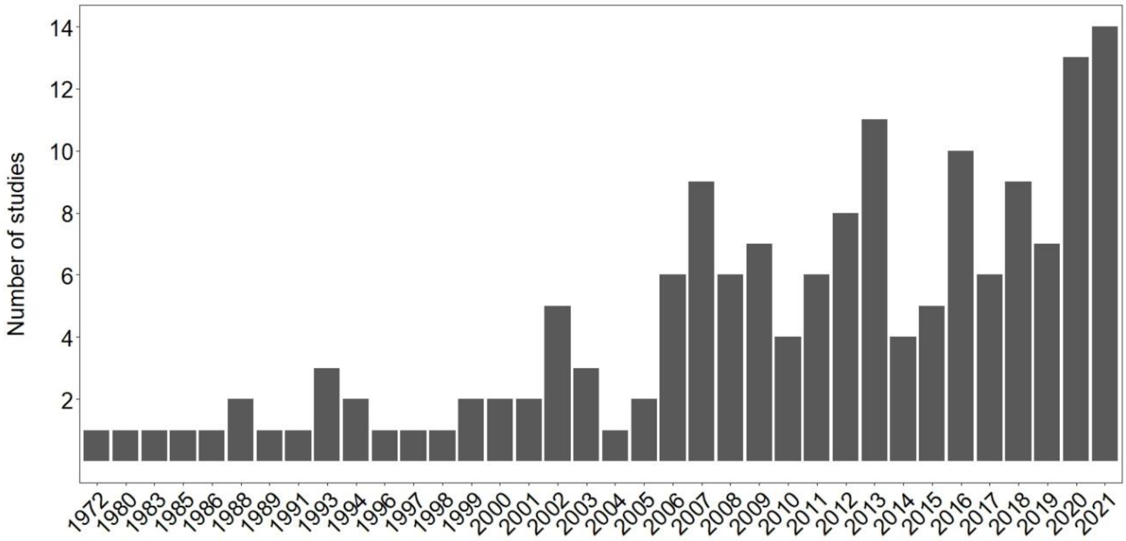


Figure 2.2: Number of studies quantifying the diet of urban-inhabiting birds from 1972 to 2021. Data came from the 155 studies included in this review.

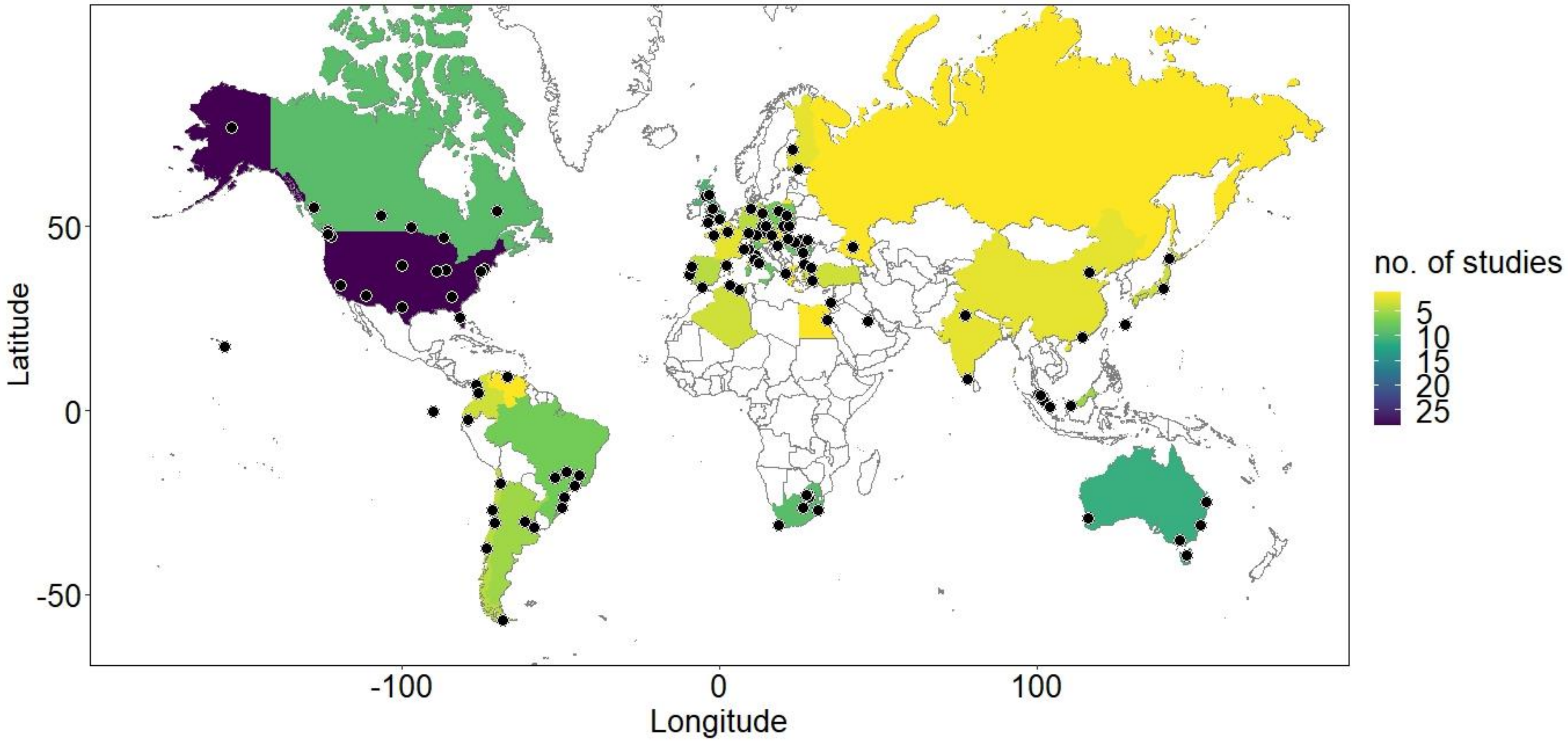


Figure 2.3: Global distribution across 35 countries of the 155 studies quantifying the diet of 132 urban-inhabiting species included in this review. Each point represents a study in which the diet of one or more urban-inhabiting bird species was quantified.

2.3.1. Distribution of studies and estimates in space, between species and across techniques

Studies came from 35 countries with most studies conducted in USA (n= 28, 17.61% of studies), followed by Australia (n= 11, 6.92% of studies). An equal number of studies were carried out in Canada, South Africa and the UK (n= 9, 5.66%). Subsequently, South American countries Brazil and Argentina had 7 and 5 (4.40% and 3.14%) studies respectively. Two and one study represented both the lowest and most common number of studies conducted across countries such as India, China and Russia (Figure 2.3).

Bird families from which the highest number of estimates were obtained were owls (n= 98 estimates, 23.1%) followed by gulls (n= 71 estimates, 16.7%) (Figure S1.2). The most frequently sampled species were the Common kestrel (*Falco tinnunculus)*, Long-eared owl (*Asio otus*), White ibis (*Eudocimus albus*) and Yellow-legged gull (*Larus michahellis*) from which I obtained the same number of estimates (n= 23 estimates, 5.4%), followed by the Barn owl (*Tyto alba;* n= 20 estimates, 4.7%), Tawny owl (*Strix aluco,* n= 18 estimates, 4.2%) and Blue tit (*Parus caeruleus,* n= 16 estimates, 3.8%) (Figure S1.3).

Of the different techniques used to quantify avian diet, regurgitates and prey remains were the most frequently used (n= 192 estimates, 45.3%), followed by direct observations (n= 95 estimates, 22.4%), then faecal sampling (n= 63 estimates, 14.8%) followed by stomach analysis (n= 47 estimates, 11.1%). Finally, the least most common method used was isotope analysis (n= 21 estimates, 5.0%) and few studies used a mixture of these techniques (n= 6 estimates, 1.4%) to quantify diet (Figure S1.4).

2.3.2. Sources and types of anthropogenic food consumed

From the 424 estimates, the source of the anthropogenic food was provided for 175. Most species obtained anthropogenic food from discarded food items (79.4% of those 175 studies), followed by provisioned food (15.4%) and then from landfill sites (5.7%) (Figure S1.5). The majority of studies (58.7% of a total of 424 estimates) provided estimates without detailed descriptions of the anthropogenic food items consumed (Figure 6). From those which provided this information, human food was the most common food item consumed (65.7%). Provisioned food sources consisted mostly of bird seed followed by human food (e.g., bread). Non-food items such as synthetic materials were predominantly sourced from discarded refuse and landfill sites and included items such as paper, glass, plastic, polystyrene foam and metal (Figure S1.5, Table S1.1).

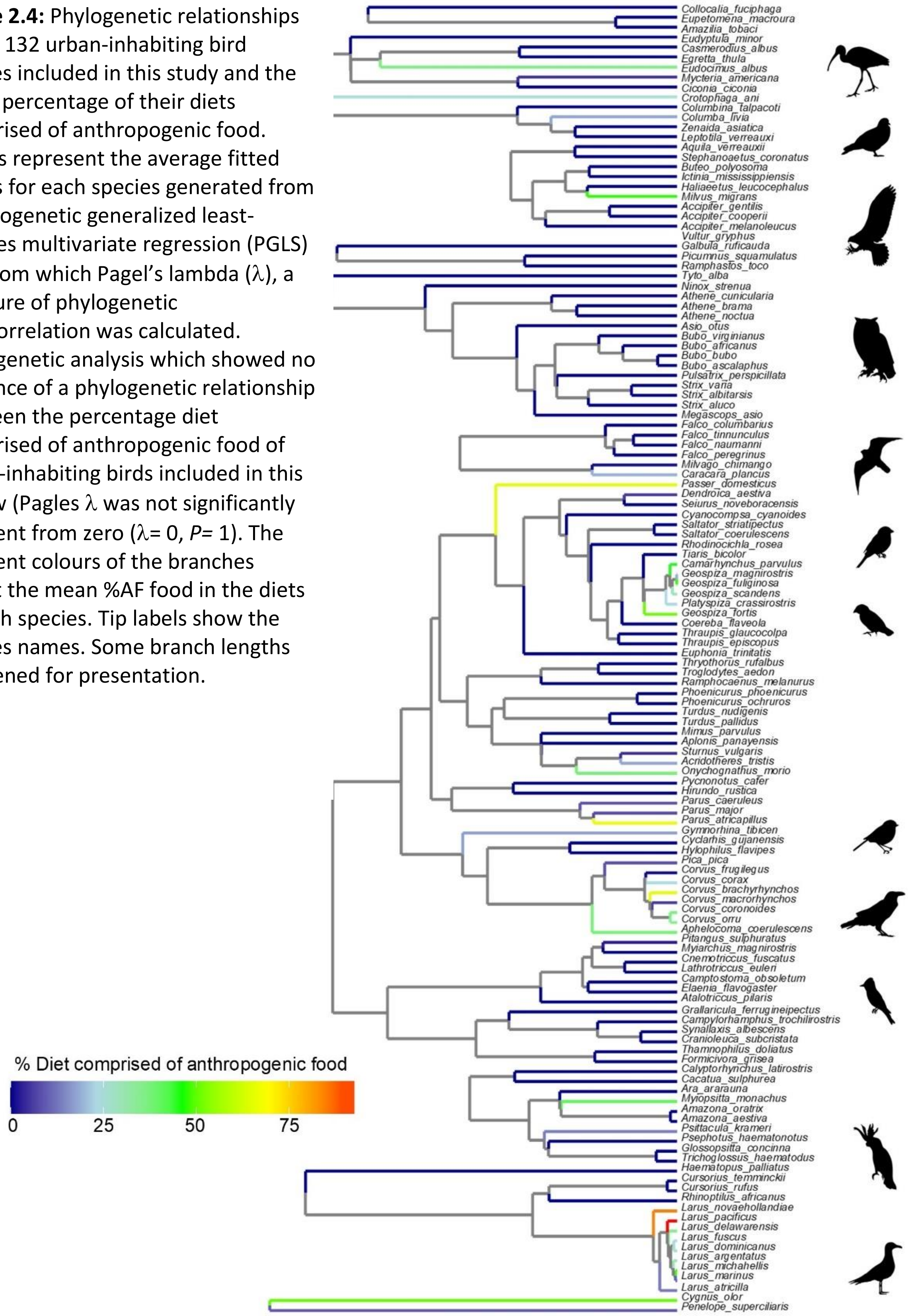
2.3.3. Distribution of estimates across different traits

Carnivores and aquatic species had the largest number of estimates (n= 144 estimates, 34.0%: n= 104 estimates, 24.5%, respectively). Generalists and carnivores were the next most frequently sampled dietary guild (both, n= 64 estimates, 15.1%), followed by granivores (n= 22, 5.2%) and frugivores (n= 20, 4.7%). The least sampled dietary guilds were nectivores and scavengers which both only had three estimates (0.7%) (Figure S1.6a). With respect to territoriality, most of the estimates came from species showing weak (n= 188, 44.3%) and no territoriality (n= 155, 36.6%), and less from species which are strongly territorial (n= 81, 19.1%) (Figure 2.6b). Finally, most of the estimates come from species with a range size between approximately 1,202,000km^2-170,000,000km^2, with the number of estimates peaking at 8,800,000km^2 and few with range sizes <1,202,000km^2 (Figure S1.6c).

2.3.4. Phylogenetic influence on anthropogenic food consumption

Values of Pagels λ (lambda) close to zero indicate phylogenetic independence in the model residuals, (i.e., trait values are random with respect to phylogeny) while values close to one indicate the existence of a phylogenetic relationship consistent with a Brownian motion model evolutionary model (i.e., closely related families have similar estimates than would be expected by chance) (Pagel, 1999). Phylogenetic analysis using PGLS demonstrated that λ= 0 (95.0% CI: [0, 0.342]) was not significantly different from zero (P= 1), providing no support for any phylogenetic autocorrelation in these data and thus supporting my further analysis, which did not include a phylogenetic component (Figure 2.4, see Table S1.2 for ANOVA results).

Figure 2.4: Phylogenetic relationships of the 132 urban-inhabiting bird species included in this study and the mean percentage of their diets comprised of anthropogenic food. Means represent the average fitted values for each species generated from a phylogenetic generalized least-squares multivariate regression (PGLS) and from which Pagel's lambda (λ), a measure of phylogenetic autocorrelation was calculated. Phylogenetic analysis which showed no evidence of a phylogenetic relationship between the percentage diet comprised of anthropogenic food of urban-inhabiting birds included in this review (Pagles λ was not significantly different from zero (λ= 0, *P*= 1). The different colours of the branches depict the mean %AF food in the diets of each species. Tip labels show the species names. Some branch lengths shortened for presentation.



2.3.5. Estimates of, and traits associated with, anthropogenic food consumption

For many species of urban living birds, no anthropogenic food was found in the diet. For species which did consume anthropogenic food, the average percentage ranged from 0.35% for Burrowing owls (*Athene cunicularia*) to 85.0% and 92.5% for Pacific gulls (*Larus pacificus*) and Silver gulls (*Chroicocephalus novaehollandiae*) respectively. These two gulls were the only species in the 80%-100% percentile. The next highest percentages were observed for American crows (*Corvus brachyrhynchos*), Black-capped chickadees (*Poecile atricapillus*), House sparrows (*Passer domesticus*) and Ground finches (*Geospiza* spp.) which all had diets comprising approximately between 55-65% anthropogenic food (Figure 2.5).

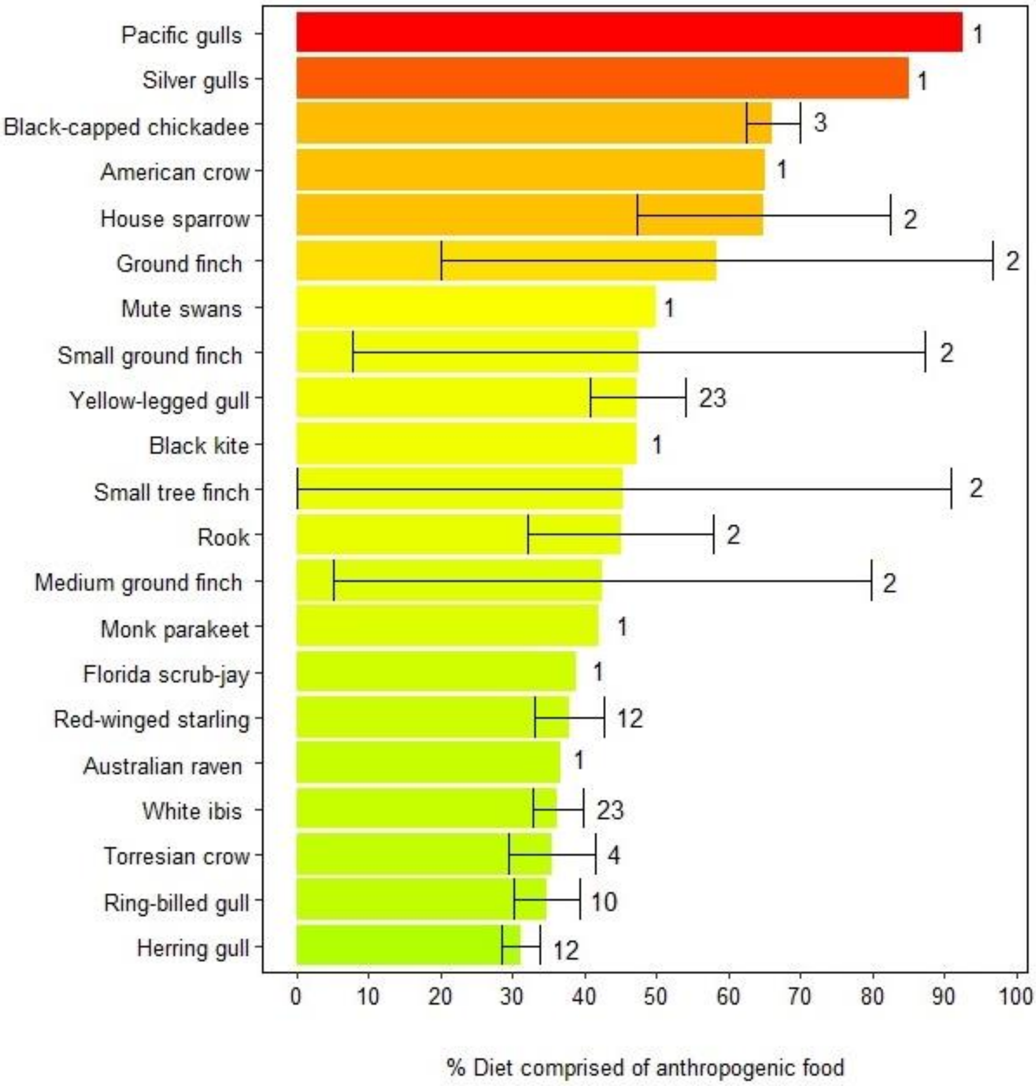


Figure 2.5: The average % of the diet comprised of anthropogenic food by urban-inhabiting bird species included in this review. The plot displays all those species whose diet comprised >30% anthropogenic food (n= 22 bird species). The values above the bars represent the number of estimates derived for each species and standard error bars are shown for those species with more than 2 estimates. Data were derived from 424 estimates taken from 155 publications included in this review and comprise 132 species (16.5% of species shown here).

Aquatic species, granivores, generalists and scavengers were amongst those who consumed the highest percentage of anthropogenic food (herbivores who were also high exploiters only consisted of a single observation). I found a significant difference in the %AF depending on the dietary guild of the species (ANOVA: $\chi^2_{8, 410}$= 33.58, $P < 0.001$; Figure 2.6). Scavengers and generalists consumed significantly greater %AF than insectivores. Aquatic species, scavengers and generalists also consumed a significantly greater %AF than carnivores. (Figure 2.6, see Supplementary Table S1.3 for pairwise comparisons).

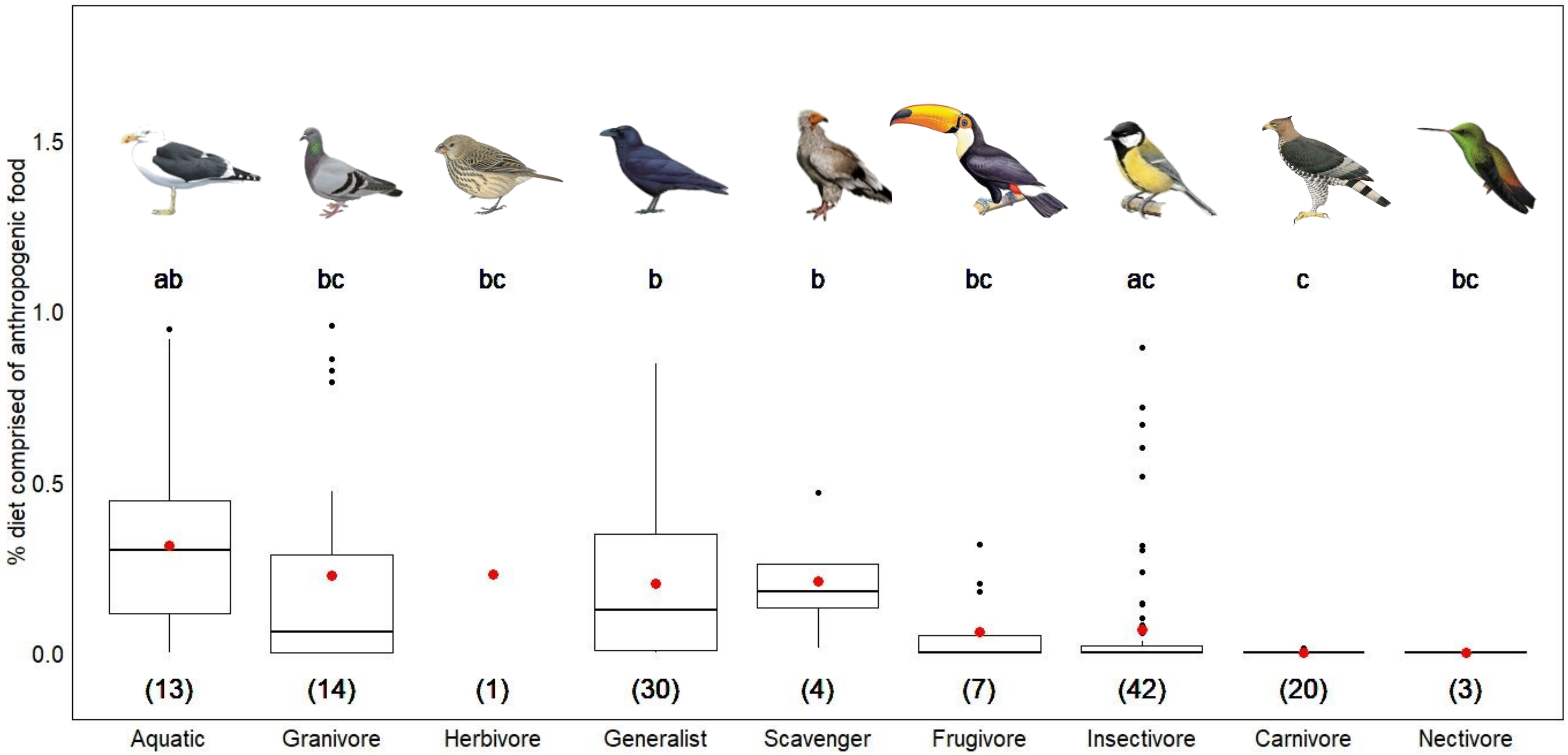


Figure 2.6: Box and Whisker Plot Illustrating the distribution of the percentage of anthropogenic food in the diet of species across different dietary guilds. Red dots represent the mean percentage generated from GLMER. The percentage of the diet comprised of anthropogenic food was significantly different with dietary guild (*P*< 0.001, $\chi^2_{(8; 424)}$ = 33.58). Means sharing the same letter were not significantly different. Sample sizes are indicated in parentheses. Data were derived from 155 studies describing the diet of urban-inhabiting birds and included 132 species and 424 estimates.

The %AF in the diet showed no significant difference with species' body mass (ANOVA: $\chi^2_{1,\,410}$= 0.18, *P*= 0.67), corrected brain size (ANOVA: $\chi^2_{1,\,410}$= 1.00, *P*= 0.32), level of territoriality (ANOVA: $\chi^2_{2,\,410}$= 3.97, *P*= 0.14), or species range size (ANOVA: $\chi^2_{1,\,410}$= 2.64, *P*= 0.10). However, I found a significant difference in %AF within the diets of species from urban areas across different hemispheres with species from urban areas in the Northern Hemisphere containing a higher %AF in their diets compared to those in the Southern Hemisphere (estimate= -2.29 ± 0.99, *z*= -2.31, *P*= 0.02, ANOVA: $\chi^2_{1,\,410}$= 5.32, *P*= 0.02; Figure 2.7).

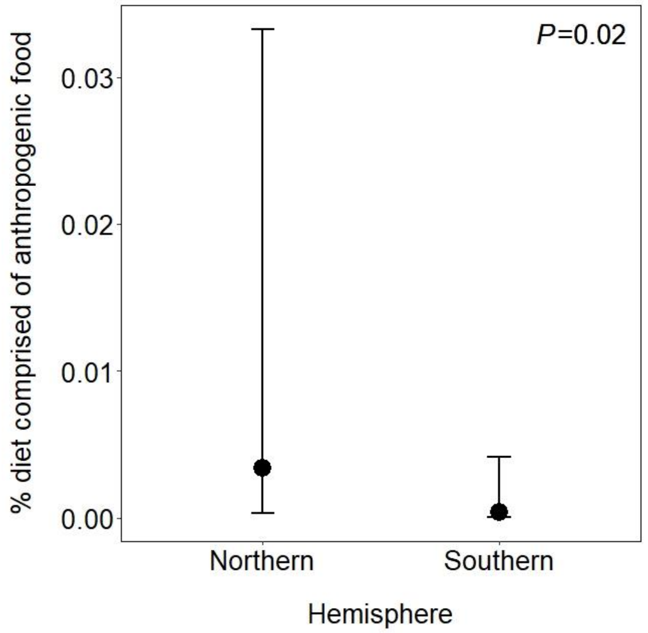


Figure 2.7: The average proportion of anthropogenic food in the diet for species from different hemispheres with standard error bars shown. The percentage of the diet comprised of anthropogenic food was significantly different with hemisphere ($\chi^2_{(1;\,424)}$ = 5.32, *P*= 0.02). Means and standard error bars were generated from GLMER. Data were derived from 155 studies describing the diet of urban-inhabiting birds and included 132 species and 424 estimates.

2.4. Discussion

This literature review uncovered numerous studies worldwide that reported on the inclusion of anthropogenic food in avian diets, but with a high number of publications from cities in the Northern Hemisphere. The majority of studies came from Europe (42% of studies) and North America (28%), but a reasonable number of studies were from the Southern Hemisphere, which is often underrepresented in the field of urban avian ecology (Chace & Walsh, 2006; Aronson, et al., 2014; Marzluff, 2016; Martin, et al., 2012). The number of publications containing information on the diet of urban inhabiting birds has increased remarkably since 1972, likely reflecting the rapid growth in urbanization since the 19th century (Ritchie & Roser, 2018; United Nations, 2018) and concerns for the consequences on biodiversity.

Although studies spanned a surprisingly large number of different species (n= 132), taxa were biased towards raptors (particularly owls and kestrels), gulls and corvids, which were the most frequently studied bird groups in urban avian literature. Raptors, due to their position at the top of food chains, are often the focus of research as the composition of their diets has been shown to be an effective surrogate measure for wider biodiversity (Sergio, et al., 2006; Natsukawa & Sergio, 2022). Furthermore, gathering dietary information from raptors is often straightforward due to their ease of observation through direct means, and the convenient collection of their faecal and prey remains (Real, 1996). Both crows (family *Corvidae*) and gulls (family *Laridae*) are classical subjects for the study of urban avian diets, which is not surprising as crows and gulls are among the most abundant and proficient exploiters of urban environments throughout the world (Marzluff, et al., 2001; Blair, 1996). In both cases their population trends have been attributed to rapid urbanization (Auman, et al., 2011; Auman, et al., 2008) and the exploitation of anthropogenic food sources (Marzluff & Neatherlin, 2006; Webb, et al., 2011).

Urban birds exploit a diverse range of anthropogenic food such as meat, hotdogs, pizza, crisps, french-fries, pasta/noodles, cheese as well as dogfood. Most of the food items presented here were processed foods which are typically high in carbohydrates and fats (Heiss, et al., 2009; Townsend, et al., 2019; Coogan, et al., 2018) and which may lead to nutritional imbalances or worse, reduced fitness and survival, as predicted by the ‘junk-food hypothesis’ (Alverson, 1992). Even more concerning was the high prevalence of non-digestible anthropogenic debris in the diet of urban-inhabiting species. These included materials commonly used for food packaging (polystyrene foam, paper, plastic, and foil), fabric (leather, thread, twine, nylon, rubber), metal, wood, and glass, and of which seabirds (Family *Laridea*) represented the most frequent exploiters (C. 80%). For several of the studies anthropogenic materials consumed were used as a proxy for anthropogenic food consumption, which may not be ideal as these are often non-digestible items and could potentially overestimate the actual amount of anthropogenic food in a species' diet.

The results show no evidence for a phylogenetic signal in the mean %AF in the diet of urban-inhabiting bird species, instead showing marked differences in anthropogenic food consumption by closely related species. Furthermore, the trait-based analysis showed that %AF in the diet of urban-inhabiting birds was not influenced by their body mass, corrected brain size, level of territoriality, nor range size but instead was influenced by species dietary guild. Aquatic species, scavengers and generalists consumed significantly more anthropogenic food than specialist groups. These results support the idea that some species are more adept for urban areas than others (Callaghan, et al., 2019; Bonier, et al., 2007; Evans, et al., 2011) and that their larger densities in urban areas may be partly assisted by their greater exploitation of anthropogenic food (Oro, et al., 2013; Robb, et al., 2008; Clergeau, et al., 1998).

2.4.1. Phylogenetic influence on anthropogenic food consumption

The lack of evidence for a phylogenetic signal in the mean %AF in the diet of birds suggests that there is no underlying evolutionary lineage which allows birds to exploit anthropogenic food. Thus, many closely related species showed marked differences in the %AF consumption, as well as many distantly related species which have high anthropogenic food consumption. The lack of phylogenetic signal in terms of anthropogenic food exploitation by urban-birds contrasts with many other analyses that have explored exploitation of urban habitats and all of which provide strong evidence that the phylogenetic relatedness of species increases in urban areas (Callaghan, et al., 2019; Ibáñez-Álamo, et al., 2017; Sol, et al., 2017; Morelli, et al., 2016; Palacio, et al., 2018).

The absence of a phylogenetic signal in my study suggests several possibilities. Firstly, it could reflect limitations related to the lack of phylogenetic representation in my dataset, which included only 132 bird species. In contrast, other global analyses that successfully detected phylogenetic signals benefited from a broader taxonomic range within regions. They often conducted comparative studies, assessing the phylogenetic diversity of urban versus non-urban bird communities (e.g., Ibañez-Álamo et al., 2017) or comparing the phylogenetic diversity of urban communities with specific regions (e.g., Sol et al., 2017), whereas my study was primarily focused on the species level.

Many of these studies which were able to detect a phylogenetic signal also differ from mine in terms of both scope and scale. For example, Morelli et al. (2016) successfully identified a phylogenetic signal when comparing bird communities between urban and rural areas across six different European cities. Similarly, Callaghan et al. (2019) detected a phylogenetic signal in species adaptability to urban environments by assessing the urban tolerance of birds on a continental scale, covering the majority of Australia's bird species (approximately 80%) and utilizing a comprehensive dataset exceeding 5,000,000 bird observations. Detecting a true phylogenetic signal is likely easier when conducted on a smaller-scale and with ample phylogenetic data, in contrast to my analysis, which was conducted on a global scale and lacked sufficient phylogenetic data (132 species).

Species with similar traits are generally more closely related (Böhning-Gaese & Oberrath, 1999; Morelli, et al., 2016). Hence, the absence of a phylogenetic signal could imply that the traits linked to increased anthropogenic food facilitate such exploitation independent of evolutionary relationships. Instead, these traits may be shaped by different environmental factors within their respective urban environments. Furthermore, my results also suggest that ability to adapt to urban environments is likely influenced by factors other than a higher consumption of anthropogenic food sources, or that this factor alone does not exclusively determine urban tolerance. Some of these urban adapted species which exhibit higher densities in urban environments include, for example, Common starlings (*Sturnus vulgaris*), House sparrows (*Passer domesticus*) (Croci, et al., 2008; Lancaster & Rees, 1979; Evans, et al., 2009) and Feral pigeons (*Columba livia domestica*) (Rose, et al., 2006; Kark, et al., 2007) all exhibit minimal consumption of anthropogenic food from my data. The ability to consume anthropogenic food sources may have its benefits but may not be a prerequisite for urban living; instead, it may be a characteristic gained through increased encounters with anthropogenic food in urban areas (De León, et al., 2019).

2.4.2. Anthropogenic food consumption has no relationship with body mass and territoriality

When food resources are locally scarce and clumped in distribution, the opportunity arises for larger or more aggressive individuals to monopolize food resources (Maher & Lott , 2000; Tobias, et al., 2016). In contrast, when food resources are abundant or evenly distributed, which may be the case in most urban environments, frequent intrusion of territories increases the cost of resource defence which may ultimately lead to the abandonment of territorial behaviour and resource dominance (Carpenter, 1987; Meretsky & Mannan , 1999; Gill & Wolf, 1975). The daily continuous input of anthropogenic food in urban environments thus likely shifts selective pressure to low competition and dominance for food, resulting in the equal exploitation of anthropogenic food across all levels of territoriality and body masses. This observation is supported by previous work showing that urban tolerant species tend to be less territorial (Neate-Clegg, et al., 2023). Urban tolerant species tend to be more social and gregarious (Sol, et al., 2014; Croci, et al., 2008; Kark, et al., 2007). This has also been demonstrated in for some territorial species in natural environments that shifted from being highly territorial over resources to foraging with minimal aggression with conspecifics when supplementary food is provided (Wilson, 2001; Carlier & Lefebvre, 1997).

2.4.3. Anthropogenic food consumption had no relationship with corrected brain size

My prediction that larger brained species tend to exploit more anthropogenic food was not supported. Again, this contrasts with studies examining urbanization tolerance, which have found that birds with larger brain birds were better adapted to urban habitats (Maklakov, et al., 2011; Sayol, et al., 2020). Several studies have shown that relatively larger brain size is positively associated with greater exploitation of novel resources, increased human tolerance and exploratory behaviour and enhanced ability to learn new feeding techniques (Lefebvre, et al., 1997; Lefebvre, et al., 2002; Sol, et al., 2005), all of which could facilitate greater anthropogenic food consumption. Instead, my findings showed that smaller-brained species (e.g., pigeons) possess an equal ability to exploit anthropogenic food to larger-brained species (e.g., crows, gulls, and starlings). It’s been suggested that because the brain is a complex organ, with countless neurons, synapses, neurotransmitters, and regions that work together to facilitate various cognitive, sensory, and motor functions, that brain size may not be the best indicator for cognition (Kark, et al., 2007) and therefore better exploitation of novel resources. This point is extensively argued by Healy & Rowe (2007). The scope of the data might possibly be disregarding the specialization or multi-functionality of different parts of the brain in different species. Although urbanization may be exerting strong pressure for the selection of certain traits, the exploitation of anthropogenic food may be a by-product of increased encounters with urban food resources, if the resources fall within the niche of the species. This is further discussed below.

2.4.4. Anthropogenic food consumption had no relationship with distributional range size

While I did not specifically investigate migration status, the absence of a correlation between the %AF in the diet of species and their geographical range distributions raises interesting questions.

Range-restricted species such as resident bird species may have a competitive advantage over wide-ranging species such as migrants in that they arrive earlier than migrants to exploit food resources in urban areas (Croci, et al., 2008; Lancaster & Rees, 1979; Bonnet-Lebrun, et al., 2020). However, my results suggest that year-round food sources in urban areas (Tryjanowski, et al., 2015), may benefit migrant in such a way that they exploit anthropogenic food to a similar extent as range-restricted species. Support for this idea that wide-ranging species may also exhibit anthropogenic food at considerable levels comes from suggestions that the provisioning of supplementary food may have facilitated range expansion in some species. For instance, the northern cardinal rapidly expanded its range over a 40-year period which coincided with a substantial increase in the number of households participating in bird feeding (Robb, et al., 2008). The provisioning of supplementary foods may have also be responsible for the growing trend of birds choosing to remain in one place rather than embarking on long migrations (Jokimäki, et al., 1996; Courter, et al., 2013). In this context, wide-ranging species may benefit similarly to range-restricted species. However, their benefits result from different strategies: wide-ranging species possibly benefit from greater dispersal capabilities that allow them to explore and find anthropogenic food sources, while range-restricted species benefit from their closer proximity to these food sources.

2.4.5. *Anthropogenic food consumption differs between hemispheres*

I also found differences in the %AF that birds incorporated into diets with hemisphere with bird species from urban environments in the Northern Hemisphere exploiting a greater proportion of anthropogenic food than bird from urban environments in the Southern Hemisphere. This was not surprising as participation in bird feeding may differ significantly between the two hemispheres and likely drives the level of anthropogenic food exploitation. The practice of bird feeding has shown to be more established in the Northern Hemisphere, specifically in European countries and during winter (Jones & Reynolds, 2008; Jones, 2011) where participants' motivations for bird-feeding are often linked to improve the survival of birds during the extreme winter conditions in the Northern Hemisphere (Fuller, et al., 2008; Reynolds, et al., 2017). These species have likely become accustomed to the reliable supplementary food sources in the Northern Hemisphere, possibly leading to greater exploitation or even dependence.

2.4.5. Anthropogenic food consumption differs between dietary guilds

Aquatic species, generalists and avian scavengers incorporated a greater proportion of anthropogenic food into their diets compared to other dietary specialists. It’s not surprising that aquatic bird species were high exploiters of anthropogenic food as most of the species in the aquatic feeding guild were made up of gulls and ibises, both of which have been highlighted as some of the most proficient exploiters of anthropogenic food resources. Aquatic species have also adapted well to urban environments (Auman, et al., 2011; Méndez, et al., 2020). This has been attributed to their adaptation to living in highly dynamic systems which requires the ability to travel long distances to locate food (Botson, et al., 2016) and likely facilitates a greater consumption of anthropogenic food. Some gull species also exhibit the extraordinary ability to match their foraging time to coincide with peak human activity (e.g., school breaks or peak operating times of waste disposal facilities) (Spelt, et al., 2020) thereby taking advantage of greater food opportunities. Similarly, ibises have demonstrated their the ability to switch to using anthropogenic food when natural food is limited and is allowed them to occur in high densities in urban areas (Calle & Gawlik, 2011; Ross, 2004; Dorn, et al., 2011; Murray, et al., 2018).

Ther %AF in the diet of granivores was not significantly different from these high exploiters of anthropogenic food. Granivores, despite being specialists were also high consumers of anthropogenic food. In many urban areas, particularly in the Northern Hemisphere, intentional supplementary anthropogenic food predominantly consists of seeds, nuts and grains provided at bird feeders (Jones & Reynolds, 2008; Davies, et al., 2009) which may favour granivore species (Kark, et al., 2007; Chace & Walsh, 2006). A classic example is the House Sparrow (*Passer domesticus*) which is granivorous species and a successful worldwide urban exploiter (Chamberlain, et al., 2007). Other studies suggest that despite being dietary specialists, the increased exposure of granivores to year-round anthropogenic food that fit well within their ecological niche, could erode this diet specialization to such an extent that they shift to showing a stronger preference for anthropogenic food (De León, et al., 2019). De León et al., (2014) has referred to generalists as ‘imperfect’ or ‘opportunistic generalists’. Further support for this idea comes from studies on Darwin’s finches, one of the most well-known examples of species specialization due to their remarkable diversity in beak morphologies. These finches have shown increased preference for anthropogenic foods and collapsed ecological segregation within urban settings (De León, et al., 2019; Hendry, et al., 2009) suggesting that although granivores are dietary specialists, anthropogenic foods can modify and erode ecological uniqueness and thereby promote urban living (Callaghan, et al., 2020; De León, et al., 2019).

As expected, generalists were also high consumers of anthropogenic food. Generalist species are the most successful guild in urban environments (Callaghan, et al., 2019; Evans, et al., 2011; Kark, et al., 2007) and their ability to exploit a broad niche may allow them to readily find and exploit appropriate resources, including anthropogenic food. Besides broader dietary requirements, numerous studies have also suggested that generalists are more behaviourally flexible, and have enhanced innovation and problem-solving abilities, which may be beneficial when navigating novel food environments such as urban settings (Griffin & Guez, 2014; Møller, 2009; Sol, et al., 2013; Sol, et al., 2011; Sol, et al., 2002).

That avian scavengers exploited anthropogenic food in large amounts was not surprising. Avian scavengers are particularly associated with rubbish dumps where there may be a high predictability and abundance of organic waste and anthropogenic food (Pomeroy, 1975; Gangoso, et al., 2013; Plaza & Lambertucci, 2018). For example, the American black vulture (*Coragyps atratus*) is an example of an avian scavenger whose presence in some urban areas is highly associated with the prevalence of anthropogenic food sources (Novaes & Cintra, 2013). Their exploitation of these resources is so extensive that some scavengers rely on anthropogenic food for potentially over half of their daily food intake (Augé, 2017). Some scavengers are particularly efficient at finding anthropogenic food sources because they have a developed olfactory sense and do not rely solely on visual clues for finding food (Graves, 1992). However, it Is important to mention that although scavengers exhibited the greatest consumption of anthropogenic food across all groups, my data only consisted of two scavengers and there are also inconsistencies between what other studies classify as scavengers (e.g., gulls and crows) compared to the diet classification used by Tobias et al., (2019).

Frugivores, nectivores, and carnivores exhibited significantly lower amounts of anthropogenic food in their diets compared to the aforementioned species. These dietary specialists possess specific food requirements and morphological adaptations tailored for the exploitation of their specialized diets, which can likely never be met by exploiting anthropogenic foods.
However, many of these species; e.g., frugivores and nectivores may still be abundant in urban areas where they may be able to exploit gardens or public spaces with abundant fruit-bearing trees and flowerbeds (Walther, et al., 2018; Rigacci, et al., 2021) or where supplementary food is provided in the form of fruit and sugar water (Reynolds, et al., 2017).

In the case of carnivores, which consisted mainly of birds of prey, a variety of human commensals occur at higher densities in urban areas which provide important sources of prey (Chace & Walsh, 2006). As specialists, the diets of carnivores which include owls, falcons and hawks may be less flexible for the exploitation of anthropogenic food. Additionally, the energy and nutrient content of anthropogenic food may not be suitable for raptors, which have higher energy and nutrient requirements (Joseph, 1998) for sustained flight and hunting compared to smaller bird species and other larger but more generalist species.

This could have implications for the provisioning of ecosystem services and disservices in urban areas. For example, scavengers provide important ecosystem services in urban environments namely, the stabilization of food webs, waste-disposal services and disease mitigation (DeVault, et al., 2016; O'Bryan, et al., 2018). Given that scavengers were the highest consumers of anthropogenic food in my study, this raises concerns regarding their role in urban environments. Additionally, their presence in urban environments might also lead to increased ecosystem-disservices if the consumption of anthropogenic food leads to large aggregations in urban environments (Fletcher, et al., 2010; Rees, et al., 2015), such as increased disease transmission (Monaghan, et al., 1985) and human-wildlife conflicts (Soulsbury & White., 2015). Likewise, the increasing populations of several crow and gull species (aquatic species and generalists) in urban areas likely attributed to their heightened consumption of anthropogenic food may lead to increased conflict with humans, impact soil and vegetation or present sanitary risks in urban areas (Soh, et al., 2002; Belant, 1997).

Conclusion

This review has revealed the widespread nature of anthropogenic food consumption across a wide range of different bird species globally. I highlight the need for more representation of studies conducted in the Southern Hemisphere in the literature as this may hinder my ability to make generalisations about the effects of urbanization (Reynolds et al., 2021). These effects may contrast strongly due to the difference in the climate, rates of urbanization, city dynamics and socioeconomic inequality between the Global South and the Global North (Cilliers, et al., 2011; Shackleton, 2012).

Unlike some prior studies that have identified phylogenetic relationships among urban-tolerant species, my research, which did not find such a relationship between species and their degree of anthropogenic food exploitation, implies that thriving in urban environments may not necessarily hinge on this specific characteristic. Using a trait-based approach I found that dietary guild is a key determinant of anthropogenic food exploitation by birds inhabiting urban environments. Identifying which ecological traits promote anthropogenic food consumption is important to understand the trajectory of biodiversity in urban areas. Understanding which traits promote anthropogenic food exploitation can inform planning and conversation actions in urban environments. My study highlights that scavengers, generalists and aquatic species are more prone to increased anthropogenic food consumption. These findings align with previous studies that have examined more general filtering for urban environments of avian species, with scavengers, aquatic species, generalists and granivores often managing better in urban habitats compared to specialists (Bonier, et al., 2007; Kark, et al., 2007; Croci, et al., 2008; Callaghan, et al., 2019; Evans, et al., 2011). This indicates the potential significance of exploiting anthropogenic food as an adaptation strategy for thriving in urban environments.

Appropriate management of anthropogenic food sources could reduce the attractiveness of scavengers, generalists and aquatic species to anthropogenic food sources in urban areas and prevent their dominance in urban avian communities and the likelihood of ecosystem disservices such as human-wildlife conflict. Some of these management actions may include regularly cleaning outdoor eating areas, disposing of waste more securely, or installing lockable/bird-proof refuse bins. My results also highlight the importance of maintaining patches of natural food sources such as fruit- and nectar-bearing vegetation, forests, shrubby, open and aquatic landscapes to support the occurrence of dietary specialists (Kark, et al., 2007; Callaghan, et al., 2020) and secure the ecosystem services they may provide in urban areas.

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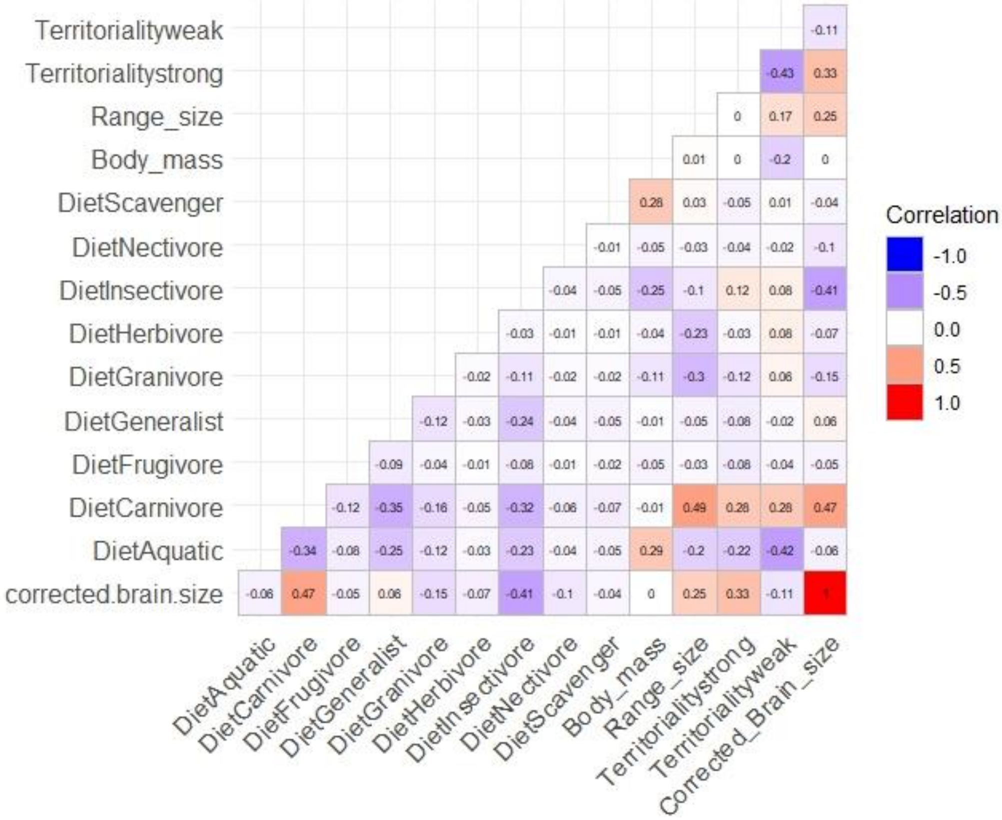
2.6. Supplementary material



	DietAquatic	DietCarnivore	DietFrugivore	DietGeneralist	DietGranivore	DietHerbivore	DietInsectivore	DietNectivore	DietScavenger	Body_mass	Range_size	Territorialitystrong	Territorialityweak	Corrected_Brain_size
Territorialityweak														-0.11
Territorialitystrong													-0.43	0.33
Range_size												0	0.17	0.25
Body_mass											0.01	0	-0.2	0
DietScavenger										0.28	0.03	-0.05	0.01	-0.04
DietNectivore									-0.01	-0.05	-0.03	-0.04	-0.02	-0.1
DietInsectivore								-0.04	-0.05	-0.25	-0.1	0.12	0.08	-0.41
DietHerbivore							-0.03	-0.01	-0.01	-0.04	-0.23	-0.03	0.08	-0.07
DietGranivore						-0.02	-0.11	-0.02	-0.02	-0.11	-0.3	-0.12	0.06	-0.15
DietGeneralist					-0.12	-0.03	-0.24	-0.04	-0.05	-0.01	-0.05	-0.08	-0.02	0.06
DietFrugivore				-0.09	-0.04	-0.01	-0.08	-0.01	-0.02	-0.05	-0.03	-0.08	-0.04	-0.05
DietCarnivore			-0.12	-0.35	-0.16	-0.05	-0.32	-0.06	-0.07	-0.01	0.49	0.28	0.28	0.47
DietAquatic		-0.34	-0.08	-0.25	-0.12	-0.03	-0.23	-0.04	-0.05	0.29	-0.2	-0.22	-0.42	-0.06
corrected.brain.size	-0.06	0.47	-0.05	0.06	-0.15	-0.07	-0.41	-0.1	-0.04	0	0.25	0.33	-0.11	1

Figure S1.1: Correlation matrix for ecological traits used in the analysis namely dietary guild, territoriality, range size, body mass and brain size plotted using the package *ggcorrplot* (Kassambara, 2019)**.** Blue and red squares correspond to negative and positive correlations respectively. The highest correlation coefficient observed was 0.49, which occurred between carnivores and range size. However, this value did not surpass the commonly used threshold of 0.7, which typically signifies highly correlated variables (Dormann, et al., 2013).

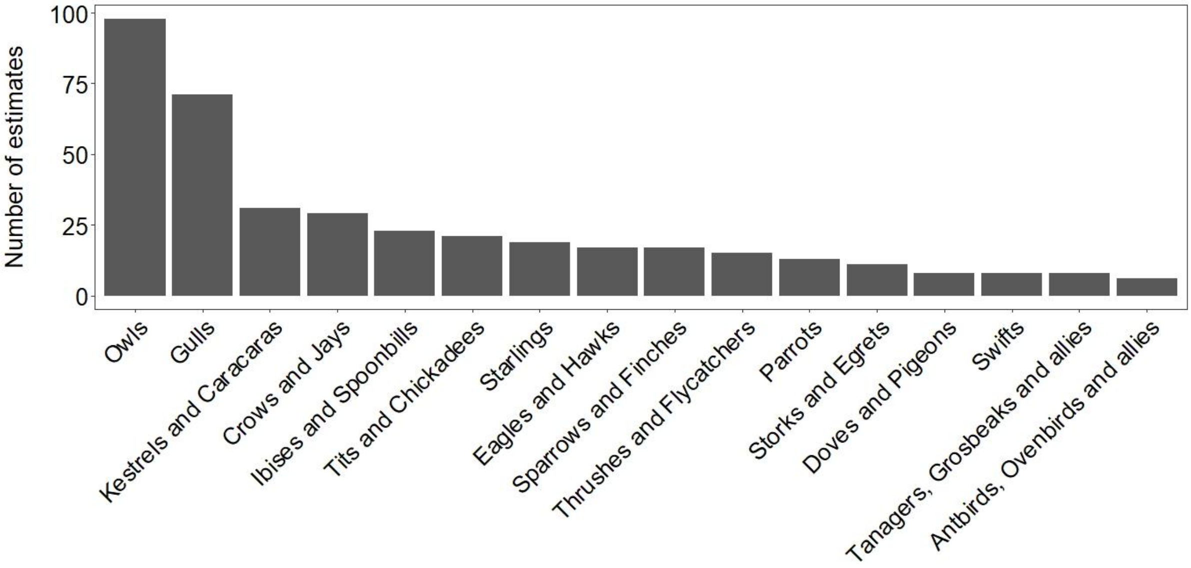


Figure S1.2: Number of estimates within each bird species represented in the literature, showing all species with >4 estimates (n= 16 out of 31 species groups). Data were derived from 155 publications quantifying the diet of urban-inhabiting birds and from which I obtained 424 estimates from 132 species and 31 bird type groups. Bird types with <4 estimates (n= 15 bird types) are not shown here.

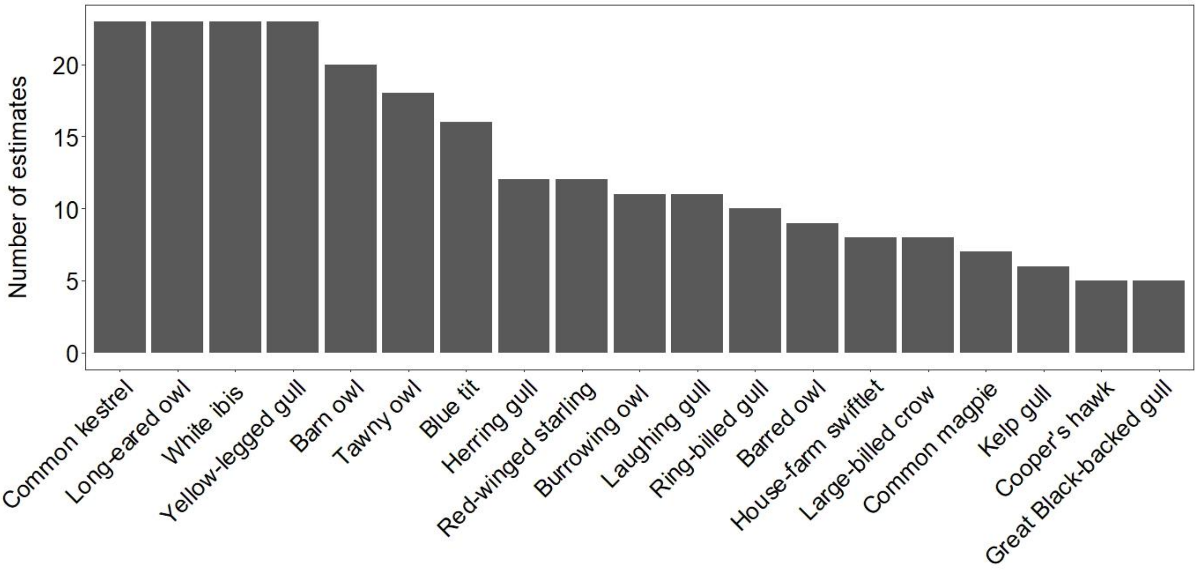


Figure S1.3: Number of estimates within each bird typerepresented in the literature, showing all bird species with ≥5 estimates (n= 19 species). Data were derived from 155 publications quantifying the diet of urban-inhabiting birds and from which I obtained 424 estimates from 132 species and 45 bird families. Species with <5 estimates are not shown here (n= 116 species).

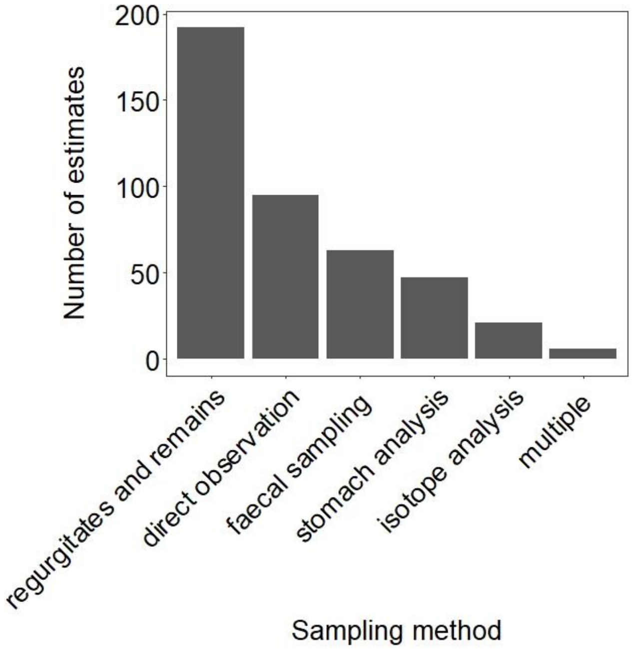


Figure S1.4: Number of estimates obtained using different techniques used to quantify the diet of urban-inhabiting birds. Data were derived from 424 estimates from 132 species and 155 publications.

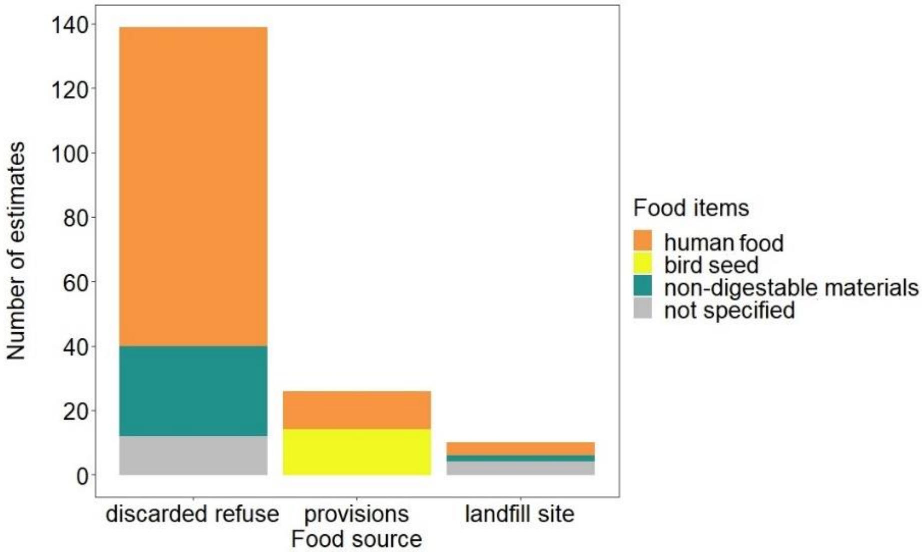


Figure S1.5: The sources and food items of anthropogenic food consumed by the urban-inhabiting birds included in this review as well as the number estimates within each category. Data were derived from 155 publications and includes a total of 424 estimates of which only 175 (displayed here) included details of the anthropogenic food consumed.

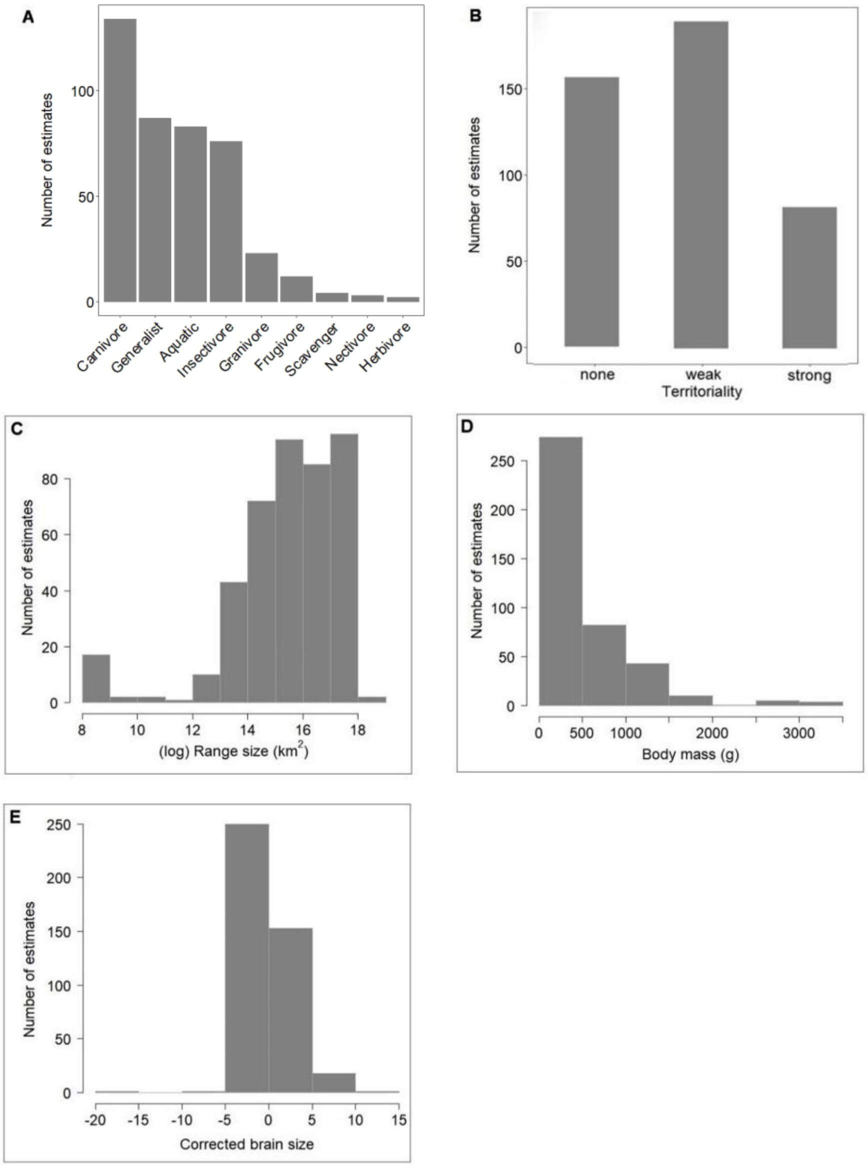


Figure S1.6: The number of estimates of anthropogenic food consumption within each (a) dietary guild and (b) level of territoriality and the distribution of estimates with (c) log range size (km^2), (d) body mass (g) and corrected brain size (e). All plots included 424 estimates in total obtained from 132 species and 155 publications, except for plot (d) which only includes species with body mass <4000g (n=129, excluding Verreaux's eagle (*Aquila verreauxii*), Andean condor (Vultur gryphus), Bald eagle (Haliaeetus leucocephalus) and Mute swan (*Cygnus olor*)).

Table S1.1: Descriptions of anthropogenic food items consumed by the 132 bird species inhabiting urban environments used in this review, taken from 155 publication.

Food items	Description
Human food	Meat (offal, seafood, red-meat, chicken, bones), baked goods (pizza, hot-dogs, pies, bread, muffin, biscuits), fruit (watermelon, apple, grape, banana, avocado), vegetables (cucumber, lettuce, tomato, sweet corn, french-fries), chips (popcorn, crisps), eggshell, pasta/noodles, peanut butter, beans, chocolate, cheese, commercial cereal (rice, corn, oats, wheat, peanut, sunflower seeds, maize, barley, millet).
Bird seed	Commercial bird seed (millet, milo, sunflower)
Non-digestible materials	Polystyrene foam, wood plastic (including nurdle, microplastics), metal (including aluminium/tin foil), cellophane, fabric (leather, thread, twine/textile, nylon), glass, paper, plastic, sheet, pipes, culverts, rubber.

Table S1.2: Analysis of variance (ANOVA) for the phylogenetic generalized least-squares multivariate regression (PGLS) fitted to explore whether the percentage of diet comprised of anthropogenic food showed evidence for a phylogenetic signal.

Explanatory variable	df	Sum of squares	Mean sum of squares	F value	*P*
Dietary guild	**8**	**81.73**	**11.68**	**4.69**	**0.001***
Territoriality	2	11.492	5.75	2.31	0.10
Range size	1	8.18	8.18	3.29	0.07
Body mass	1	2.09	2.09	0.84	0.36
Brain size	1	2.06	2.06	0.83	0.36

Table S1.3: Pairwise comparisons with Bonferroni correction of the %AF consumed between dietary guilds. Significant differences are highlighted in bold.

Contrast	odds.ratio ± S.E.	z value	P value
Aquatic - Carnivore	**10347 ± 2.54e+04**	**3.76**	**0.01**
Aquatic – Frugivore	0 ± 38 8.40e+01	1.66	0.77
Aquatic – Generalist	0 ± 1.00e+00	0.59	0.99
Aquatic – Granivore	7 ± 1.30e+01	0.97	0.99
Aquatic - Herbivore	0 ± 2.00e+00	0.20	1.00
Aquatic - Insectivore	146 ± 2.58e+02	2.81	0.11
Aquatic - Nectivore	27832878 ± 1.63e+09	0.29	1.00
Aquatic – Scavenger	0 ± 0.00e+00	1.43	0.89
Carnivore – Frugivore	0 ± 0.00e+00	2.07	0.50
Carnivore – Generalist	**0 ± 0.00e+00**	**4.59**	**<0.01**
Carnivore – Granivore	0 ± 0.00e+00	-2.91	0.09
Carnivore - Herbivore	0 0.00e+00	2.21	0.39
Carnivore - Insectivore	0 0.00e+00	1.99	0.55
Carnivore - Nectivore	2690 ± 1.58e+05	0.13	1.00
Carnivore - Scavenger	**0 ± 0.00e+00**	**4.10**	**<0.01**
Frugivore – Generalist	0 ± 0.00e+00	2.31	0.34
Frugivore - Granivore	0 ± 0.00e+00	0.80	1.00
Frugivore – Herbivore	0 ± 0.00e+00	1.03	0.98
Frugivore - Insectivore	4 ± 8.00e+00	0.67	1.00
Frugivore – Nectivore	725946 ± 4.27e+07	0.23	1.00
Frugivore - Scavenger	0 0.00e+00	2.53	0.22
Generalist - Granivore	17 ± 2.80e+01	1.66	0.77
Generalist – Herbivore	1 ± 4.00e+00	0.02	1.00
Generalist – Insectivore	**361 ± 4.99e+02**	**4.26**	**<0.001**
Generalist – Nectivore	68925530 ± 4.05e+09	0.31	1.00
Generalist – Scavenger	0 ± 0.00e+00	1.11	0.97
Granivore – Herbivore	0 ± 0.00e+00	0.67	0.99
Granivore - Insectivore	22 ± 3.60e+01	1.85	0.65
Granivore – Nectivore	4145264 ± 2.44e+08	0.26	1.00
Granivore – Scavenger	0 ± 0.00e+00	1.98	0.56
Herbivore – Insectivore	340 ± 1.39e+03	1.42	0.89
Herbivore – Nectivore	64894782 ± 3.82e+09	0.31	1.00
Herbivore – Scavenger	0 ± 0.00e+00	0.58	1.00
Insectivore – Nectivore	191057 ± 1.12e+07	0.21	1.00
Insectivore – Scavenger	**0 ± 0.00e+00**	**3.29**	**0.03**
Nectivore – Scavenger	0 0.00e+00	0.35	1.00

CHAPTER 3

Who benefits from the rich? Differential responses of avian ecological traits to socioeconomic conditions of urban areas in a developing country.

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Abstract

Within urban areas there is considerable evidence that biodiversity and abundance correlate positively with increasing socioeconomic status, a pattern termed the ‘luxury effect’. However, which types of species show the strongest responses to increasing socioeconomic status has rarely been investigated. Here using citizen science data from the Southern African Bird Atlas 2 (SABAP2), I explored how species with varying diets, habitat types, nest locations, clutch sizes, body mass, levels of territoriality, migration status, endemism, residency, and conservation status respond to household income levels within urbanised areas across South Africa. With respect to diet and habitat type, I found that generalists, carnivores, granivores, aquatic species and species associated with desert-rock, forest-woodland and aquatic habitats showed the strongest positive response to income. In relation to migration status, I found that both sedentary species and full migrants showed evidence of a luxury effect. I found evidence that the luxury effect was steeper for species endemic to South Africa and for species which were locally threatened. In contrast, species with differing nesting location, clutch size, body mass, residency and territoriality responded similarly to income. The results show support for increased availability of food resources including supplementary foods, resource stability in high-income areas as key drivers of the luxury effect, as well as the occurrence of wealthier neighbourhoods in areas with more habitat cover and greater habitat diversity to act as refuges for locally endemic species and species of conservation concern. It will be revealing for future research to investigate whether the patterns identified here are found for other urbanised areas in different parts of the world and can contribute to our understanding of what drives the luxury effect within urban areas.

3.1. Introduction

A fundamental component of ecology and natural resource conservation is understanding the spatial patterns of biological diversity and how they are influenced by environmental drivers (Gaston, 2000). The best-known predictors of species richness are primary productivity and habitat heterogeneity (Blackburn & Gaston., 1996; Evans, et al., 2005), such that primary productivity (the rate of carbon fixed via photosynthesis) is positively correlated with species richness, such that more productive environments, such as forests and grasslands provide more food resources to support more species (Waide, et al., 1999; Hurlbert & Haskell, 2003) compared to less productive habitats such as deserts (Dugarsuren & Lin, 2016). Similarly, at a local scale, greater vegetation structural complexity, typically seen in forests are thought to support a greater number of species, by providing a variety of microhabitats and microclimates (Vogeler, et al., 2014; Tews, et al., 2004), compared with structurally more simple habitats such as grasslands (Hurlbert, 2004).

The United Nations (2019) estimates that 55.3% of the world's human population live in urbanized areas and this is expected to increase to 60% by 2030. Because urbanization typically results in significant loss of habitat, loss of species, biotic homogenization, alien species invasions and depletion of ecosystem services (Grimm, et al., 2008), urban residents are often thought to live in biological deserts (Turner, et al., 2004; Pickett, et al., 2008; Aronson, et al., 2014). On the other hand, urban environments are unique mosaics of roads, residential, industrial, and commercial property interspersed with remnants of less modified, indigenous, and exotic vegetation. Recent studies have shown that urban environments have the potential to support a variety of wildlife (Bateman & Fleming, 2012; Ives, et al., 2016; Baldock, et al., 2015; Menke, et al., 2011) however, opportunities of humans to experience wildlife are not equally distributed across all levels of society.

Within urban areas there is considerable evidence that biodiversity and abundance correlate positively with socioeconomic status of neighbourhoods (Chamberlain, et al., 2020; Hope, et al., 2003; Luck, et al., 2009; Martin, et al., 2004; Kinzig, et al., 2005), such that wealthier residents occupy areas that support disproportionately higher levels of species diversity and abundance than low-income groups. This pattern has been termed the 'luxury effect' (Hope, et al., 2003). Within urban areas the traditional resource-diversity relationship has been modified by human activities. Instead of natural resources being limiting factors, financial resources may shape the biodiversity patterns in urban areas. The luxury effect has been found globally for plant species richness and vegetation cover (Leong, et al., 2018). Fewer studies have examined the luxury effect for animals, yet it has been found for bird, bats, mammals, lizards, and arthropods (Leong, et al., 2018; Magle, et al., 2021; Chamberlain, et al., 2020).

Urban biodiversity provides a means through which urban residents, often detached from nature (Chiesura, 2004), can appreciate its wider benefits. These include improved physical and psychological wellbeing (Sandifer, et al., 2015; Fuller, et al., 2007; Keniger, et al., 2013; Hartig, et al., 2014; Bell, et al., 2018; Lovell, et al., 2014) and improved immune health (Hanski, et al., 2012). Access to biologically diverse spaces also promotes social and cultural interaction and in turn can strengthen social cohesion and community empowerment (Costanza, et al., 1997; Coley, et al., 1997; Jennings & Bamkole, 2019). It has been shown to be associated with lowered crime rates (Leong, et al., 2018). Numerous studies conducted during the COVID-19 lockdowns, have stressed the importance of access to nature in helping people cope with the lack of social activity (Labib, et al., 2022; Pouso, et al., 2021; Slater, et al., 2020; Desrochers, et al., 2022; Robinson, et al., 2021). Urban biodiversity is thus an important component of the quality of life of urban inhabitants, but the existence of the luxury effect implies that these benefits are not equally distributed across all levels of society, particularly in low-income neighbourhoods.

Various hypotheses for the underlying cause of the luxury effect in urban environments have been proposed. These include that residents, city officials or policymakers invest more resources in the modification and management of biodiverse spaces in wealthier areas (Leong, et al., 2018; Kinzig, et al., 2005; Hope, et al., 2003; Loss, et al., 2009; Grove, et al., 2014). This may attract more species and wealthy individuals and in turn raises property prices. In contrast, little investment in low-income neighbourhoods may limit the biodiversity that can persist there (Wolch, et al., 2014). Additionally, individuals' practises, often shaped by their social and cultural background, can favour the presence of wildlife while discouraging that of others (e.g., provisioning of supplementary food). In this manner, the socioeconomic conditions of an area may limit or enable the biodiversity that urban inhabitants may choose to maintain or actively eliminate (Kinzig, et al., 2005; Martin, et al., 2004; Hope, et al., 2006).

While multiple studies support the existence of the luxury effect, most of these have been done in large cities in developed countries (e.g., Shanahan, et al., 2014; Hope, et al., 2003; Loss, et al., 2009; Tratalos, et al., 2007, Chamberlain, et al., 2020). Evidence for the luxury effect is therefore derived from relatively short socioeconomic gradients and is biased towards high levels of socioeconomic conditions in comparison to the range of such conditions seen globally. Developing regions typically have higher population growth rates, higher rates of urban expansion and higher levels of poverty and inequality but are also often richer in biodiversity (United Nations, 2018; Fisher & Christopher, 2007). These differences in conditions therefore highlight the importance of exploring the luxury effect within developing areas outside of the Northern Hemisphere.

Chamberlain et al. (2019), in one of the few studies exploring the luxury effect in a developing country, found higher bird species richness in wealthier urban areas in South Africa. This pattern was observed in all but the most urbanised areas where the relationship was reversed. This implies that the luxury effect may be mediated by urban cover. Initially, biodiversity may increase with socioeconomic development however, as urban cover expands, the once positive influence of socioeconomic status on biodiversity weakens. This decline can be attributed to increasing adverse effects of the built environment on biodiversity, which begin to manifest as urban land cover exceeds 38% in their study.

In South Africa, the range of socioeconomic conditions present an ideal opportunity to study how species vary in relation to socioeconomic conditions in urban areas. South Africa is ranked the most unequal country in the world (Sulla, et al., 2022) and has urban areas varying from wealthy neighbourhoods with highly developed infrastructure to informal settlements comprising of makeshift shacks with extreme poverty. Social histories of cities can also influence the distribution and composition of species (Schwarz, et al., 2015; Brooks, et al., 2016) and necessitate the importance of conducting such research in cities of South Africa. During the apartheid regime (1940s-1993) in South Africa, urban areas were geographically segregated based on race (Shackleton, et al., 2014). These laws controlled the movement of black South Africans and dictated where people of colour were to live and work. White South Africans were allocated in middle-upper class suburbs with formal, freestanding housing, on large plots, while people of colour were forcefully relegated to low-income suburbs with high-density social housing and rapidly expanding informal settlements (Western, 1981; Seekings, 2011). Apartheid segregation relied on inequitable distribution of economic, social, and infrastructural resources between racial groups (Western, 1981; Seekings, 2011; Turok, 2001) and created the steep socioeconomic gradient still highly prevalent today (Shackleton & Gwedla, 2021; Lubbe, et al., 2010).

In this study, I build on the work of Chamberlain et al. (2019) to test whether species from different functional groups show similar or differing relationships with socioeconomic status. Understanding whether the species which increase in wealthier areas are just a random subset of species, or come disproportionately from certain functional groups, can also help substantiate the different hypotheses that have been proposed to drive the luxury effect. Not all species may respond in the same manner across a gradient of socioeconomic conditions. For example, studies have reported differential responses to the luxury effect by species of different residency with the greater diversity of birds in high-income neighbourhoods being driven by native species (Kinzig, et al., 2005; Lerman & Warren, 2011; Melles, 2005; Chamberlain, et al., 2020). However, to the best of my knowledge differential responses to the luxury effect for other ecological traits have not yet been investigated for any taxa. Any such response, whereby different groups are selectively lost from poorer neighbourhoods, may be particularly consequential if the species lost provide important ecosystem services, such as pollination, or disservices, such as the spread of disease.

The availability of food resources (natural and supplementary), nesting opportunities, habitat, vegetation complexity and level of disturbance (i.e., human density) may all correlate positively with socioeconomic status (Hope, et al., 2003; Iverson & Cook, 2000). These conditions may be more favourable to certain groups of species, and they may increase disproportionally compared to other groups. In this study, I explore whether the luxury effect response differs depending on species' (1) dietary guild, (2) habitat type, (3) nest location (*cavity, elevated or ground nests*), (4) body mass, (5) clutch size, (6) level of territoriality (*none, weak, strong*), (7) migration status (*full-migrant, partial-migrant, sedentary*), (8) endemism (*endemic, not endemic*), (9) residency (*resident, introduced*) and (10) conservation status (*threatened, least-concern*). For some of these traits, any differential relationship (within these traits) with socioeconomic status could provide support for certain hypotheses proposed for the driving the luxury effect (e.g., dietary guild). I detail my expectations (if any) based on the traits and the hypotheses proposed for the luxury effect in Table 1.

Table 3.1: The ecological traits for which I explored differential responses to the luxury effect, the rationale for including the trait and the expected outcome for its relationship with income.

Ecological trait	**Rationale**	**Expected outcome**
Dietary guild	• Prey abundance for carnivores may be higher in wealthier areas as a consequence of the luxury effect ("LE" hereafter) • Flowering plants, fruiting trees and seed-bearing trees may be more common in wealthier areas which may benefit nectivores, frugivores and granivores. • The LE is stronger in arid areas[1]. Thus, aquatic food resources may be greater in wealthier areas (e.g., pools, bird baths, fountains irrigated lawns)[2; 3.] • Generalists consisting of opportunistic species, have ubiquitous feeding requirements, and tend to be more successful in exploiting urban resources [4;5.] • Enhanced plant diversity with income could benefit insectivores. Alternatively, its occupancy could be discouraged by increased use of insecticides with income[6].	• Carnivores would show a stronger increase to socioeconomic status income than all other groups. • Nectivores, frugivores and granivores show a strong positive relationship with income. • Insectivores show a strong positive relationship with income. • Species consuming aquatic food would show a strong positive relationship with income. • Generalists may be equally abundant across all socioeconomic levels, as they are more adaptable. • Insectivores may show a positive or negative relationship with income.
Habitat type	Wealthier areas may offer better opportunities for species more closely associate with certain habitat types. E.g., more aquatic habitat, more established trees, more grass lawns, and locations closer to mountain slopes.	Species associated with rocky habitat, aquatic habitat, forest habitat and grasslands show a disproportionately stronger relationship with income.

Nest location	Wealthier areas may feature more older/taller trees, tall-standing vegetation, building cover or higher proximity to mountains, providing enhanced nesting opportunities for cavity and elevated nesters.	While all groups may show a LE, cavity and elevated nesters might show more pronounced LE compared to ground nesters.
Clutch size	According to the-pace-of-life theory, slower-paced species, typically have longer lifespans and lower reproductive outputs, whereas those species on the fast end tend to show opposite patterns[7]. Increased food resources, a likely primary driver of the luxury effect, are suggested to favour slower life histories[8; 9].	Species with smaller clutch sizes show a stronger association with income compared to those with large clutch sizes.
Body mass	Food resources may correlate positively with income, and larger species may only be able to exist in urban areas where food resources are sufficiently abundant.	Larger species show a disproportionately stronger relationship with income.
Territoriality	The increase in habitat availability with income[12] might also lead to an increase in food availability, suitable habitat, and nesting opportunities. The rise in habitat availability associated with SES[12] may result in an increase in food accessibility, suitable habitats, and nesting opportunities. As a result, this could encourage decreased competition for resources and a reduction in territorial behaviour among species in wealthier neighbourhoods compared to low-income neighbourhoods, where there might be a heightened necessity to defend such resources that could be in limited supply.	• Non-territorial species show a stronger positive relationship with income. • Territorial species show a negative relationship with income.
Migration status	Migratory species usually select for resource stable habitats [9; 10;11] which may be more prevalent in wealthier neighbourhoods.	Migratory species show a stronger relationship with income than sedentary species.
Endemism	The presence of endemic and non-endemic bird species in urban areas is likely associated with the characteristics of vegetation. Given that both exotic	Both endemic and non-endemic birds would increase with income.

	and native vegetation have been observed to increase with income[12; 13], I anticipate that birds of varying endemic status would exhibit similar distribution patterns.	
Residency	No general expectation for when income might favour native versus introduced species has emerged however, it has been said that the greater plant diversity seen in high-income neighbourhoods is often driven by non-native ornamental species. [11]	I expect a stronger relationship with income from Introduced bird species than native species.
Conservation status	In addition to increased habitat availability with income[12], the luxury effect could also be driven by enhanced habitat quality, improved habitat connectivity, and reduced disturbances within wealthier neighbourhoods. All of these factors might enable wealthier neighbourhoods to support a greater number of species of conservation concern compared to low-income neighbourhoods.	Threatened species exhibit a significantly stronger relationship with income compared to non-threatened species, for which the relationship with income might be more gradual or even absent

(1) Chamberlain et al., 2020; (2) Fuller et al., 2008; (3) van Heezik & Hight, 2017; (4) Coetzee et al., 2008; (5) Faeth et al., 2005; (6) Cook et al., 2012; (7) Williams et al., 2010; (8) Reznick et al., 1990; (9) Somveille et al., 2015; (10) Kinnunen et al., 2022; (11) Davoren et al., 2016; (12) Hope et al., 2003; (13) Martin et al., 2004

3.2. Methods

3.2.1. Selection of study areas

Bird occurrence data were acquired from the citizen science programme Southern African Bird Atlas Project 2 (SABAP2) (http://sabap2.birdmap.africa/), which is based on pentad areas (ca. 9 x 9km square). I extracted data from the same urban pentads as those selected by Chamberlain et al. (2019). These pentads were chosen based on their level of urbanisation. Across all the pentads in South Africa, the number of urban areas were quantified using the South African National Land-Cover Dataset from 2013 to 2014 (Department of Environmental Affairs, 2015), which categorizes each 30m x 30m raster grid cell into dominant land cover types using multi-seasonal Landsat 8 imagery. The focus was on the '*urban*' parent class and the proportion of the pentad covered by urban land by using the sum of the area of urban land covered grid cells and dividing this by the total land area in the pentad was calculated. Using these data on urban land cover, three urbanized land cover subclasses were defined: peri-urban (5%–20% urban), suburban (21%–50% urban) and urban (>50% urban) (Figure S2.1). Pentads with <5% urban cover were not included. Only those peri-urban pentads that were adjacent to at least one other pentad of a different urban land cover sub-class (i.e., either suburban or urban) were included, to ensure that pentads were sampled from larger urban landscapes, rather than small, relatively isolated rural settlements. For more details see Chamberlain et al. (2019).

3.2.2. Bird data

I used reporting rate data from SABAP2, a citizen science program where observers record the presence of all species on an atlas card (a species list made on each visit) during timed visits (mean ± SD = 160 ± 90 min) to pentads (Supplementary data). Using the original data from Chamberlain et al. (2019), all surveys collected from 01/01/2012 to 31/12/2014 were included. Only cards where the observer fully complied with the protocol rules; i.e., listed as '*full protocol*' were used in the analysis. To control for sampling effort between pentads, pentads with less than 5 atlas cards were excluded. In terms of sampling effort across income levels, the number of cards submitted within each income group ranged from 443 to 4875 cards (Figure S2.3). For each pentad and each species, I had the number of atlas cards where the species was present and the total number of atlas cards that were completed for that pentad. This acted as the response variable which has been described as the reporting rate for a pentad (Amar, et al., 2016; Lee , et al., 2018), and see the statistical analysis below; reporting rates have been shown to vary (albeit in a non-linear manner) within density (Lee , et al., 2018), and thus for this study, reporting rate was used as a proxy for abundance of a species in a pentad. For each species, I only included data from pentads that were within the species range to minimize the likelihood of mistakenly identifying false positive associations between species reporting rates and socioeconomic status. To select which pentads were potentially within a species range, the data were divided into degree squares (e.g., areas approximately 100km x 100km). If the species was not detected in any pentad within that degree square, then data for that species within that degree square were excluded from the rest of the analysis.

3.2.3. Socioeconomic data

Annual household income was used as a proxy measure for socioeconomic status, as it provides the most direct test of the luxury effect (Leong, et al., 2018). The median annual household income from Chamberlain et al. (2019) (hereafter 'income') (in South African Rands, where 1R was equivalent to c. US$0.06 in 2022; http://x-rates.com/historical/?from=USD&amount=1&date=2022-05-24) was used, which was derived from approx. 15 million household surveys during the 2011 South African National Population Census (Statistics South Africa, 2012, data available at www.statssa.gov.za). Median income was more representative of the typical income of a pentad, which in some cases had highly skewed data distributions due to a few extremely wealthy households in the same pentad as very poor areas. The lowest spatial resolution of the data was a small area unit (85,907 polygons for South Africa, where a polygon was a variable sized small area unit containing approximately 200 households), and median income per pentad was derived as the median proxy income value for all small area units with their polygon centroid located within a pentad. Median annual income was log-transformed prior to analysis and varied between R14,000 and R443,500 (between US$2,102 and US$66,525 median= R27,874 US$4,182) across the pentads (Figure S2.2).

3.2.4. Species functional traits

Data on bird species traits were obtained from four sources; Tobias & Pigot (2019), Tobias et al. (2022) and Wilman et al. (2014). The diet classification as assigned by Tobias & Pigot (2019) was used. For the 27 species for which Tobias & Pigot (2019) lacked data, Tobias & Pigot (2022) was consulted for 25 species and Wilman et al. (2014) for the remaining two. The only adjustments made to the diet categories involved combining species with a diet classification of 'aquatic plants' and 'aquatic animals' into a single category termed 'aquatic'. Dietary guilds were classified into nine categories: generalists, aquatic, herbivores, granivores, frugivores, nectivores, insectivores, scavengers and carnivores (Table 3.2a).

I used species' habitat type classification as assigned by Tobias et al. (2022) and included six final categories: *aquatic* (habitat type classified as coastal, marine, riverine and wetland), *desert-rock* (habitat type classified as desert and rocky), *forest-woodland* (habitat type classified as forest and woodland), *grassland, shrubland* and *human-modified* (Table 3.2b). Species' nest location and clutch sizes were obtained from Tobias & Pigot (2019) and Hockey et al. (2005) (Table 3.2c). I took the average clutch size within species from Tobias & Pigot (2019) and Hockey et al. (2005) and consulted the *Roberts – Birds of southern Africa* bird guide directly for those species that had no data (Table 3.2d). Body mass of species was obtained from Wilman et al. (2014), Tobias & Pigot (2019) and Tobias et al. (2022) and I calculated the average across all databases (Table 3.2e). The territoriality classification from Tobias & Pigot (2019) was used and Robert's bird guide was consulted directly for 26 species for which Tobias & Pigot (2019) lacked data (Table 3.2f). Species migration status from Tobias et al. (2022) was used, listed as either *migratory, partially migratory* or *sedentary* (Table 3.2g). Species' endemism (*endemic* versus *non-endemic*) (Table 3.2h) and residency (*native* versus *introduced*) (Table 3.2i) was obtained from the Robert's bird guide database and Bird Life South Africa (https://www.birdlife.org.za/media-and-resources/bird-checklists, date accessed 16 March 2021). The regional conservation status of species for 2021 was obtained from the Bird Life South Africa website (https://www.birdlife.org.za/media-and-resources/bird-checklists). Due to small sample sizes within some threat categories, I grouped species into one of two categories: *least concern* and *threatened*, the latter including all species listed as critically endangered, endangered, vulnerable and near threatened (Table 3.2j). Prior to the analysis I checked for collinearity among traits by plotting a covariance matrix using the package ggcorrplot (Kassambara, 2019) which showed no strong collinearity (maximum correlation coefficient <0.47; Figure S2.4). None of the correlation coefficients exceeded the commonly accepted threshold of >0.7 for assessing collinearity (Dormann, et al., 2013).

Table 3.2: Ecological traits used in this analysis and their categories for categorical variables, their sources, and final sample sizes. Sample sizes included in parentheses. I had information for all 492 native species for all traits except clutch size for which I only obtained data for 486 species.

Ecological trait	**Categories**	**Source**
(a) Dietary guild	*aquatic (81), scavenger (4), carnivore (46), frugivore (22), nectivore (10), generalist (51), herbivore (13), granivore (60), insectivore (214)*	Tobias et al. (2022), Tobias & Pigot (2019), Wilman et al. (2014)
(b) Habitat type	*aquatic (coastal, marine, riverine and wetland) (104), desert-rock (16), forest-woodland (145), grassland (112), shrubland (108) and human-modified (7)*	Tobias et al. (2022)
(c) Nest location	*cavity (198), ground (116), elevated (178)*	Tobias & Pigot (2019), Hockey et al. (2005)
(d) Clutch size	ranging from 1 – 13 eggs	Hockey et al. (2005), Tobias & Pigot (2016)
(e) Body mass	ranging from 5.96g - 8193.45g	Tobias & Pigot (2016), Tobias et al. (2022), Wilman et al. (2014)
(f) Territoriality	*none (132), weak (228), strong (132)*	Tobias & Pigot (2019), Hockey et al. (2005)
(g) Migration status	*full migrant (66), partial migrant (72), sedentary (354)*	Tobias et al. (2022)
(h) Endemism	*endemic (94), non-endemic (398)*	BirdLife South Africa website, Hockey et al. (2005)
(i) Residency	*native (492), introduced (6)*	BirdLife South Africa website, Hockey et al. (2005)
(j) Conservation status	*threatened (41), least concern (450)*	BirdLife South Africa website, Hockey et al. (2005)

3.2.5. Statistical analysis

Chamberlain et al. (2019) examined changes in species richness with income and found a significant interaction in this relationship across different levels of urbanisation; species richness increased with income up to a certain level of urbanisation (38%), above which the nature of the relationship reversed, becoming negative. I used the same data for urban land cover and socioeconomic measurement as Chamberlain et al. (2019) but used a different metric for the bird data (reporting rates as a proxy for abundance). Thus, I first established whether the same interaction was also present in the species-specific reporting rate data, and whether the inflection point (e.g., 38%) was the same. Once any inflection point was established, pentads with urbanisation levels above that value were excluded since in this analysis I was interested in exploring whether the luxury effect differed across traits (e.g., dietary guild etc), without the added complication of an interaction with income and urbanisation.

All analyses were performed within the R statistical environment version 4.0.0. (R Development Core Team, 2019). The explanatory variable in all models was the ratio of the number of cards which reported the species as present or absent within a pentad to the total number of cards submitted for that pentad (fitted with *cbind* syntax) and for ease of writing I use the term 'reporting rate'. Data were analysed using generalised linear mixed effects regression models with Template Model Builder (glmmTMB) (Magnusson, et al., 2017). In all analyses, continuous explanatory variables (e.g., urban cover, income etc.) were centred and scaled using z-score standardization, resulting in all variables having a mean of zero a standard deviation one, thus making variables more comparable. The final models included urban cover and the interaction between each trait and income. Species was fitted as a random term to account for multiple observations taken for the same species.

First I investigated the interaction between income and urban cover, and established the best fitting distribution for the data by fitting four separate generalised linear mixed effects regression models with Template Model Builder (glmmTMB) (Magnusson, et al., 2017); fitted with either 1) a beta-binomial error distribution with a *logit* link, 2) a beta-binomial error distribution with a *cloglog* link, 3) with a binomial error distribution with a *logit* link and 4) a binomial error distribution with a *cloglog* link. Based on Akaike's information criterion (AIC), ΔAIC and Akaike weights (ω_i), the best model (with the lowest AIC value) was fitted with a beta-binomial error distribution with a *logit* link and thus all models were fitted using this error distribution (Table S2.1).

I investigated for differential responses for the different categories within each trait, testing for an interaction between median income and each ecological trait on species reporting rates in separate models, controlling for urban cover. Where significant results were found in the final model of each functional group, linear trends (estimates ± standard error (SE)) were extracted using the *emtrends* function from the *emmeans* package in R (Lenth, 2018), which allowed comparisons of the slopes for each category of a trait. Statistical significance was taken as $P < 0.05$.

3.3. Results

For most of the analyses I had information from 492 species that were spread across a total of 239 urbanised pentads. The number of pentads included for each species varied, depending on the species distribution, with data ranging from a minimum of three pentads to a maximum of 239 pentads per species and an average of 138.66 ± 3.07 (SE) pentads. The number of surveys within each pentad varied from five to 443 per pentad over the two years of the surveys, between 2012 and 2014.

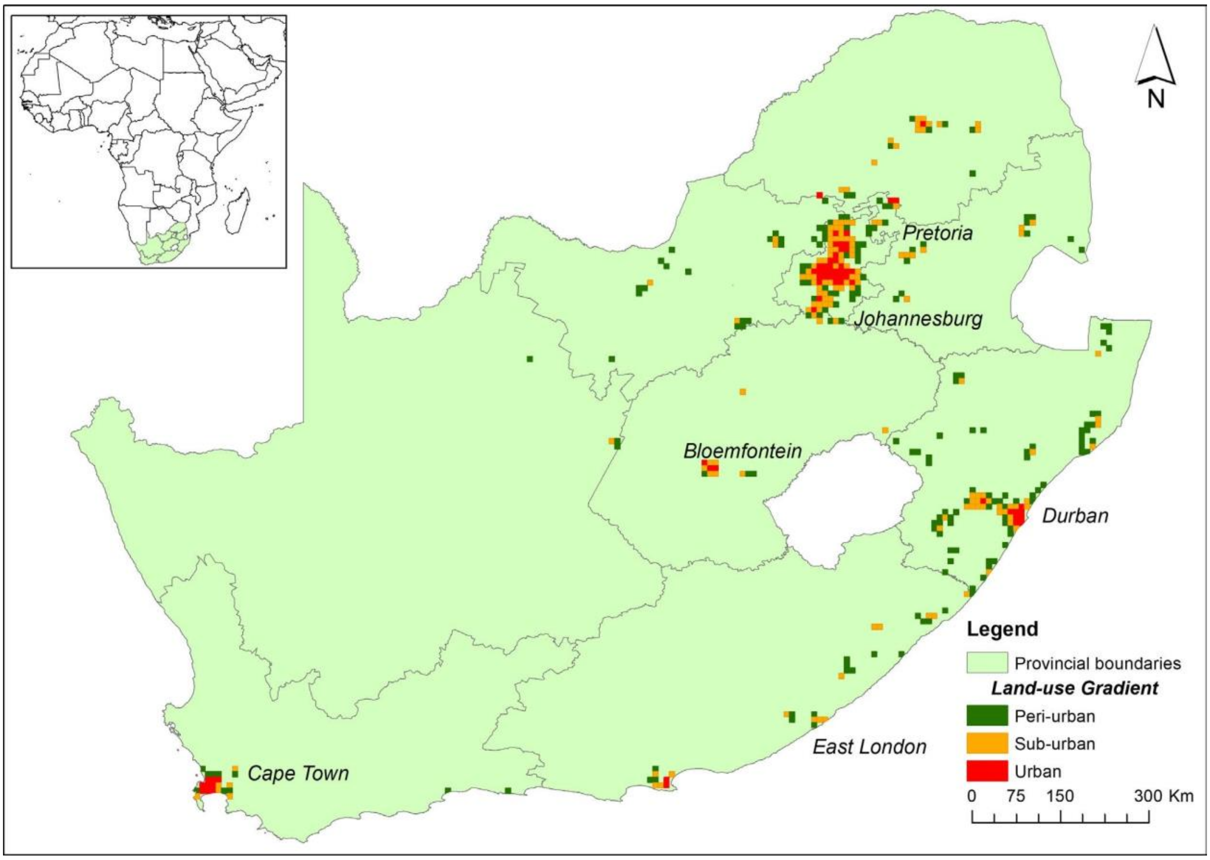

Figure 3.1: Location of pentads within South Africa within which bird abundance data were extracted (see inset top-left for geographical location within Africa). Pentads were defined into two subclasses: peri-urban (circular points, 5%–20% urban cover), suburban (triangular points, 21%–43% urban cover). Pentads with urban cover >43% were excluded from analyses because the relationship between bird abundance and income become negative, i.e., the luxury effect was reversed (Figure 2) (image taken from Chamberlain et al., (2019)).

3.3.1. Relationship in overall reporting rates and income across different levels of urbanisation

I first explored whether there was evidence for an overall luxury effect with reporting rates of all species and if there was an interaction between income and urbanisation. I found a significant interaction between urbanisation and income with a positive relationship with income up until urbanisation passed 43% (Figure 3.2). Thus, for all the subsequent analysis I excluded all pentads (n= 76, 24.13% of pentads) with an urban cover of over 43%.

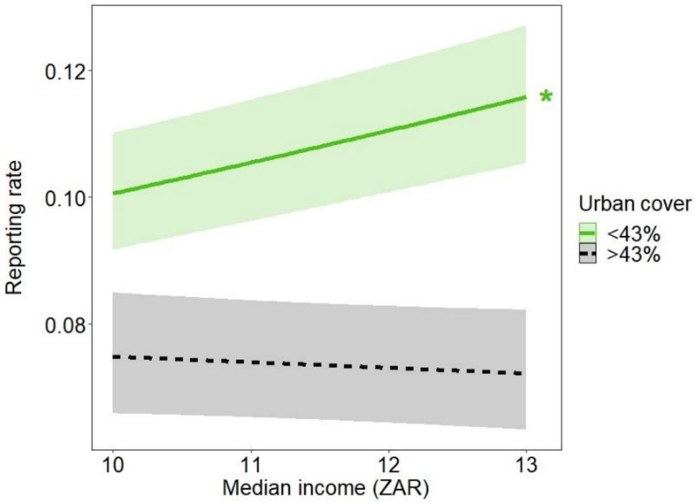

Figure 3.2: The interactive effect of median income and urban cover on species reporting rate, showing the response of species reporting rate to income at urban cover <43% (solid, green line) and >43% (dashed, black line). Median income is the $\log_{10}$-transformed median household income, in Rands, at the pentad level. Trend lines were producued from a glmmTMB and the analysis was performed on centred and scaled predictor variables, but are presented here as unscaled, uncentred values to aid interpretation. There was a significant interaction between income and urban cover (ANOVA: χ^2= 40.23, df= 1, *P*< 0.001). For urban cover <43% species reporting rate increased by 4% wih every 1 unit increase in income (estimate= 0.04 ± 0.01, *P*< 0.001, n= 492 species and 239 pentads), after which the relationship with income becomes non-significant (estimate= -0.04-1 ± 0.01, *P*= 0.28, n= 484 species and 76 pentads). Asterisks on the right of trendlines indicate which slopes are significant.

I found a significant interaction with income for dietary guild, habitat type, migration status and endemism, and a marginally non-significant interaction with income for territoriality and conservation status. However, I found no significant interaction between income and either nest location, clutch size, body mass, nor residency. I report here in more detail by comparing the slope estimates for variables for which there was a significant or marginally non-significant interaction with income (Table 3.1a-j).

3.3.2. Relationship with income for species belonging to different dietary guilds.

There was a strong significant interaction seen between median income and dietary guild (Table 3.1a). Only generalists, carnivores, granivores and aquatic species showed a significant increase with income where the relationship with income was non-significant for other diet groups (Table 3.1a; Figure 3.3). Carnivores showed a significantly more pronounced increase with income compared to granivores and aquatic species whereas the increase with income was not significantly different between aquatic and granivore species (*see Table S2.2 for pairwise comparisons)*.

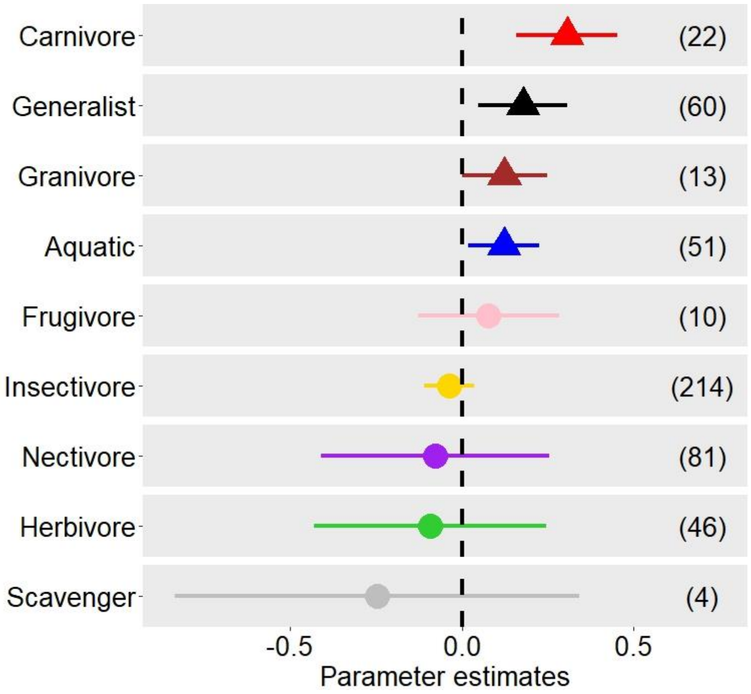

Figure 3.3: Parameter estimates of the relationship with household income (with S.E. bars) for species belonging to different dietary guilds, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and dietary guild was significant (Table 3.1a). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

3.3.3. Relationship with income for species associated with different habitat types

Species associated with certain habitat types showed different responses to income levels, with a strong significant interaction seen between income and habitat (Table 3.1b). Species associated with desert-rock habitats had the largest estimate indicating the steepest increase with income. The estimates of aquatic and forest-woodland suggest that these species also increased with income albeit with effect sizes around half as that of desert-rock species (Table 3.1b; Figure 3.4). For those species which showed evidence for a luxury effect, the increase with income for species associated with desert-rock habitats was significantly higher than that observed for species associated with forest-woodland and aquatic habitats whereas the increase with income for aquatic species and forest-woodland habitat was not significantly different from each other (*see Table S2.3 for pairwise comparisons)*. The relationship for species associated with grassland, shrubland and human-modified habitats was not significant with income (Table 3.1b; Figure 3.4).

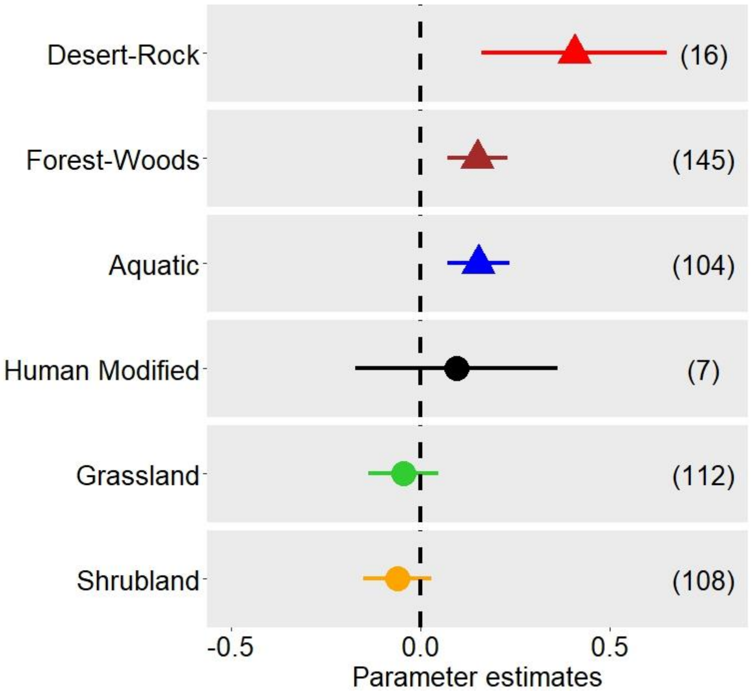

Figure 3.4: Parameter estimates of the relationship with household income (with S.E. bars) for species of different habitat types, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and habitat type was significant (Table 3.1b). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

3.3.4. Relationship between income and territoriality

There was an indication that the relationship between reporting rates and income differed depending on the territoriality of the species (Table 3.1f), the interaction being marginally non-significant (*P*= 0.06, Table 3.1f; Figure 3.5). The estimates for non-territorial and weakly territorial were significant indicating evidence for a luxury effect, whereas the estimate for territorial birds was non-significant.

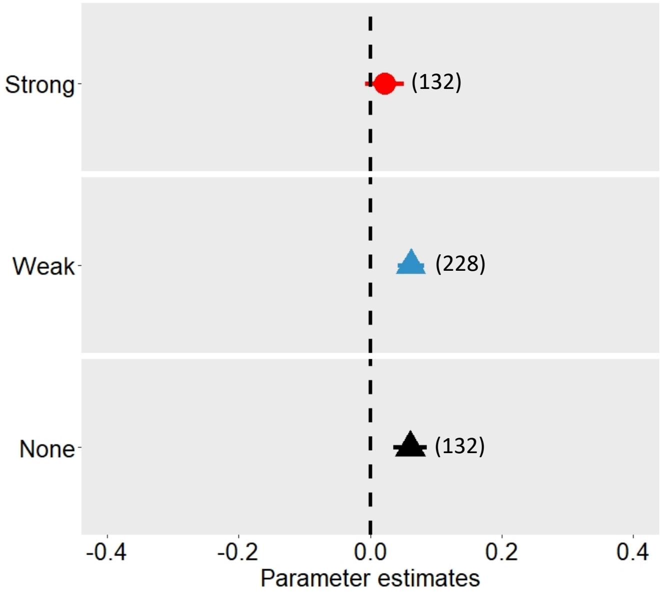

Figure 3.5: Parameter estimates of the relationship with household income (with S.E. bars) for species with different levels of territoriality, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and territoriality was marginally non-significant (Table 3.1f). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

3.3.5. Relationship between income and migration status

Species migration status significantly influenced the relationship between estimates and income, with a highly significant interaction (Table 3.1g). The estimates for sedentary species and full migrants indicate a significant increase with income whereas the estimates for partial migrants were non-significant (Table 3.1g; Figure 3.6). The increase with income for full-migrants was significantly higher that of sedentary species (*see Table S2.4 for pairwise comparisons)*.

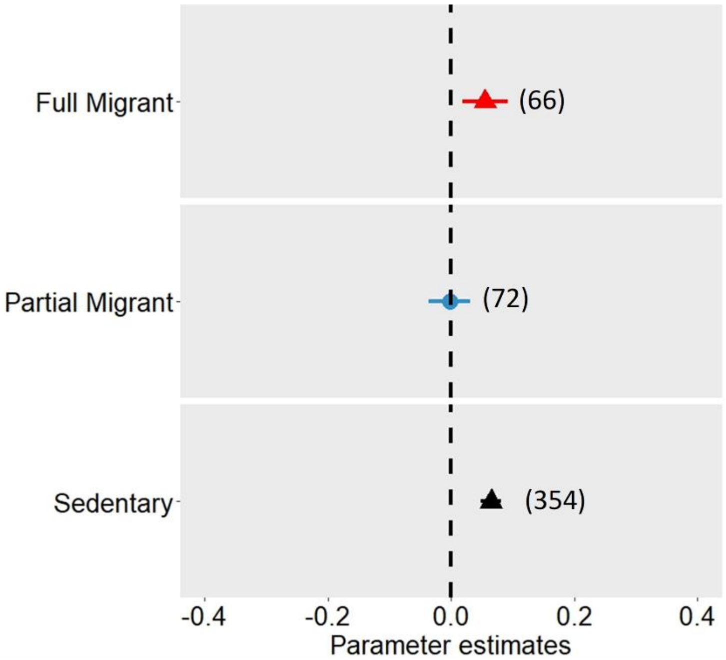

Figure 3.6: Parameter estimates of the relationship with household income (with S.E. bars) for species with different migration status, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and migration status was significant (Table 3.1g). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

3.3.6. Relationship with income and species endemism

The interaction between species endemism and income was highly significant suggesting species of different levels of endemism respond differently to income (Table 3.1h). The estimates for both endemic and non-endemic species indicate an increase with income however the estimate for endemic species was larger indicating a steeper increase with income than non-endemics (Table 3.1h; Figure 3.7).

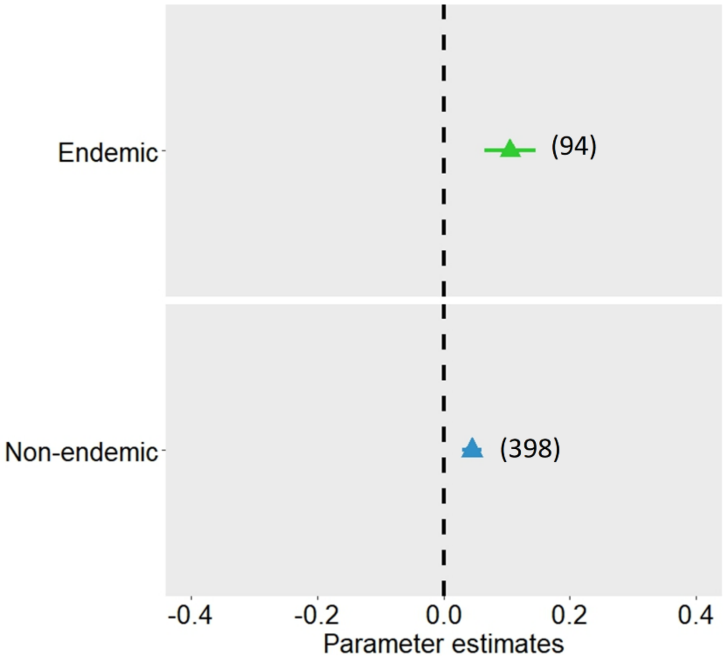

Figure 3.7: Parameter estimates of the relationship with household income (with S.E. bars) for species with different endemism, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and endemism was significant (Table 3.1h). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

3.3.7. Relationship with income and species with different conservation status

The results show a tendency of species conservation status to influence the relationship between income and parameter estimates, with the interaction between income and conservation status being marginally non-significant (*P*= 0.05) (Table 3.1j). The estimates of both threatened and least-concern species indicate an increase with income, however, threatened species had a larger estimate indicating a sharper increase (Figure 3.8).

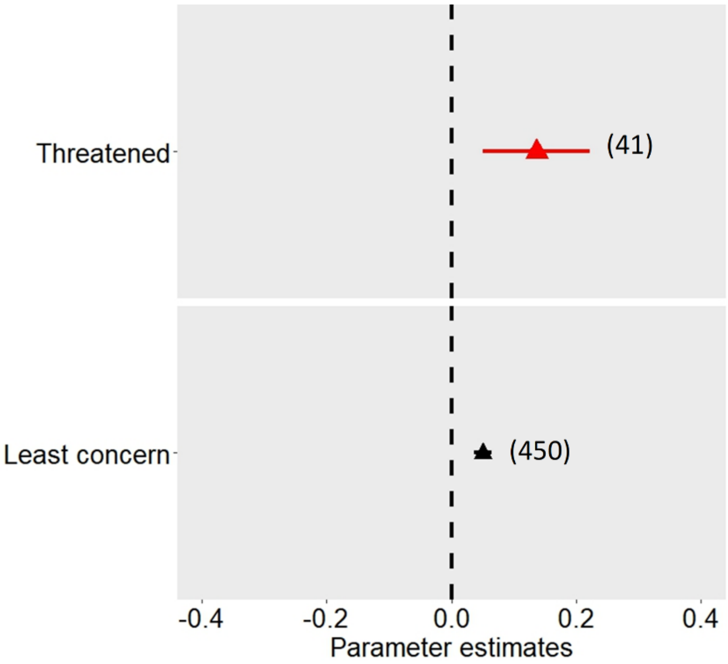

Figure 3.8: Parameter estimates of the relationship with household income (with S.E. bars) for species with different conservation status, where a triangle represents significant effects. Estimates were produced from a glmmTMB and the interaction between income and conservation status was marginally non-significant (Table 3.1j). Data were derived from the reporting rates of 492 bird species across 239 pentads. Sample sizes are provided in parentheses.

Table 3.1: Summary of Analysis of Deviance (ANOVA) performed on glmmTMBs fitting the interactive effect between income and each ecological trait and the slope of the relationship with income for the category within each ecological trait are provided. Significant relationships are indicated in bold.

Ecological trait	Explanatory variable	Estimate ± S.E.	χ^2	df	*P*	Factors	Estimate ± S.E.	*P*
(a) Dietary guild	**Diet**		**18.0**	**5**	**0.003**			
	Income	**0.05 ± 0.01**	**54.56**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.72**	**1**	**0.004**			
	diet*income		**23.91**	**5**	**0.002**	**Aquatic**	**012 ± 0.03**	**<0.001**
						Carnivore	**0.31 ± 0.05**	**<0.001**
						Frugivore	0.08 ± 0.06	0.22
						Generalist	**0.18 ± 0.04**	**<0.001**
						Granivore	**0.02 ± 0.04**	**<0.001**
						Herbivore	-0.09 ± 0.10	0.37
						Insectivore	-0.04 ± 0.02	0.10
						Nectivore	-0.08 ± 0.10	0.44
						Scavenger	-0.25 ± 0.18	0.17
(b) Habitat type	habitat type		5.74	5	0.33			
	Income	**0.06 ± 0.01**	**54.57**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.69**	**1**	**0.004**			
	habitat type*income		**32.74**	**5**	**<0.001**	**Desert-rock**	**0.04 ± 0.08**	**<0.001**
						Forest-woodland	**0.15 ± 0.02**	**<0.001**
						Aquatic	**0.15 ± 0.03**	**<0.001**
						Grasslands	-0.04 ± 0.03	0.13
						Human-modified	0.09 ± 0.09	0.28
						Shrubland	-0.06 ± 0.02	0.05
(c) Nest location	**nest location**		**13.54**	**2**	**0.001**			
	Income	**0.03 ± 0.01**	**4.42**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.70**	**1**	**<0.001**			
	nest location*income		2.85	2	0.24			

(d) Body mass	body mass	$-7.57x10^{-6} \pm 1.16x10^{-5}$	0.41	1	0.52			
	Income	**$4.18x10^{-2} \pm 6.62x10^{-3}$**	**53.62**	**1**	**<0.001**			
	urban cover	**$-2.09x10^{-2} \pm 5.86x10^{-3}$**	**12.70**	**1**	**0.004**			
	body mass *income	$1.41x10^{-6} \pm 8.44x10^{-6}$	0.03	1	0.87			
(e) Clutch size	clutch size	0.01 ± 0.03	0.13	1	0.72	clutch size	0.01 ± 0.03	0.71
	Income	**0.05 ± 0.01**	**52.95**	**1**	**<0.001**	**income**	**0.05 ± 0.01**	**0.001**
	urban cover	**-0.02 ± 0.01**	**12.30**	**1**	**0.004**	**urban cover**	**-0.02 ± 0.01**	**0.005**
	clutch size *income	$-3.01x10^{-3} \pm 3.49 x10^{-3}$	0.75	1	0.39			
(f) Territoriality	territoriality		0.30	2	0.86			
	Income	**0.049 ± 0.01**	**54.21**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.74**	**1**	**0.004**			
	territoriality*income		5.50	2	0.06	**none**	**0.06 ± 0.01**	**<0.001**
						strong	0.02 ± 0.01	0.15
						weak	**0.06 ± 0.01**	**<0.001**
(g) Migration status	**migration status**	**-**	**12.04**	**2**	**0.002**			
	Income	**0.05 ± 0.02**	**54.34**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.65**	**1**	**0.004**			
	migration status*income		**12.08**	**2**	**0.002**	**full migrant**	**0.06 ± 0.02**	**0.004**
						partial migrant	-0.002 ± 0.02	0.91
						sedentary	**0.07 ± 0.01**	**<0.001**
(h) Endemism	**Endemism**		0.28	1	0.60			
	Income	**0.09 ± 0.02**	**54.31**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.70**	**1**	**<0.001**			
	Endemism*income		**7.48**	**1**	**<0.001**	**endemic**	**0.11 ± 0.02**	**<0.001**
						non-endemic	**0.05 ± 0.01**	**<0.001**

(i) Residency	Residency		0.16	1	0.69			
	Income	**0.01 ± 0.03**	**26.21**	**1**	**<0.001**			
	urban cover	**-0.10 ± 0.01**	**382.61**	**1**	**<0.001**			
	residency*income		0.16	1	0.69	**introduced**	0.02 ± 0.04	0.68
						native	**0.03 ± 0.01**	**<0.001**
(j) Conservation status	**conservation status**		**28.91**	**1**	**<0.001**			
	Income	**0.04 ± 0.01**	**54.42**	**1**	**<0.001**			
	urban cover	**-0.02 ± 0.01**	**12.73**	**1**	**0.004**			
	conservation status*income		**3.84**	**1**	**0.05**	**threatened**	**0.14 ± 0.04**	**0.002**
						least concern	**0.05 ± 0.01**	**<0.001**

3.4. Discussion

In common with Chamberlain et al. (2019), but using a differently derived response variable, I found evidence for an overall luxury effect for birds across the urban landscape of South Africa (below a threshold of urbanisation – 43% urbanised). Chamberlain et al. (2019) found that as median income increased, the total number of species increased. In this study I attempted to understand the nature of this pattern and found that not all species respond to the socioeconomic status of an area in the same way, with a species' response dependent on their ecological traits. The response of a species to improving socioeconomic levels was dependent on dietary guild, habitat type, migration status, level territoriality and regional conservation status. In contrast, responses were apparently unrelated to species nest location, body mass, clutch size and species residency. These results reflect that the availability of food resources, habitat cover and level of environmental disturbance (i.e., human density) may correlate positively with income and act as key drivers of ecological filtering of the species inhabiting urban environments.

Carnivores, generalists, granivores and aquatic species showed the strongest response to increasing wealth of an area, while other diet groups specifically scavengers, frugivores, nectivores, herbivores and insectivores showed no increase with wealth. Species associated with forest/woodland, desert/rocky and aquatic habitats showed the strongest response to increasing wealth of an area, whereas species associated with grassland, shrubland and human-modified habitats were not influenced by the wealth of an area. I also observed a steep increase in the abundance of sedentary and migratory species with income and a tendency of non-territorial and weakly territorial species to increase with income. This study also highlights how the legacy of apartheid racial segregation and spatial planning of urban landscapes of South Africa can affect the distribution of biodiversity and thus the ecosystem services they provide and may further exacerbate the luxury effect.

Reporting rates vary albeit in a non-linear manner with abundance (Lee , et al., 2018) thus supporting the notion that it provides a reasonable direct and indirect measure of local abundance (Robertson, et al., 1995; Amar, et al., 2016; Lee & Barnard, 2017; Royle & Nichols, 2003; Huntley, et al., 2012). Although reporting rates can offer a general sense of bird abundance, because its reliability depends on variables such as habitat, species characteristics, and observer effort (Lee & Barnard, 2017; Lee, et al., 2018; Robertson, et al., 1995; Amar, et al., 2016), studies do highlight the importance of exercising caution when depending solely on reporting rates to estimate bird abundance. Using reporting rates to explore species abundance within urban areas in relation to income can provide valuable insights into the relationship between human socioeconomic factors and urban diversity.

3.4.1. Relationship between income and dietary guild

Carnivores exhibited the strongest increase with income across all diet groups. Carnivores were primarily represented by raptor species. Hence, the rise in reporting rates with income is likely a reflection the luxury effect (the increase in species richness and abundance with income), leading to an increased availability of prey to support carnivore species in wealthier neighbourhoods. The increased availability of lawns, gardens, shade trees, food plants and supplementary food (e.g., bird feeders) which are likely more prevalent with improving socioeconomic conditions, attract wildlife into urban areas in South Africa (Downs, et al., 2021) and are in turn important prey sources for various raptors in urban areas (McPherson, et al., 2016; Van der Meer, et al., 2018; Suri, et al., 2017). For example, some studies have demonstrated an increase in the availability of non-avian prey, including mammals and reptiles in affluent urban areas (Tricam, 2020; Magle, et al., 2016). In addition to a range of vertebrate prey, raptors also typically require tall trees to persist in urban areas (McPherson, et al., 2021) a habitat type which my results suggest also increases with income. For example, many South African raptors benefit from the use of exotic trees in urban areas (Smith, 1974). Retaining forest patches in the urban mosaic landscapes encouraged the persistence of a population of Crowned Eagles (*Stephanoaetus coronatus*) in KwaZulu-Natal, South Africa (McPherson, et al., 2019).

My expectation that generalists would be equally abundant across the income gradient was not supported; instead, generalists exhibited the second strongest response to income across all dietary groups. Generalists are the most urban-tolerant of bird species (Callaghan, et al., 2019; Lancaster & Rees, 1979) and have broad dietary requirements (Palacio, 2020; Bonier, et al., 2007), which may provide a competitive advantage over other dietary guilds in exploiting urban food resources both natural and anthropogenic. Aquatic species also showed an increase with income and is likely associated with an increase in aquatic habitats in wealthier neighbourhoods (Chamberlain, et al., 2020; Jenerette, et al., 2011; Leong, et al., 2018; Mahan, et al., 2000) which include irrigated laws, ponds, rivers, fountains and other water features. The steep increase observed by both generalists, and granivores may also be indicative of an increase in a variety of food resources with improving socioeconomic conditions including food provisioning. Food provisioning is another important predictor of urban biodiversity (Leong, et al., 2018; van Heezik & Hight, 2017) and has been shown to be higher in wealthier urban areas (Hope, et al., 2003; Davies, et al., 2012). This is likely because wealthier individuals have excess disposable income to purchase birdseed or can afford to allocate excess leftover food resources to provision urban-exploiting birds (Davies, et al., 2012; van Heezik & Hight, 2017; Fuller, et al., 2008). This result demonstrates a similarity between urban areas in European cities and cities across South Africa in that intentional supplementary anthropogenic food primarily consists of seeds, nuts, and grains provided at bird feeders (Jones & Reynolds, 2008; Davies, et al., 2009) which favour the presence of granivores (Kark, et al., 2007; Chace & Walsh, 2006).

Although studies suggest that nectivores are very sensitive to urban areas and tend not to venture far into suburbia (Pauw & Louw, 2012), the overall lack of a luxury effect for frugivores and nectivores was surprising and ran contrary to my expectations. Even after conducting a repeated analysis that incorporated pentads representing all urban cover levels in South Africa, there remained no statistically significant increase in the reporting rates of frugivores and nectivores associated with income. Previous studies have shown that high-income neighbourhoods in medium-sized towns in the Eastern Cape of South Africa, support more frugivore and nectivore communities, likely due to increased investment in the maintenance of flowering and fruit-bearing trees (Tricam, 2020). In contrast, Lubbe et al., (2010) found higher abundance of frugivores in low-income neighbourhoods of the city of Tlokwe, South Africa, suggesting people in poorer communities grew more fruit trees. These studies show that there may be differences in how socioeconomic factors drive frugivore and nectivore diversity between urban areas which may not be reflected when using a multi-city/nation-wide approach.

The overall lack of a luxury effect response observed for frugivores, nectivores, herbivores, insectivores, and scavengers may be indicative of their inability to contend with other urban stressors as specialists have been repeatedly shown to be less tolerant of urban areas (Callaghan, et al., 2019; Patankar, et al., 2021). Furthermore, the absence of a discernible luxury effect among these diet groups may signal the presence of unique urban characteristics within low-income neighbourhoods that serve to mitigate the expected response to luxury. For example, studies on bird species diversity in urban green spaces of Johannesburg, South Africa found no evidence of a luxury effect; instead, historical urban spatial planning decisions, specifically the use of water bodies to separate racial groups, likely buffered low-income neighbourhoods from reduced avian diversity (Howes & Reynolds, 2021). Additionally, different urban management protocols between cities could also explain the absence of a luxury effect seen for certain foraging guilds (Howes & Reynolds, 2021).

3.4.2. Relationship between income and habitat type

The racial segregation imposed by the Apartheid regime resulted in the overlap of socioeconomic and racial patterns, which are still seen within society today (Shackleton, 2016). Wealthy suburbs consisting predominantly of white South Africans are located in well vegetated areas with freestanding housing on large plots, whereas low-income suburbs housing people of colour are located in densely populated areas, with more urban cover, little vegetation and receiving less infrastructural support from municipalities (Western, 1981; Seekings, 2011). The responses from species with different habitat requirements highlight the differences in the ecological attributes that likely exist along socioeconomic gradients of South African urban areas. The luxury effect was absent for species associated with grassland, shrubland and human-modified habitat whereas species associated with deserts and rocky habitat exhibited the steepest increase with income, followed by species associated with forests, woodland and aquatic species which had a similar rate of increase. This suggests that tree cover, rocky habitat and water reserves become more abundant with improving socioeconomic conditions whereas within poorer areas habitat requirements were not being met. For example, Verreaux's eagles *(Aquila verreauxii))* were one of the 35 species in the rocky-desert category. This species requires relatively large open areas (agriculture or natural habitats), with good densities of medium-sized mammals and birds for hunting (Murgatroyd, et al., 2016) and cliffs for breeding, habitats that would likely be more associated with wealthier neighbourhoods.

Greater vegetation cover in wealthier neighbourhoods is associated with an increased availability of resources, fostering a greater number of species of sustainable avian populations. Expansive areas of vegetation also tend to exhibit more diverse habitats and environments, facilitating a broader range of species (Palmer, et al., 2008; van Heezik, et al., 2013; Mayorga, et al., 2020; Svein, 2018). Diverse habitats with a mixture of trees, shrubs, water resources and grasses have more structural complexity that could provide more diverse habitat, resources and protection for a wide range of bird species (Evans, et al., 2009). Furthermore, neighbourhoods with ample vegetation cover have larger core areas that are less vulnerable to edge effects (Antos & White, 2003).

3.4.3. Relationship between income and nest location

I found no interaction between nest type and income, instead elevated nesters, ground nesters and cavity nesters exhibit a similar increase in their reporting rates with income for the selected level of urban cover I investigated. This suggests that the availability of possible nest sites to support these species increases similarly with improving socioeconomic conditions in urban areas. The availability of suitable habitat for ground nesters, trees and man-made structures such as buildings, roof-tops for elevated nesters and the availability of suitable natural habitat and nest-boxes for cavity nesters was likely increases at a similar rate across urban areas of South Africa.

3.4.4. Relationship between income and territoriality

I expected that species showing strong territoriality would exhibit a sharper increase with income than less territorial species. On the contrary, I observed the opposite, whereby the abundance of non-territorial and weakly territorial species showed a tendency to increase with improving socioeconomic conditions whereas strongly territorial species did not. Although this result was marginally non-significant, this pattern may be indicative of increased resource abundance favouring group-living over solitary living or more transient/nomadic species over resident species. Evidence for the former comes from studies exploring the evolution of cooperative breeding. They suggest that family living is more likely in more productive, resource stable environments, where prolonged associations may be less costly (Covas & Griesser, 2007; Griesser, et al., 2017). Therefore, non- and weakly territorial species which may consist of more gregarious and cooperative breeding species exhibiting a significant association with income whereas strongly territorial species do not.

3.4.5. Relationship between income and species migration status

Migration is associated with resource availability that allows species to cope with periods of low resource availability and migratory species generally select for resource-rich stable habitats (Somveille, et al., 2015). I expected that increased food availability and green space in wealthier neighbourhoods would act as refuges (Morelli, et al., 2017; Ferenc, et al., 2014) and might favour migratory species. This assumption is supported by a recent study by Kinnunen et al. (2022) who found that as median income increased, cities in the United States tended to support more migratory species than other groups. Contrary to these expectations, I found that both sedentary species and full migrants were favoured by improving socioeconomic conditions, whereas partial migrants responded less strongly. Partial migrants are those species, for which some section of the population migrate whereas others remain on the breeding ground year-round. It is not clear why species with this trait would not respond as strongly.

3.4.6. Relationship between income and species endemism

Both endemic and non-endemic species increased with income however, species endemic to South Africa exhibited a stronger increase with income. This is a result which is also supported by other studies (Kinzig, et al., 2005; Lerman & Warren, 2011; Melles, 2005). This likely reflects the higher occurrence of wealthier neighbourhoods in areas with greater coverage of ecologically specialised vegetation such as ornithophilous floral species, e.g., plants specialized for pollination by birds, or greater and lower environmental disturbance. Since a species' geographical range can provide a reliable index of its environmental tolerance (Symonds & Johnson, 2006), it follows that endemic species which occupy distinct habitats, have restricted geographic ranges and smaller populations (Işik, 2011; Carrascal, et al., 2008) and can only tolerate a narrow range of habitats. In contrast, non-endemic species which survive and reproduce across a wide range of environmental conditions, therefore have broader environmental tolerance (Bonier, et al., 2007) and may fare better across all income areas. For example, the Olive thrush (*Turdus olivaceus*), is one of 94 locally endemic species included in this dataset. The Olive Thrush is a common garden bird in most regions of South Africa (Vernon & Herremans, 1997). In natural settings, the Olive Thrush occurs predominantly in montane forest, forest edge and riverine thickets (Urban, et al., 1997), which may be more abundant in affluent neighbourhoods. Another common garden bird, the Southern double-collared sunbird (*Cinnyris chalybeus*), is a nectivore, which commonly pollinates fynbos vegetation, a Mediterranean-type shrubland restricted to coastal and mountainous areas of the Western Cape of South Africa (Geerts & Pauw, 2009). The results suggest that species adapted to arid, rocky and aquatic habitats, such as those restricted to the fynbos biome, increase in wealthier neighbourhoods.

3.4.7. Relationship between income and conservation status

I also found an interesting relationship between income and conservation status, with threatened species showing the strongest response. This indicates that within poor neighbourhoods there are fewer resources to support these more vulnerable species. It is likely that wealthier neighbourhoods have greater coverage of good-quality habitat to buffer threatened species from environmental stressors such as human disturbance, pollution (e.g.., air, noise, light, chemical) and exposure to disease-causing pathogens (Seress & Liker, 2015). Additionally, neighbourhoods with ample vegetation cover have larger core areas to host species that are more vulnerable to edge effects (Antos & White, 2003). For example, the Blue crane (*Anthropoides paradiseus*), one of the 41 threatened species in the dataset, is a large terrestrial bird, classified as a *vulnerable* species on the

IUCN Red List largely attributed to loss of habitat due to mining, agriculture and development (BirdLife International, 2022). An increased availability of grasslands and lower human disturbance with improving socioeconomic conditions could strongly promote the presence of Blue Crane, populations which are dependent on extensive home ranges of open grassland for successful breeding (Meine & Archibald, 1996). In most cities, wealthier individuals are often attracted to luxury housing along the coast while low-income housing is provided at the urban edges of the city (Van Ham, et al., 2021). This is certainly the case in the Cape Metropolitan Area where the coastline areas attract super-rich international homebuyers and tourists and where there has been little integration of the low-income, African majority (Trail, 2006). Endangered seabirds such as the Cape cormorant (*Phalacrocorax capensis*), also occur predominantly in coastal and estuarine environments on the South-Western parts of South Africa where they feed predominantly on small pelagic fish (Berry, 1976). Limited exposure of poorer communities to species of conservation concern may have implications for their willingness to participate in practices aimed for their conservation (Alcock, et al., 2020; Richardson, et al., 2020; Rosa, et al., 2018).

Conclusion

In conclusion, the steep socioeconomic gradient present in South Africa, a consequence of racial segregation during the apartheid era, provides an opportunity to explore the luxury effect in more detail, and to understand how socioeconomic conditions of urban areas affect selection of ecological traits exhibited by birds. This study shows that the legacy of the socioeconomic inequalities that stem from the apartheid era are reflected in the types of biodiversity observed in urban landscapes today, and thus the types of species people encounter and the ecosystem services that they benefit from within these urban areas. I found a significant change in the abundance of birds with specific traits across socioeconomic gradients in South African urban areas, likely driven by the increased abundance of food resources, increased availability of habitat associated with specialists and likely lower environmental disturbance with improving socioeconomic conditions. Wealthier neighbourhoods benefit from a greater abundance of carnivores, generalists, granivores, aquatic species as well as more endemic and threatened species compared to low-income neighbourhoods. Although the use of different urban areas as replicates in studies of urban wildlife and the assumption that different cities are comparable should be made with caution, these findings are likely indicative of unequal distribution of food resources, vegetation cover and environmental disturbance which result in unequal opportunities to host a heterogeneous suite of avian species particularly in low-income neighbourhoods.

Consequently, I expect a loss of ecosystem services in communities already disadvantaged by inadequate infrastructural, economic, and social services. With respect to this study, the loss of specific ecosystem services in low-income communities may include the regulation of pest populations by carnivores, scavenging on garbage and decaying matter by generalists and seed dispersal by granivores, as well as the overall recreational and aesthetic value added to urban communities through the presence of diverse avian communities (Heyman, et al., 2017; Whelan, et al., 2008; Sekercioglu, et al., 2016; Whelan, et al., 2015). Future studies should investigate the consequences of such ecological trait selection and resulting urban bird communities in urban areas on daily human life, motivations to interact with nature and to participate in environmentally conscious behaviour.

While encouraging private garden planting to create suitable habitat and promote the occurrence of species may be useful, this may be constrained by income in low-income neighbourhoods. There needs to be greater effort on the part of city management to ensure public spaces within low-income areas are restored to host avian communities with a diverse range of ecological traits and ecosystem services. As urban development continues to intensify and new cities emerge, it’s important that city-planners implement more sustainable solutions in urban development to ensure the luxury effect does not manifest within these communities.

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3.6. Supplementary material

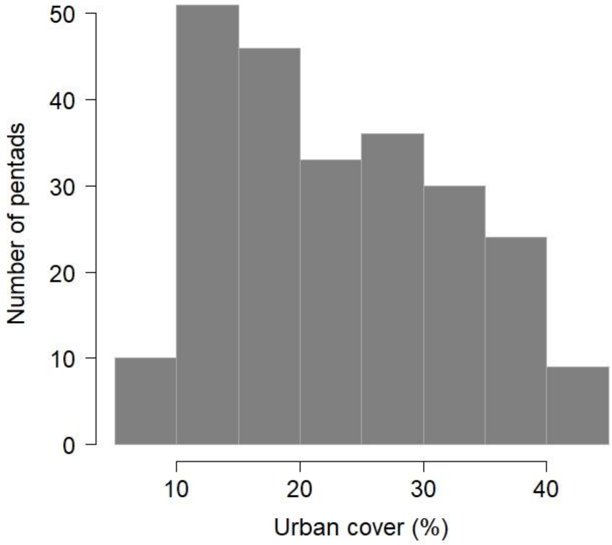

Figure S2.1: Distribution of urban cover of sampled pentads (*n* = 239). Urban cover was derived from the South African National Land-Cover Dataset from 2013 to 2014 (Department of Environmental Affairs, 2015) and varied from 6%-43% across all pentads. There was a significant interaction between income and urban cover (ANOVA: χ^2= 40.23, df= 1, *P*< 0.001). There was evidence for a luxury effect for the reporting rates of species occurring in pentads with <43% urban cover (estimate= 0.04 ± 0.01, *P*< 0.001), after which the relationship with income became non-significant (estimate= -0.04-1 ± 0.01, *P*= 0.28) and these pentads (n= 76 pentads) were therefore excluded from the analysis.

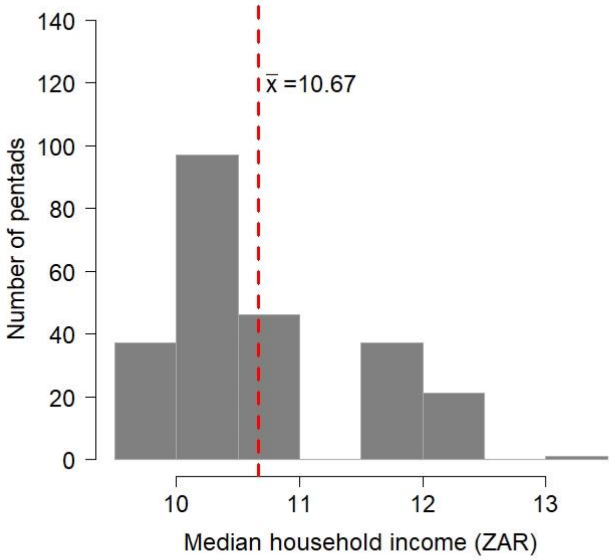

Figure S2.2: Distribution of median annual household income (ZAR, $\log_{10}$-transformed) of sampled pentads (*n* = 239). The red, dashed line indicates the mean income across all pentads. Median annual household income (in South African Rands, where 1R was equivalent to c. US$0.15 in 2011; http://www.x-rates.com/historical/?from=USD&amoun t=1&date=2011-06-01) derived from the 2011 South African National Population Census (Statistics South Africa, 2012) in which 15 million households were surveyed (data available at www.statssa.gov.za). Mean annual household income ranged between R14,011 and R443,452 (between US$872,180 and US$27,602.60 median = R27,874, 221US$1734.24).

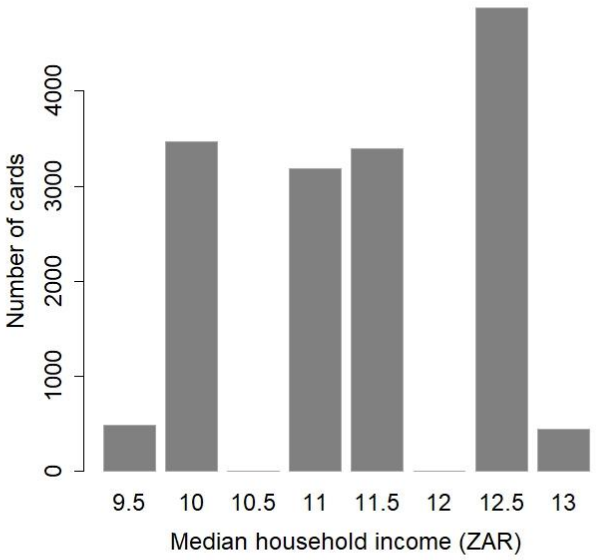

Figure S2.3: Distribution of the total number of atlas cards submitted across median annual household income (ZAR, $\log_{10}$-transformed). Data were obtained from Chamberlain et al. (2019), and were from surveys collected from 01/01/2012 to 31/12/2014 and include 239 pentads. Data include only cards where the observer fully complied with the protocol rules; i.e., listed as '*full protocol*' and data excludes pentads with less than 5 atlas cards.

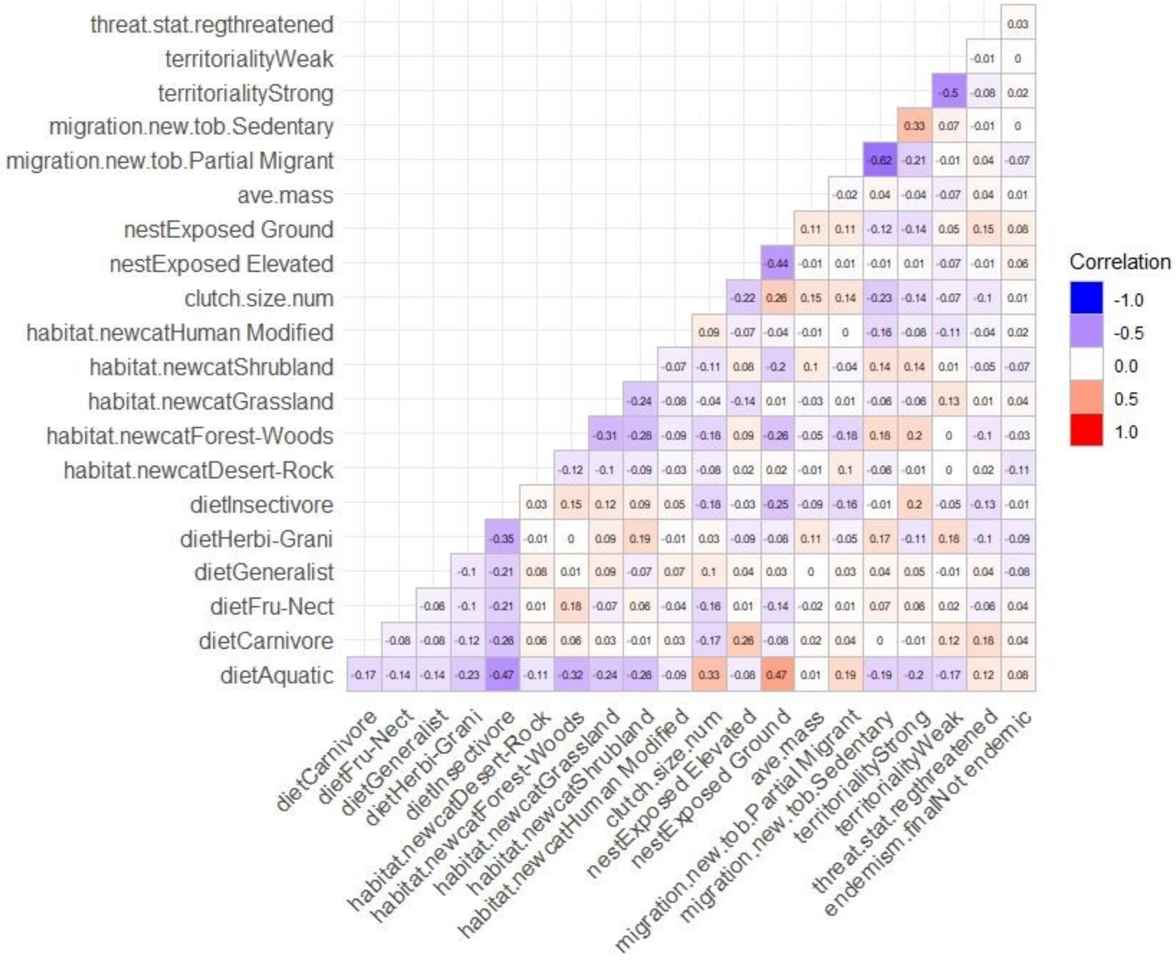

Figure S2.4: Correlation matric of the ecological traits used in the analysis plotted using the package *ggcorrplot* (Kassambara, 2019)**.** Blue and red squares correspond to negative and positive correlations respectively.

Table S2.1: Model structure of the four competing generalised linear mixed models to explore the interaction between income and urban cover and their respective Akaike's information criterion (AIC), ΔAIC and Akaike weights (ω_i) which was used to select the best competing model. The best model (with the lowest AIC value).

Model	**AIC_C**	**ΔAIC_C**	**ω_i**
diet*scale(income) + (1|scientific name), family=list (family="betabinomial", link="logit")	258335.5	0	0.996
diet*scale(income) + (1|scientific name), family=list (family="betabinomial", link="cloglog")	258346.9	11.40	0.003
diet*scale(income) + (1|scientific name), family=list (family="binomial", link="logit")	710274.4	451938.82	0
diet*scale(income) + (1|scientific name), family=list (family="binomial", link="cloglog")	710267.7	451932.18	0

Table S2.2: Pairwise comparisons with Bonferroni correction of the relationship with income between dietary guilds. Significant differences are highlighted in bold.

Contrast	**estimate ± S.E.**	**P value**
Aquatic - Carnivore	**-0.18 ± 0.05**	**0.02**
Aquatic - Frugivore	0.04 ± 0.07	0.99
Aquatic - Generalist	-0.05 ± 0.05	0.97
Aquatic - Granivore	-0.00 ± 0.05	1.00
Aquatic - Herbivore	0.21 ± 0.11	0.55
Aquatic - Insectivore	**0.16 ± 0.04**	**<0.001**
Aquatic - Nectivore	0.20 ± 0.11	0.63
Aquatic - Scavenger	0.36 ± 0.18	0.53
Carnivore - Frugivore	**0.23 ± 0.08**	**0.08**
Carnivore - Generalist	0.12 ± 0.06	0.45
Carnivore - Granivore	**0.18 ± 0.06**	**0.05**
Carnivore - Herbivore	**0.40 ± 0.11**	**0.01**
Carnivore - Insectivore	**0.34 ± 0.05**	**<.0001**
Carnivore - Nectivore	**0.38 ± 0.11**	**0.02**
Carnivore - Scavenger	**0.55 ± 0.19**	**0.07**
Frugivore - Generalist	-0.10 ± 0.07	0.91
Frugivore - Granivore	-0.04 ± 0.07	0.99
Frugivore - Herbivore	0.17 ± 0.12	0.89
Frugivore – Insectivore	0.11 ± 0.06	0.73
Frugivore - Nectivore	0.15 ± 0.12	0.93
Frugivore - Scavenger	0.32 ± 0.19	0.74
Generalist - Granivore	0.05 ± 0.05	0.98
Generalist - Herbivore	0.27 ± 0.11	0.25
Generalist - Insectivore	**0.21 ± 0.05**	**<0.001**
Generalist - Nectivore	0.25 ± 0.10	0.31
Generalist - Scavenger	0.42 ± 0.18	0.34
Granivore - Herbivore	0.21 ± 0.11	0.56
Granivore - Insectivore	**0.16 ± 0.04**	**<0.001**
Granivore - Nectivore	0.20 ± 0.10	0.64
Granivore - Scavenger	0.37 ± 0.18	0.53
Herbivore - Insectivore	-0.06 ± 0.11	0.99
Herbivore - Nectivore	-0.02 ± 0.14	1.00
Herbivore - Scavenger	0.15 ± 0.21	0.99
Insectivore - Nectivore	0.04 ± 0.10	1.00
Insectivore - Scavenger	0.21± 0.18	0.96
Nectivore - Scavenger	0.17 ± 0.20	0.99

Table S2.3: Pairwise comparisons with Bonferroni correction of the relationship with income between habitat type. Significant differences are highlighted in bold.

Contrast	**estimate ± S.E.**	**P value**
Aquatic – Desert-Rock	**-0.25 ± 0.08**	**0.03**
Aquatic – Forest-Woods	0.00 ± 0.04	1.00
Aquatic - Grassland	**0.19 ± 0.04**	**<0.001**
Aquatic – Human-modified	0.06 ± 0.09	0.98
Aquatic - Shrubland	**0.21 ± 0.11**	**<0.001**
Desert-Rock – Forest-Woods	**0.25 ± 0.08**	**0.03**
Desert-Rock – Grassland	**0.45 ± 0.08**	**<0.001**
Desert-Rock – Human-modified	0.31 ± 0.12	0.09
Desert-Rock – Shrubland	**0.47 ± 0.09**	**<0.001**
Forest-Woods - Grassland	**0.19 ± 0.04**	**<0.001**
Forest-Woods – Human-modified	0.06 ± 0.09	0.99
Forest-Woods – Shrubland	**0.21 ± 0.04**	**<0.001**
Grassland – Human-modified	-0.14 ± 0.09	0.66
Grassland – Shrubland	0.02 ± 0.04	0.99
Human-modified – Shrubland	0.15 ± 0.09	0.55

Table S2.4: Pairwise comparisons with Bonferroni correction of the relationship with income between migration status. Significant differences are highlighted in bold.

Contrast	**estimate ± S.E.**	**P value**
Full-migrant – Partial migrant	**0.15± 0.05**	**<0.001**
Full migrant – Sedentary	0.05 ± 0.04	0.40
Partial migrant – Sedentary	**-0.10 ± 0.04**	**0.02**

CHAPTER 4

Staying cool and eating junk: Influence of heat dissipation and anthropogenic food on foraging and body condition in an urban passerine.

Source: Author

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Abstract

Climate change and urbanization are two of the most important current global change processes affecting wildlife today. However, studies have largely focused on these issues in isolation, limiting my ability to predict how they impact species simultaneously. During hot weather conditions, many birds reduce activity to minimise heat gain, which can result in an inability to maintain body mass. In urban environments, however, higher anthropogenic food or water availability could buffer individuals from these potential costs. In this study, I explore the impacts of elevated ambient temperature on the foraging behaviour and body mass of an urban-inhabiting passerine, the Red-winged starling, *Onychognathus morio*. In this study system (a university campus), anthropogenic food abundance fluctuates over short timescales, with food being more abundant on weekdays and less abundant on weekends. This allowed me to explore how birds respond to elevated temperatures during days with varying availability of anthropogenic food. My result showed that individuals increased heat dissipation behaviours with temperature, while foraging effort declined. Despite reduced foraging with rising temperature, starlings were able to maintain constant food intake rate and body mass irrespective of the short-term food fluctuations. This suggests that overall food and water abundance in this urban environment buffered individuals from the effects of elevated temperature, at least within the current range experienced in this system and during the non-breeding season.

4.1. Introduction

Climate change and urbanization are two of most important human-induced environmental changes threatening biodiversity today (McKechnie & Wolf, 2010; Aronson, et al., 2014). Despite the substantial challenges these global change processes pose for wildlife, most studies have focused solely on one of these factors, independent of the other. For example, most research has investigated the effects of climate warming on natural environments, limiting my ability to predict how urban environments will respond in a warming world. Understanding how multiple global change processes simultaneously affect species' survival and distributions will become increasingly important as both temperatures and urbanization continue to increase (Chamberlain, et al., 2020).

The Earth's climate is warming at an unprecedented rate (IPCC, 2007) with projections predicting increases in maximum air temperatures and the frequency, intensity, and duration of heat waves in coming decades (Meehl & Tebaldi, 2004). These changes are likely to present many animal populations with new thermoregulatory challenges. Extreme hot weather events have already led to several mass mortalities in the last century (Finlayson, 1932; Towie, 2009; Welbergen, et al., 2008; Bega, 2020). Birds are particularly at risk as they heavily rely on water to stay cool through evaporative heat dissipation (e.g., panting) (Bartholomew, 1972; Dawson, 1982). Even with access to sufficient water, they could succumb to hyperthermia due an inability to dissipate heat rapidly enough (McKechnie & Wolf, 2010; Finlayson, 1932).

High temperature conditions may also be exacerbated in urban environments (Luber & McGeehin, 2008), where temperatures regularly exceed those measured in natural areas due to a phenomenon termed the Urban Heat Island (UHI) effect (Oke, 1982; Voogt & Oke, 2003; Grimmond, 2007). The UHI effect is primarily due to the high percentage cover of non-evaporative, impervious artificial surfaces such as bricks, concrete and asphalt, which have a relatively lower albedo and absorb heat more effectively than vegetation (Oke, 1982; Arnfield, 2003; Fischer, et al., 2012). This makes urban environments an excellent natural experiment for quantifying the impact of climate warming on organisms (Angilletta Jr, et al., 2007). As cities continue to grow in size, they become warmer, exacerbating the UHI effect (Oke, 1973). This interaction and the projected increases in climate warming and urbanization, necessitate the importance of investigating the response of animal populations to elevated temperature.

At thermal extremes, mobile individuals can respond behaviourally by seeking refuge in thermally buffered microsites (Ricklefs & Hainsworth, 1968; Austin, 1976; Clark, 1987; Cunningham, et al., 2015). The use of cooler microsites may reduce the need to employ evaporative heat dissipation (Wolf, et al., 1996) or may also allow birds to continue to forage at high temperatures (Austin, 1976). Alternatively, individuals can reduce the risk of exposure to elevated body temperatures by suppressing their activity under elevated temperature conditions (Ricklefs & Hainsworth, 1968; Cunningham, et al., 2015; du Plessis, et al., 2012). However, behavioural thermoregulation can result in costly trade-offs, particularly energetic constraints that result from reduced foraging opportunities under less favourable conditions (Goldstein, 1984; Clark, 1987; Cunningham, et al., 2015). For example, when temperatures exceeded 30°C, Southern pied babblers *(Turdoides bicolor)* spent a significant amount of their time panting while foraging and were unable to obtain enough food to offset overnight weight loss (du Plessis, et al., 2012). Similarly, when switching to use cooler microsites during elevated temperature conditions, Southern fiscals (*Lanius collaris)* experienced a 50% reduction in their foraging returns due to their vision being obstructed in cooler, shaded hunting perches (Cunningham, et al., 2015). These foraging trade-offs associated with thermoregulation have also been observed in the provisioning rates of breeding individuals with potentially far-reaching implications for breeding success (Van de Ven, et al., 2020; Van de Ven, et al., 2019; Cunningham, et al., 2013).

Given the above-mentioned trade-offs and their associated costs, access to abundant food and water resources may buffer animals from the costs associated with thermoregulation (Tieleman & Williams, 2002). Urban environments are typically more abundant in food resources (Anderies, et al., 2007; Shochat, et al., 2006; Møller, 2009), the consumptiom of which has been shown to allow many species to devote less time to foraging (Sol, et al., 2013; Lowry, et al., 2013) and improve foraging efficiency (Fleischer Jr, et al., 2003; Lill & Geraldene, 2016). As such, abundant urban food resources may mitigate or buffer impacts of, for example, foraging-thermoregulation trade-offs, on the ability to maintain body mass. Additionally, access to abundant water resources in urban environments can make it easier for urban-inhabiting species to cope with heat stress by lowering the risk of dehydration during elevated temperatures by improving excess water reserves needed to employ evaporative cooling and effectively maintain body temperatures below lethal limits.

Using a food supplementation experiment, Tieleman and Williams (2002) explored how arid-adapted Hoopoe-larks (*Alaemon alaudipes)* optimized time allocated to thermoregulation and foraging depending on their energy reserves and hydration state. Their study showed that birds with access to additional food spent less time foraging and more time on behavioural thermoregulation and self-maintenance. Additionally, they showed that with access to additional food, the onset of behavioural thermoregulation occurred earlier, while the recommencement of foraging was delayed until prevailing temperatures were lower. Similar patterns could occur in urban environments where abundant anthropogenic food sources are available.

In this study I explore the impacts of air temperature during the austral summer on the foraging behaviour and body mass of an urban-inhabiting passerine, the Red-winged starling (*Onychognathus morio),* resident at the University of Cape Town, South Africa. The Red-winged starling is a highly opportunistic bird which takes advantage of the rich foraging opportunities available at the university campus by scavenging on human-derived food (Stofberg, et al., 2019). I explored whether the impacts of maximum daily air temperature on foraging behaviour and body condition are different between times of high human presence, which is associated with abundant anthropogenic food (i.e., weekdays during term time, hereafter 'high human presence days' or 'HHP days') and times when low human presence on campus (i.e., weekends, vacation, hereafter 'low human presence days' or 'LHP days') and anthropogenic food is therefore less abundant (Risi, et al., 2021). Using focal observations, I explored the relationship between (1) panting, (2) foraging effort and (3) food consumption rate with daily maximum temperature and their effects on (4) daily body mass change. I then, explore (5) whether these patterns differ between HHP and LHP days. I hypothesized that abundant anthropogenic foods on HHP days could buffer the effects of elevated temperatures such that the (1) onset of panting would occur earlier with access to higher water resources from some forms of anthropogenic food (e.g., apples or grapes), and (2) foraging effort would decline more rapidly with elevated temperatures as birds avoid prolonged activity under unfavourable temperature conditions. Furthermore, I predicted that any declines in (3) food consumption and (4) diurnal body mass gain with increasing temperature would be less pronounced on HHP days than LHP days.

4.2. Methods

4.2.1. Study site and population

The study took place at the main campus of the University of Cape Town (hereafter 'UCT'; 33°57'31.5''S 18°27'36.4''E). The campus is located at the periphery of Cape Town (population estimate 4.62M. inhabitants), Western Cape, South Africa, on the slopes of Table Mountain overlooking the residential areas and the city. Cape Town has a Mediterranean climate, with warm, dry summers (December-March) and cool, rainy winters (May-July). The study took place during the austral summers (January-April) of 2018 and 2019.

The study commenced after the conclusion of the breeding season of a population of resident, urban Red-winged starlings, (hereafter ‘starlings’). Starlings in this population were colour-ringed for individual identification and are habituated to close human contact which allows them to be closely observed (within 1-2m) without affecting their normal behaviour (Stofberg, et al., 2019). Since 2017, as part of a larger long-term project and prior to the commencement of this study, the birds had also been habituated to stand on a portable, top-pan, digital scale (Ohaus, New Jersey 500 x 0.1 g). This was done to monitor daily mass change in exchange for a small food reward (a raisin) (following methods used by Ridley and Raihani, 2007) (see Stofberg, *et al.,* 2019 for further details on capture, ringing and weighing).

Starlings are highly opportunistic and well-adapted to urban areas, taking advantage of the abundant nesting and food opportunities. In their natural environments they feed on fruit, seeds, nectar and invertebrates, but at UCT the resident population also forage on anthropogenic food, such as fries, apples, grapes, muffins, cheese, bread and crisps (Stofberg, et al., 2019).

4.2.2. *Temperature data (T_{max})*

Temperature data were obtained from the South African Weather Services (SAWS) from a weather station set 15m above the ground and in a location (33°93’30’’S 18°47’70’’E) approximately 3.5km from the study site. The weather station recorded maximum temperature (°C) (hereafter ‘T_{max}’) at hourly intervals throughout the study period. However, it was suspected that the study site could be cooler than the adjacent urban areas due to its higher elevation and greater vegetation cover by green space (Table Mountain National Park, and sports fields). Therefore, hourly T_{max} data were also obtained from a weather station directly located at the study site, but I was only able to obtain data from it for the first summer (2018) of the study period. I therefore calibrated these two datasets against each other for the year 2018 (Figure S3.1), then used the following linear equation $y= 0.84x + 3.3$ to convert the data obtained from SAWS station for both years to better approximate the likely T_{max} on campus.

4.2.3. *Behavioural observations: Time activity budgets*

I collected behavioural data from 100 ca 20-minute focal observations (mean ± S.D: 18 min 58 sec ± 2 min 41 sec) (hereafter 'focals') (Altmann, 1974), following methods used by Stofberg *et al.* (2019). Focals were carried out from distances of 2-3m on individually marked and habituated individuals, from 12h00 till 16h00. Focal individuals were selected by choosing the first encountered colour-ringed starling whilst walking along one of four main transects on the university campus and prioritising those from which mass recordings (see later) had been obtained that morning. I sampled two individuals per transect and two transects daily, reversing the order in which the transects were most recently sampled to randomize the focal individuals in time. All focals were recorded by a single observer using a smartphone with CyberTracker software (CybterTracker Version 3.443). I recorded six main behaviours during focals: foraging, panting, perching (while not engaging any of the other behaviours), preening, calling and flying. These behaviours were the primary activities observed during focals of starlings and all needed to be recorded to determine their respective time allocations during the twenty-minute focal observation. However, my particular focus was on investigating how the duration of foraging, food consumption rate, and the likelihood of panting was influenced by temperature. If a focal individual was lost for 2-minutes or longer during the focal (i.e., out of sight), the focal was abandoned and a new focal commenced once the bird was re-found or a new colour-ringed individual was located.

The percentage of time engaged in foraging within each focal was calculated using the total time engaged in foraging divided by the total time the individual was in sight during the focal. Panting was quantified as the presence/absence of panting behaviour within a focal. The number of beakfuls of food consumed within the focal was used as the measurement of food consumption (see Stofberg, et al., 2019 for details).

4.2.4. *Diurnal change in body mass (ΔM_b)*

Diurnal body mass of focal individuals was measured twice daily on HHP and LHP days, in the morning between 08h00-11h00 (w_1) and in the late afternoon between 16h00-18h00 (w_2) to allow diurnal change in body mass (hereafter 'ΔM_b') to be calculated. The average time between two weight measurements was 6 hours, 27 minutes. ΔM_b was calculated as a percentage change in morning body mass (w_1) divided by the time elapsed (Δt) between the morning (t_1) and late afternoon (t_2) measurements, and standardized to 6hrs using the following equation modified from du Plessis et al. (2012):

$$\Delta M_b = [100 \times \frac{w2 - w1}{w1}] / \frac{t2 - t1}{6}$$

Where t_1= time weighed prior to the start of focal observations; t_2= time weighed at the end of the day's focal observations; w_1= mass at t_1; w_2= mass at t_2.

4.2.5. *Statistical analysis*

Statistical approach: The effects of T_{max} on panting, foraging and body mass gain were investigated using mixed-effect models implemented with *lme4* (Bates et al., 2015) and *MuMIn* (Barton, 2009) within the R statistical environment version 4.0.0. (R Development Core Team, 2019). Generalized linear mixed models (GLMMs) and linear mixed models (LMMs) were fitted to behavioural and ΔM_b data. Forward stepwise model selection was used to determine those variables useful in developing regression models (see below). All models included 'bird identity' (from the colour rings) as a random term, and the continuous predictor variable (T_{max}), which was centred and scaled before model-fitting.

This study focused on behavioural trade-offs with elevated T_{max} and such relationships may be expected to be quadratic due to underlying non-linear relationships between T_{max} and physiological performance. Thus, I explored the presence of a quadratic relationship between T_{max} and each behaviour of interest (except for probability of panting – detailed below) and T_{max} and ΔM_b. Where quadratic relationships were significant, I used a break-point analysis to find the turning point of the relationship with T_{max} using the *segmented* function in package '*segmented'* (Muggeo, 2003) then, modelled the linear relationship of the variable with T_{max} values above the break point. Next, I explored the relationship between the behavioural variables and sex and excluded this predictor from the final models thereafter if non-significant. Finally, I explored the relationship between the behaviour and the interaction between T_{max} and day type (HHP and LHP), and, where the interaction was not significant, fitted T_{max} and day type (HHP and LHP) as separate additive terms. Statistical significance was taken as $P < 0.05$, with data presented as mean estimates ± standard error (SE) unless otherwise stated.

Model structures

Panting: The presence/ absence of panting during a focal was fitted using a binomial error distribution and a logit link function. Focal length (minutes the focal individual was in sight) was fitted as a weighted term.

Foraging effort: The proportion of the focal spent foraging was arcsine square root transformed to improve normality, then modelled with a Gaussian error distribution. Foraging effort models included the square-root of the focal length (minutes) as a weighted term, to account for the foraging effort being less well estimated during shorter focals.

Food consumption: The response variable was food intake rate, calculated as the number of beakfuls consumed per minute. Food intake rate was fitted with a Gaussian error distribution and with the focal length (in minutes) as a weighted term. There were three outlying data points (>three beakfuls per minute) which were excluded from the analysis.

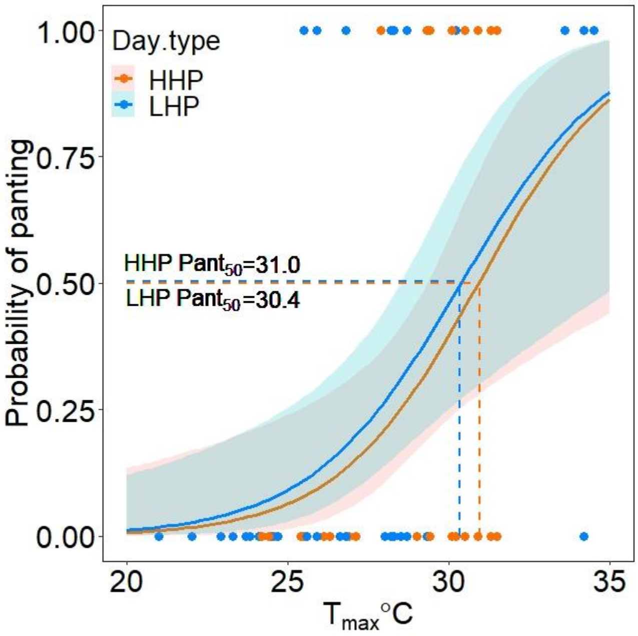
Diurnal ΔM_b: This was the mass gain over six hours in the morning before noon and expressed as a percentage of M_b. This was fitted in a linear model with a Gaussian error distribution.

4.3. Results

A total of 100 twenty-minute focals were collected from 46 known individuals (21 female and 25 male) on 50 HHP days and 50 LHP days over the course of the study.

4.3.1. *Influence of* T_{max} *on panting*

The probability of starlings panting increased with T_{max}. Starlings began panting at a T_{max} of 24.8°C and the T_{max} at which panting was present in 50% of focals (i.e., $Pant_{50}$) was 30.8°C (31.0°C for HHP days and 30.4°C for LHP days). The probability of panting did not differ with day type, nor was there an interaction between T_{max} and day status (Table 3.1a; Figure 4.1), suggesting that the increase in panting with T_{max} did not differ between HHP and LHP days.



2940

Figure 4.1: The probability of panting (heat dissipation via evaporative heat loss) with temperature (T_{max}) in urban Red-winged starlings on high human presence days (HHP: orange points, orange line) and low human presence days (LHP; blue points, blue line). Each point represents the presence (1) or absence (0) of panting of a single individual within a C. 20-minute focal. 'Pant$_{50}$' is calculated as the T_{max} at which 50% of observed individuals are displaying panting, following Smit et al., 2016. Trend lines are the logistic regressions, generated from predictions of a logistic GLMM. The interaction between day type and T_{max} was not statistically significant (Table 3.1a). Data were from 100 (50 HHP and 50 LHP focal observations collected from 45 colour-ringed urban Red-winged starlings during the non-breeding summer season in 2018 and 2019.

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4.3.2. *Influence of T_{max} on foraging effort and food intake*

There was a significant quadratic relationship between T_{max} and foraging effort (Table S3.1; Figure S3.2). The break-point analysis showed that foraging effort began to decline at T_{max} >26°± 1.15°C. There was no relationship between T_{max} and foraging effort at T_{max} cooler than 26°C (across these T_{max} birds foraged C.40% of the time). Above 26°C, there was a significant decline in foraging effort as T_{max} increased, and at 34°C starlings foraged for less than 1% of time. There was no difference in foraging effort between HHP and LHP days, nor was there any interaction between T_{max} and day status (Table 4.1b; Figure 4.2a), indicating that the rate of decline in foraging effort with T_{max} was similar between HHP and LHP days. Despite declines in foraging effort with T_{max}, starlings were able to maintain their food intake rate (Table 4.1c). Food intake rate was also not influenced by day type (Table 4.1c) nor the interaction between T_{max} and day type (Table 4.1c; Figure 4.2b).

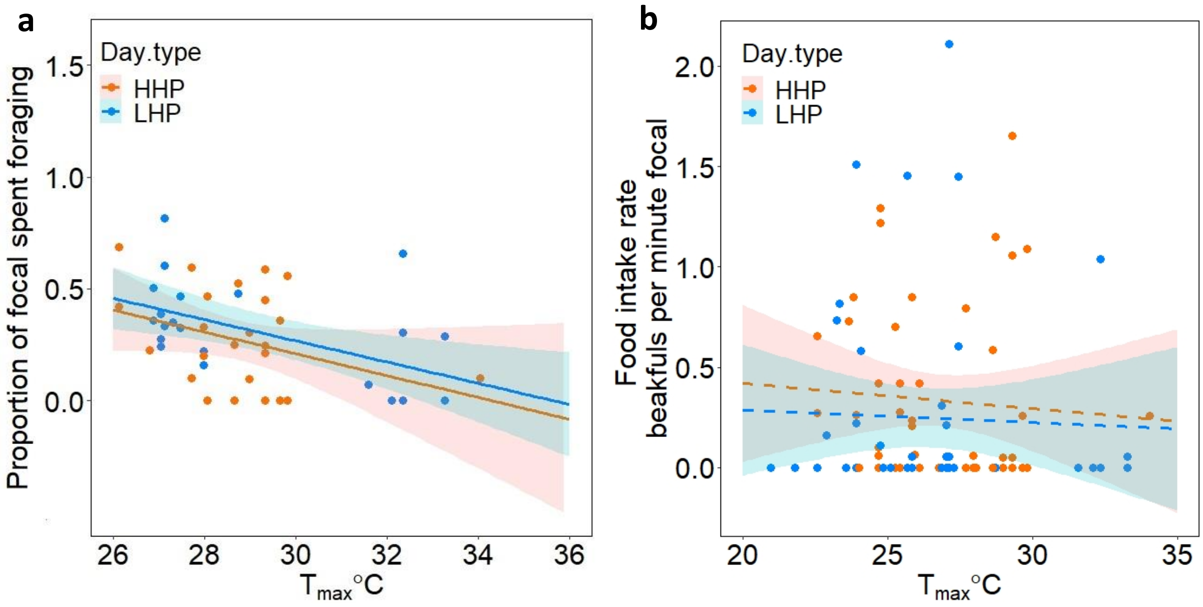

Figure 4.2: (a) The proportion of a time spent foraging and with temperature (T_{max}) by urban Red-winged starlings on HHP (orange dots, orange line) and LHP (blue dots, blue line) days. Each point represents the proportion of the focal spent focal spent foraging within a C. 20-minute focal. Trend lines are the predictions of a linear mixed model. The interaction between day type and T_{max} was not significant (Table 4.1b). Data were from 48 (25 HHP and 23 LHP) focal observations collected from 21 urban Red-winged starlings (9 female and 12 male) during the non-breeding summer season in 2018 and 2019. **(b)** The food intake rate with temperature (T_{max}) of urban Red-winged starlings on high human presence days (HHP; orange dots, orange line) and low human presence days (LHP; blue dots, blue line). Each point represents the number of beakfuls consumed within a C. 20-minute focal. Trend lines are the predictions of a linear mixed model. The dashed lines indicate a non-significant relationship with T_{max} (Table 4.1c). The interaction between day type and T_{max} was not significant (Table 1). Data were from 97 (48 HHP and 49 LHP) focal observations collected from 45 urban Red-winged starlings (21 female and 24 male) during the non-breeding summer of 2018 and 2019.

4.3.3. *Influence of T_{max} on diurnal ΔM_b*

I obtained 507 ΔM_b records, from 60 unique individuals (31 females and 29 males), 264 records collected on HHP days and 243 on LHP days. I found no relationship between T_{max} and ΔM_b with starlings able to maintain body mass despite increasing T_{max} (Table 4.1d). There was also no evidence that the relationship between ΔM_b and T_{max} differed between HHP and LHP days (Table 4.1d; Figure 4.3a). However, I detected differences in diurnal ΔM_b between day types (Table 4.1d; Figure 4.3b), with starlings experiencing a greater average ΔM_b of 2.43% ± 0.16% on HHP days compared to only 2.06% ± 0.22% on LHP days.

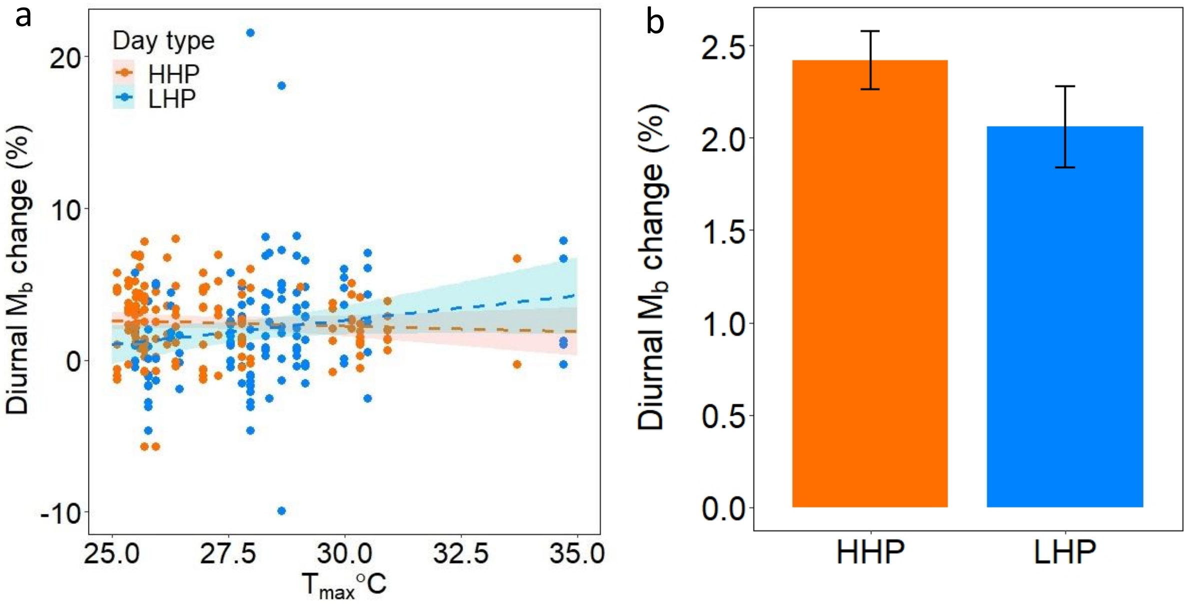

Figure 4.3: (a) Diurnal body mass change (ΔM_b) with temperature (T_{max}) of urban Red-winged starlings on high human presence days (HHP; orange dots, orange line) and low human presence days (LHP; blue dots, blue line). Each point represents a paired M_b change record over approximately C. 6 hours on a single day. The trend lines are the predictions from linear mixed models. The dashed lines indicate a non-significant relationship with T_{max} (Table 1). The interaction between day type and T_{max} was not significant (Table 1). **(b)** The mean diurnal M_b was significantly greater on HHP (orange) than on LHP days (blue) standard error bars shown. Data were from 507 paired (morning and evening) M_b change records, consisting of 264 records collected on HHP days and 243 on LHP days and from 60 starlings (31 females and 29 males). Data were during the non-breeding summer season of 2018 and 2019.

Table 4.1: Results of linear forward stepwise regression to examine the relationship of T_{max} (temperature), day type (high human presence, i.e., weekdays in term-time, HHP; vs low human presence, i.e., weekends and vacation, LHP), sex and the interaction between T_{max} and day type with behaviour and diurnal mass change (ΔM_b, %) of urban Red-winged starlings. In all cases, final models included only T_{max} and those variables that had a significant relationship with the response variable. Bird ID was included as a random term in all models, models exploring behavioural variables were weighted by square root of the focal length. Significant results are highlighted in bold.

Response variable	**Explanatory variable**	**Estimate ± S.E.**	χ^2	**df**	**n**	***P***
(a) Panting	**T_{max}**	**2.31 ± 0.32**	**50,76**	**1**	**100**	**<0.01**
	day type	-0.17 ± 0.32	0.28	1	100	0.60
	sex	0.71 ± 1.73	0.17	1	100	0.68
	T_{max}*day type	-0.01 ± 0.79	7.00	1	100	0.99
(b) Foraging effort	**T_{max}**	**-0.10 ± 0.03**	**14.48**	**1**	**48**	**<0.01**
	day type	0.03 ± 0.06	0.17	1	48	0.68
	sex	-0.04 ± 0.07	0.32	1	48	0.58
	T_{max}*day type	0.01 ± 0.07	0.01	1	48	0.94
(c) Food consumption rate	T_{max}	-0.01 ± 0.04	0.10	1	97	0.75
	day type	-0.08 ± 0.07	1.25	1	97	0.26
	sex	0.14 ± 0.15	0.82	1	97	0.36
	T_{max}*day type	0.04 ± 0.08	0.24	1	97	0.63
(d) Diurnal ΔM_b	T_{max}	0.04 ± 0.13	0.10	1	507	0.76
	day type	-0.43 ± 0.27	2.54	1	507	0.11
	sex	0.32 ± 0.43	0.54	1	507	0.46
	T_{max}*day type	0.08 ± 0.27	0.09	1	507	0.77

4.4. Discussion

In this study I explored the heat dissipation behaviours of urban-adapted Red-winged starlings and whether anthropogenic food consumption could mitigate the costs associated with thermoregulation at elevated temperatures. Starlings increased panting behaviour with temperature, while foraging effort concurrently declined. Despite lower foraging effort, starlings were still able to maintain similar overall food intake rates and body mass gain. These thermoregulatory behaviours and their associated costs did not differ between high and low human presence days likely suggesting that the overall food and water abundance in this urban environment may not differ significantly between weekends and weekdays. Although there was an indication that starlings weighed more on days with a higher abundance of anthropogenic food (HHP days), than they did on days with less anthropogenic food (LHP days) and is likely due to the consumption of more anthropogenic food on workweek days which are typically high in calories, carbohydrates, and fats (e.g., Stofberg, et al., 2019). However, the outcome regarding mass was also non-significant, which provides further support that overall food availability may not differ significantly between day types. Rather my results indicate that overall food and water abundance is abundant in this urban environment to such an extent that it buffers the costs of behavioural thermoregulation on food intake and mass gain. This finding is supported by a previous study on this population but carried out during winter, which showed no difference in the activity budgets of starlings on HHP and LHP days which was attributed to starlings not being resource-limited on LHP days (Stofberg et al., 2019). Their ability to maintain daily body mass across a range of temperatures on both HHP and LHP days could be driven by starlings maintaining food consumption rates even when foraging time was reduced under unfavourable temperature conditions – perhaps achieved by deliberately targeting larger anthropogenic food items during hot weather, at least across the range of T_{max}s sampled in this study.

4.4.1. *Buffering of evaporative water loss in urban environments*

I expected starlings to have lower access to water-rich food (e.g., grapes and apples) on LHP days and thus to exhibit lower rates of evaporative heat dissipation. Instead, the onset of panting was not significantly different between HHP and LHP days. Like other passerines, starlings in this system were increasingly reliant on evaporative heat dissipation (i.e., panting) to offset excess heat as temperatures increased (Bartholomew, et al., 1962; Bartholomew, et al., 1968; Dawson, 1982).

Starlings in this system started panting at a relatively low temperature of 25°C compared to that of other passerines studied in natural environments (temperatures in the mid-30s°C reported for arid-adapted birds in natural environments, where baseline temperatures are hotter than in Cape Town (du Plessis, et al., 2012; Cunningham, et al., 2015; Smit, et al., 2018). The only other study to investigate behavioural thermoregulation of birds in an urban environment was Edwards et al. (2015), who found that Western Australian magpies (*Cracticus tibicen dorsalis*) started panting at a temperature of 27°C, not dissimilar to the threshold seen in this study system.

Evaporative heat dissipation is physiologically costly in terms of water use (Dawson, 1954; Speakman & Król, 2010; Smit, et al., 2016) and birds may delay the onset of panting when dehydrated or when access to water reserves is limited such as in arid environments (Czenze, et al., 2020; Pattinson, et al., 2020; Tieleman & Williams, 1999). Water reserves are strongly influenced by diet (Czenze, et al., 2020) therefore, the early commencement of panting observed by passerines in this study suggests that they can afford elevated rates of evaporative water loss without the increased risk of dehydration (Smit & McKechnie, 2015; Czenze, et al., 2020; Pattinson, et al., 2020). Starlings at UCT can predictability replenish their water reserves through drinking as they have access to abundant man-made surface water sources such as drains, fountains, taps and pipes, gutters and rain sumps. Furthermore, the earlier onset of panting at lower temperatures is generally predicted for species that actively drink water as opposed to non-drinking species which rely solely on dietary and metabolic water (Smit, et al., 2016; Smit & McKechnie, 2015). Non-drinking species and rural conspecifics may in contrast be under stronger selection pressure to conserve water, as the risk of dehydration may be higher (Czenze, et al., 2020).

4.4.2. *Influence of temperature on foraging effort*

The suppression of foraging activity with increasing temperature observed in this system is in keeping with multiple other studies on other birds in both arid and mesic environments (Ricklefs & Hainsworth, 1968; Tieleman & Williams, 2002; Carmi-Winkler, et al., 1987; Clark, 1987). Increased activity increases metabolic heat production (Wolf, 2000; Smit, et al., 2016) thereby exacerbating the risk of hyperthermia when foraging under elevated temperatures (Carmi-Winkler, et al., 1987; Wolf, 2000). However, nutrition status plays an important role in the trade-off between foraging with temperature (Tieleman & Williams, 2002). Access to supplementary food allows for the earlier suppression of activity to avoid prevailing high temperatures (Tieleman & Williams, 2002). In urban environments where food resources are relatively more abundant (Schoech & Bowman, 2003;

Shochat, 2004; Anderies, et al., 2007), birds may therefore be able to afford an early suppression of foraging activity at minimal cost.

Research has shown that birds typically use thermally-buffered microsites to reduce the physiological costs associated with evaporative cooling (water expenditure) and prevent dehydration when exposed to elevated temperatures (Carroll, et al., 2015; Martin, et al., 2015; Scheffers, et al., 2014). These behavioural responses, like shade-use, typically occur as an initial response, at lower ambient temperatures to delay or avoid panting (Smit, et al., 2016; Maloney & Dawson, 1998; Wolf, et al., 1996). While urban landscapes may offer shaded areas that can help urban species to cope with extreme temperatures and continue foraging (Ackley, et al., 2015), it is unlikely from a physiological perspective that starlings use panting at earlier (lower) temperatures and rely more on behavioural means of thermoregulation later, at much higher temperatures. Furthermore, given the increased availability of surface water and lower risk of dehydration in urban areas, the conservation of water reserves may be less important (Dawson, 1954).

4.4.3. *Influence of temperature on food intake*

In this study, starlings managed to maintain foraging intake and body mass during hot days, despite reduced foraging activity and increased panting behaviour which are both associated with an inability to maintain body mass (du Plessis, et al., 2012; Van de Ven, et al., 2019). Additionally, prevailing temperatures do not only influence the behaviour of the forager but may also affect the behaviour and distribution of their ‘prey’. This may be the case for insectivores in natural environments, which may suffer reduced intake rates on hotter days due to arthropod prey being less active or burrowing into the soil during hot weather conditions (e.g., du Plessis et al., 2012, can de Ven, 2019). For species which exploit anthropogenic food sources, no such pattern would necessarily be expected as anthropogenic food remain equally available, regardless of temperature (Schoech & Bowman, 2003; Anderies, et al., 2007; Bateman & Fleming, 2012; Oro, et al., 2013). Indeed, I have observed Red-winged starlings on campus foraging close to eating students waiting opportunistically for any dropped food items or for the opportunity to snatch food from those passing by. As students also seek shade during hot periods, starlings may track the movements of students which would allow them to simultaneously escape prevailing temperature conditions whilst maximizing, and thus maintaining, their food consumption. This is in contrast to studies of birds in natural environments, where shade-seeking can result in a reduction in food intake rate as birds move away from optimal foraging locations (e.g., Shochat, 2004; Cunningham, et al., 2015; van de Ven, et al., 2019).

4.4.4. *Influence of temperature on diurnal mass gain*

Within this study system, food abundance was apparently sufficient to allow starlings to maintain food intake rates and mitigate potential costs of behavioural thermoregulation on body mass. Thermoregulation requires the use of energy which could otherwise be invested in body maintenance, as well as expenditure of water which can cause mass loss via dehydration (Speakman and Król, 2010). Therefore, the ability of starlings to maintain body mass despite increasing temperature suggests that their daily food and water intake exceeded that expended on thermoregulation (Tieleman & Williams, 2002). However, I found evidence that mass gain was affected by day status and associated anthropogenic food abundance. The rates of mass gain on LHP days were lower than on HHP days, regardless of temperature. Given that foraging effort and food intake rate were similar on both day types, this suggests that diet quality may be different on HHP and LHP days. Evidence for this suggestion stems from a previous study done on this population of starlings, where starlings feed primarily on anthropogenic food on HHP days while switching to consume natural food items such as fruit and insects on LHP days (see Stofberg et al., 2019 and Catto, 2018). Reduced mass gain on LHP days could therefore be due to the consumption of foods with a lower calorific content, or with lower carbohydrate and fat content than that being consumed on HHP days.

Conclusion

My results suggest that although starlings in this urban system increase panting and reduce foraging activity in response to increasing temperatures, they do not appear to pay costs in terms of their ability to maintain body mass. This applies at least during the non-breeding season and within the current range of temperatures observed. My results suggest that abundant urban food resources might buffer birds from the adverse effects of elevated temperature, by allowing them to reduce foraging effort under unfavourable temperature conditions while maintaining food intake rate. Urban-inhabiting birds may therefore be less threatened by adverse effects of climate warming compared to birds in natural areas where food and water resources are often more limiting. Given the effect of urban cover (built-up area) on the surrounding heat environment (e.g., heat island effect), future research should focus on investigating thermoregulatory responses and associated costs for birds inhabiting urban environments with different levels of urban cover, for example, if the heat island effect in larger cities, more heavily built-up areas or urban areas with different levels of connectivity of remnant vegetation could decrease the advantage that urban food resources offer to birds on hot days. Additionally, future studies could compare thermoregulatory behaviours and their associated costs between species with varying degrees of dependence on anthropogenic food (e.g., urban-adapted (non-dependent) versus urban-exploiting (dependent) species)).

4.5. Acknowledgements

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4.7. Supplementary material

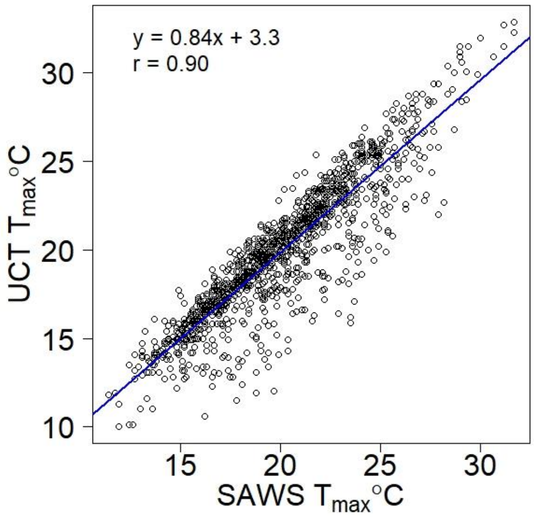

Figure 3.1: The linear regression (blue line) for the correlation between maximum temperatures (T_{max}) at the university of Cape Town (UCT) and T_{max} obtained from a South African weather station (SAWS) located in district Observatory, during the summer of 2018. The two locations are approximately 4.0 km apart. The equation of the line is shown together with the Spearman's rank correlation coefficient (r). T_{max} were highly correlated (r = 0.90) however, T_{max} at UCT were lower than Observatory. The equation 'y= 0.84x + 3.3' was used to estimate the T_{max} at UCT for the summer of 2019 as I was unable to obtain the local T_{max} data for that specific period.

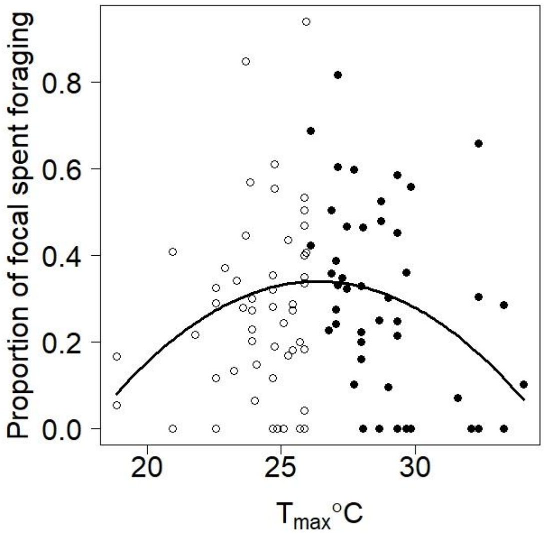

Figure S3.2: The proportion of a focal spent foraging as a function of maximum temperature (T_{max}) during the summer of 2018 and 2019 by urban Red-winged starlings. Each point represents the proportion of time an observed individual spent foraging within a 20-minute focal. The solid trend line represents the predictions from the quadratic relationship between foraging effort and T_{max}. The white points show the distribution of data for T_{max} <26°C where foraging effort is positively associated with T_{max}. The black points show the distribution of data for T_{max} >26°C where foraging effort is negatively associated with T_{max} and the portion of the data used to model the linear relationship between foraging effort and T_{max}

Table S3.1: The **r**esults from each model output exploring the quadratic relationship between temperature (T_{max}) and behavioural variables (except the model exploring the presence/absence of panting) and diurnal body mass change (ΔM_b). Significant results are highlighted in bold.

Response variable	estimate ± s.e.	χ^2	*ndf*	*ddf*	*t*	*n*	*P*
Foraging effort~	**-0.01 ± 0.00**	**10.56**	**67.39**	**1**	**-3.25**	**100**	**<0.001**
Food intake rate	-0.00 ± 0.00	0.81	51.33	1	-0.90	97	0.37
ΔM_b	0.01 ± 0.01	2.30	486.98	1	1.52	507	0.13

CHAPTER 5

An experimental test of the effects of anthropogenic ‘junk-food’ on adults and nestlings in an African urban passerine

Source: Author

Abstract

Abundant anthropogenic food together with natural food scarcity drastically alters the food quality available to urban species. At the same time, within urban settings, a healthy diet could hold particular importance, especially for species with lower tolerance to urban conditions. However, the physiological effects of anthropogenic food consumption might differ significantly between life stages and might be specifically detrimental during early life. I investigated experimentally how the quality of anthropogenic food affects the behaviour and daily body mass change of breeding adult birds, as well as the fatty acid (FA) physiology and the condition of their young. In this study, I supplemented Red-winged starlings (*Onychognathus morio)* with either a "processed" (cheese and crisps) or an "unprocessed" (mealworms and apple) diet. Using focal observations, I tested treatment effects on (1) foraging and provisioning behaviour and (2) body mass change of individually marked adults. Furthermore, I tested treatment effects on (3) the relative FA proportions in the blood plasma of nestlings, and (4) their morphology (body mass and skeletal size). The results showed no difference in adult behaviour and body mass change with diet treatment. The blood plasma of nestlings assigned to a processed diet was significantly higher in saturated FAs but lower in unsaturated fatty acids (overall polyunsaturated FAs and ω-6 polyunsaturated FAs) relative to those assigned to the unprocessed diet. However, diet quality had no effect on nestling morphology. This study offers some support for the hypothesis that anthropogenic food is tolerable by adult birds but may be detrimental for their nestlings given its effect on plasma FAs and their involvement in physiological functioning.

5.1. Introduction

Urbanization is one of the most irreversible forms of land-use change, typically leading to the loss of natural vegetation and associated natural food abundance (Meyrier, et al., 2017; McIntyre, et al., 2001). Additionally, the remaining natural food choices are often of lower nutritional quality than those in rural areas (Seress & Liker, 2015). This means that species breeding in urban environments may experience a mismatch between the availability of high-quality preferred food and reproduction when the demand for such food is high. To compensate for shortages of preferred foods in urban habitats, individuals might increase their search efforts for suitable foods (Jarrett, et al., 2020; Tremblay, et al., 2005; Isaksson & Andersson, 2007). Additionally, species that opportunistically make use of anthropogenic food sources may shift to provisioning anthropogenic food (Shawkey, et al., 2004; Mennechez & Clergeau, 2006), especially as their young grow and their energy demands increase. Urban environments typically contain large amounts of easily accessible anthropogenic foods (e.g., intentionally provided bird feeders but also unintentional through garbage bins and food scraps (Jones & Reynolds, 2008).

Another characteristic of urban environments is short-term fluctuations in food availability, following a weekly cycle of pulsing human activity and associated anthropogenic food (Stofberg, et al., 2019; Catto, et al., 2021; Risi, et al., 2021). This pattern is also described as the 'weekend effect' which describes how people living in urban areas use weekends and holidays to spend time in nature, resulting in temporary increases in recreational activities in natural areas (Barrueto, et al., 2014) and, in contrast, empty urban centres (Diniz, et al., 2021). Short-term changes in foraging behaviour following such weekly cycles have been observed for a range of urban species, for example higher anthropogenic food consumption (Stofberg, et al., 2019) and greater daily body mass gain (Catto, et al., 2021) during week days compared to weekends, or in foraging behaviour matching human time schedules (Spelt, et al., 2020).

Birds are one of most well-studied species inhabiting urban environments and are well-known for consuming anthropogenic food. However, while anthropogenic foods might be suitable for adults they may be detrimental for the health and development of their young (Isaksson & Andersson, 2007; Heiss, et al., 2009; Chamberlain, et al., 2009). Compared to natural foods, anthropogenic food is typically higher in carbohydrates, fat, and cholesterol (Coogan, et al., 2018; Townsend, et al., 2019) and lower in protein (Murray, et al., 2015; Heiss, et al., 2009). It is therefore not surprising that slower growth, poorer body condition, and increased mortality have been reported for nestlings in urban areas, and largely attributed to the consumption of anthropogenic food (Chamberlain, et al., 2009; Pollock, et al., 2017; Meillère, et al., 2015).

One of the most important nutritional aspects that differ between natural and anthropogenic foods is the composition of fatty acids (Andersson, et al., 2015; Isaksson, 2015). Fatty acids are organic compounds that serve as metabolic fuel and are involved in a range of physiological processes including controlling cell-membrane fluidity (Hazel, 1995), oxidative stress balance, thermoregulation, and immune function (Hulbert & Abbott, 2012; Ben-Hamo, et al., 2011; Hazel, 1995; Calder, 2007). There are four main classes of fatty acids, and they are categorized based on their chemical structure and properties, these are, saturated fatty acids ('SFAs'), mono-unsaturated fatty acids ('MUFAs'), omega-3 polyunsaturated fatty acids ('ω-3 PUFAs') and omega-6 polyunsaturated fatty acids ('ω-6 PUFAs'). SFAs and MUFAs can be biosynthesized or obtained from dietary sources, such as processed anthropogenic foods which are typically rich in SFAs (Jew, et al., 2009) while seeds and nuts contains high levels of MUFAs (Andersson, et al., 2015; Becker, 2008). In contrast, ω-3, and ω-6 PUFAs are obtained strictly through dietary intake (Uscian & Stanley-Samuelson., 1994), ω-3 PUFAs are obtained from green leaves and insects (Andersson, et al., 2015) and like MUFAs, ω-6 PUFAs are also obtained from seeds (Andersson, et al., 2015; Becker, 2008).

Fatty acids are essential for animals throughout their lives but are particularly crucial during early life stages, when tissues and organs grow and develop (Sanders, 1988; Maldjian, et al., 1996). For example, the importance of an adequate intake of ω-3 PUFAs for the development of growing embryos has been demonstrated in several studies (Neuringer, et al., 1988; Speake & Wood, 2005; Andersson, et al., 2015; Ben-Hamo, et al., 2011; Pierce, et al., 2005). Additionally, fatty acids play an important role on bird's health, and studies on birds inhabiting urban environments have stressed the importance of maintaining an adequate balance of ω-3 and ω-6 PUFAs given their opposing effects on inflammatory responses and oxidative stress balance (Isaksson, 2015; Romieu, et al., 2008). More specifically, a high intake of ω-6 PUFAs relative to ω-3 PUFAs, due to an unbalanced diet of these fatty acids, is associated with increased oxidative stress, heightened sensitivity to antigens resulting in increased inflammatory responses (Brown, 2016; Calder, 2009). Furthermore, concerning developmental aspects, the significance of a diet rich in ω-3 PUFAs has been demonstrated to play a crucial role in promoting health and supporting growth during the early stages of development (Twining, et al., 2016; Twining, et al., 2018).

Given that a considerable number of species exploit anthropogenic food, it is therefore important to understand the implications of anthropogenic food consumption by young animals given its potential to affect fatty acid physiology and development. Additionally, investigating the effects of nutritional conditions during early life are important given their potential long-term consequences for phenotypic development, survival and reproductive behaviour in adulthood (Hopwood, et al., 2014; Lindström, 1999; Metcalfe & Monaghan, 2001).

In this study, I conducted a supplementary feeding experiment in which I manipulated the type of food available to pairs of Red-winged starlings (*Onychognathus morio*) that breed in Cape Town, South Africa. The Red-winged starling is a suitable study species for this experiment as it excessively exploits anthropogenic food (up to 80% of the daily food intake in this population), specifically during weekdays in urban areas when human presence and associated anthropogenic food abundance is high (Stofberg, et al., 2019; Risi, et al., 2021). During the breeding season at this study site, the proportion of anthropogenic food provisioned to nestlings was higher on days with high human presence (when nestling diet was composed of up to 40% anthropogenic food) compared to days with low human presence (weekends and vacation days) (Catto, et al., 2021). Furthermore, nestlings which experienced a greater number of high human presence days between hatching and ringing age (days 15-18) were lighter and smaller than those which experienced fewer high human presence days (Catto, et al., 2021), suggesting that a high proportion of anthropogenic food in the nestling diets may have negative effects on their growth.

For this study Red-winged starling pairs with dependent nestlings were hand-fed with either processed food (corn-based snacks and processed cheese) or unprocessed food (mealworms and apple: mimicking the natural fruit-and-insect diet of this species (Chittenden, et al., 2016)) . Another control group did not receive any supplement. I then explored whether the supplementary diet influenced the breeding adults' (1) behaviour and (2) diurnal body mass change, or nestlings' (3) physiology (relative fatty acid proportions) or (4) morphology at ringing age. Based on previous findings, the overall hypothesis was that processed food might be advantageous for adults during the chick-rearing period but detrimental for nestlings. I predicted that adults would prioritize the health and development of their nestlings such that they would provision unprocessed foods to their nestlings, and that this effect might be amplified by weekly cycles.

Predictions for effects of food supplementation on adult starlings:

1. *Allocation of supplementary food to nestlings during supplementation:* experimental evidence suggests that urban birds can discriminate between the quality of natural and food sources and tend to exhibit a preference for high-quality food when provisioning their

nestlings (Støstad, et al., 2017; Sauter, et al., 2006). I hypothesized that because adults would prioritize the health and development of their nestlings, pairs from nests supplemented with processed food ('$\mathrm{PF}_{\mathrm{NESTS}}$') would allocate less of this to their nestlings compared to pairs from nests supplemented with unprocessed food ('$\mathrm{UF}_{\mathrm{NESTS}}$').

2. *Adult provisioning behaviour:* urban birds have been shown to work harder through flying further than rural birds to offset the limit availability of high-quality food for nestlings in urban environments (Jarrett, et al., 2020). I therefore predicted that pairs from $\mathrm{PF}_{\mathrm{NESTS}}$ would exhibit higher provisioning rates during focal observations (after food supplementation) than $\mathrm{UF}_{\mathrm{NESTS}}$ and individuals assigned as controls ('$\mathrm{CTRL}_{\mathrm{NESTS}}$') to make up for reduced availability of good-quality food sources. I also predicted that individuals from $\mathrm{CTRL}_{\mathrm{NESTS}}$ would show higher provisioning rates than supplemented groups because of lower overall food supply throughout the day (i.e., no supplement) under the assumption of that food is limiting during the nestling rearing period on urban birds' (Seress, et al., 2020).
3. *Adult foraging activity:* Processed food typically contains more calories, carbohydrates and fat (Bateman & Fleming, 2012; Ottoni, et al., 2009; Townsend, et al., 2019) than natural food and therefore may allow an individual to meet their metabolic demands sooner than when consuming natural food. Under this assumption, I predicted that individuals from $\mathrm{PF}_{\mathrm{NESTS}}$ would exhibit shorter foraging bouts and consumption rates than individuals from $\mathrm{UF}_{\mathrm{NESTS}}$ and $\mathrm{CTRL}_{\mathrm{NESTS.}}$ Again, I expected individuals from $\mathrm{CTRL}_{\mathrm{NESTS}}$ to exhibit longer foraging bouts and higher consumption rates than supplemented groups due to non-supplementation.
4. *Adult preening and perching during focals:* As a consequence of decreased foraging activity, I predicted that individuals from $\mathrm{PF}_{\mathrm{NEST}}$ would have more time to devote to preening and perching than individuals from $\mathrm{UF}_{\mathrm{NESTS}}$ and $\mathrm{CTRL}_{\mathrm{NESTS}}$. Individuals from $\mathrm{CTRL}_{\mathrm{NESTS}}$ would have the least time to devote to preening and perching versus supplemented groups.
5. *Adult diurnal mass change (ΔM_b):* I predicted that individuals from $\mathrm{PF}_{\mathrm{NESTS}}$ would exhibit larger ΔM_b compared to individuals from $\mathrm{UF}_{\mathrm{NESTS}}$ and $\mathrm{CTRL}_{\mathrm{NESTS.}}$ This expectation is based on the possibility that individuals from $\mathrm{PF}_{\mathrm{NESTS}}$ would reach satiation more often through food supplementation or from due to the calorie-richness of processed food (Bateman & Fleming, 2012; Ottoni, et al., 2009). Due to food supplementation, I expected $\mathrm{UF}_{\mathrm{NESTS}}$ to exhibit larger ΔM_b compared to individuals from $\mathrm{CTRL}_{\mathrm{NESTS}}$.

<u>Predictions for effects of food supplementation on nestlings:</u>

6. *Nestling plasma fatty acid ('FA') relative percentages:* despite differences in the amount of the supplement pairs from different treatment allocate to their nestlings (prediction 1), I

expect that at ringing age, the FA signature of the respective treatments to still be represented in the blood plasma of nestlings. Previous research has demonstrated that anthropogenic foods can influence the physiological parameters of birds (Herrera-Dueñas, et al., 2018; Townsend, et al., 2019). Therefore, predict that differences in the quality of processed versus unprocessed would also manifest in fatty acid physiology of nestling. I predict such changes would also materialize in fatty acid physiology an important component of health. I predicted that nestlings from PF_{NESTS} would have a higher relative percentage of SFAs as processed food is typically rich in, followed by nestlings from $CTRL_{NESTS}$ of similar age, and that nestlings from UF_{NESTS} would show the lowest percentage of SFAs. In terms of unsaturated fatty acids: mono-unsaturated (MUFAs), ω-6 PUFAs, ω-3 PUFAs and the ω-6/ω-3 PUFA ratio, I expected these to be higher in nestlings from UF_{NESTS} as they typically higher in unprocessed foods such as seeds as nuts in the case of MUFAs and ω-3 PUFAs, and invertebrates and green leaves in the case of ω-3 PUFAs, followed by nestlings from $CTRL_{NESTS}$ of similar age, and that nestlings from PF_{NESTS} would show lower relative percentage of these FAs.

7. *Nestling morphology:* prior research suggests that anthropogenic food consumption may be detrimental for the development on nestlings (Chamberlain, et al., 2009; Catto, et al., 2021; Auman, et al., 2008; Heiss, et al., 2009) therefore, I predicted that due to supplementation with lower quality processed food, nestlings from PF_{NESTS} would have smaller skeletal measurements (head, bill, wing, tarsus and tail length) and lower body mass, followed by nestlings from $CTRL_{NESTS}$ of similar age, and that nestlings from UF_{NESTS} would be in better condition and thus have the largest morphological measurements.

5.2. Methods

5.2.1. Study site and species

The experiment was carried out on a breeding population of urban Red-winged starlings, at the University of Cape Town upper campus (hereafter "UCT": 33° 57' 31.5'' S 18° 27'' 36.4'' E). Breeding in this population occurs in the austral spring (October – December) (du Plessis, 2005; Craig, 2005). This species is a frequent double brooder, and to avoid any potential confounding effects of first and second broods in the analysis, the experiment was carried out exclusively during the first broods of 2018 and 2019. UCT is located in a suburban area on the slopes of Table Mountain at the periphery of Cape Town. Red-winged starlings (hereafter "starlings") are native, medium-sized passerines (~

130g), with a widespread African distribution (Craig, 2005). At UCT, starlings forage and breed within predictable home ranges (Risi, et al., 2021). They are omnivorous birds but commonly consume anthropogenic food discards in urban areas (Stofberg, et al., 2019; Catto, et al., 2021). Nesting sites at UCT include windowsills, rain sumps, air-conditioning vents and the sheltered pillars and arches of buildings.

Birds in this study population have been colour ringed for individual identification since 2017 and have also been habituated to a portable, top-pan, digital scale (Ohaus, New Jersey 500 x 0.1 g) to monitor daily mass change (following methods used by Ridley & Raihani, 2007) as part of a larger study (see Stofberg et al., 2019 for further details on capture, ringing and weighing). They are also highly habituated to close human contact, allowing them to be observed within 1-2m without affecting their normal behaviour (Stofberg, et al., 2019).

5.2.2. Nest monitoring and treatment allocation

Nests were located by watching breeding pairs carrying building materials and nests were subsequently monitored until fledging of the first broods of the season. Experimental treatments were assigned to nests that were accessible (i.e., that could be reached with a 9m ladder) and where at least one parent was colour-ringed. This ensured that I could obtain blood samples from nestlings before they fledged and monitor the behaviour of known adults. I randomly assigned the first hatched nest within this group to either a ‘unprocessed food’ (‘UF_{NESTS}’) or ‘processed food’ treatment (‘PF_{NESTS}) (*see Supplementary feeding below*). Thereafter I allocated each subsequently hatched nest alternating between both treatments thereby ensuring similar sample sizes for each treatment and avoiding treatment type being confounded with timing of breeding. On two occasions, neighbouring pairs stole supplemented food during food supplementation, and therefore were assigned to that same treatment.

Nests that were inaccessible (e.g., those too high or too unstable to be reached) but that had at least one colour-ringed adult were assigned to a control group ($\text{CTRL}_{\text{NESTS}}$) for adult behavioural observations but were not included in the analysis of nestling FA percentages or morphology. Nests that were accessible, but from which neither parent was colour-ringed, were assigned to $\text{CTRL}_{\text{NESTS}}$ for nestling blood samples and morphometric data collection, since I could not identify adults for behavioural observation.

5.2.3. Supplementary feeding

Supplementary feeding commenced when the first egg of the brood hatched, and all pairs were fed until morphological data and blood samples were collected from nestlings 16 ± 1 days old. A maximum of ten active nests were fed at a time. When new nests hatched, I stopped feeding the oldest nests if I had already obtained blood samples from the nestlings (i.e., if they were older than 16 ± 1 days). All pairs were fed twice every day: one feeding in the morning between 08h00 and 11h00, and another in the afternoon between 13h00 and 15h00. Pairs were fed *ad-libitum* by hand for 15-minutes, within 1m (horizontal distance – nests were up to 20m high) of their nest location to reduce the incidence of neighbouring birds stealing supplemental food items. I selected a 15-minute feeding duration to efficiently feed up to 10 active nests a day within the 3-hour window in the morning (8h00-11h00), factoring in a 3-minute walk between nests.

PF_{NESTS} were fed pre-grated processed cheddar cheese and $1cm^3$ pieces of cheese flavoured corn snacks (Nik-Naks brand manufactured by Simba, hereafter "corn snacks"). The processed diet was designed after an observational study on the same population which showed that these food items were frequently consumed (Stofberg, et al., 2019). UF_{NESTS} were fed mealworms (*Tenebrio molitor*) and $1cm^3$ pieces of apple.

When feeding, I presented each pair with one to three pieces of the food items of their assigned treatment, alternating between each of the two food items (within treatment). Both the male and female parent were fed as far as possible. When individuals were not interested in a food item, the item was left on the ground and I fed them a piece of the other food item in their assigned treatment. When individuals showed interest in the abandoned food item, the alternating between the presentation of the two food items was resumed. At each feeding event *Cybertracker* software (http://www.cybertracker.org/) was used to record the food item and the fate of the food item (loaded to provision nestlings versus eaten by the adult directly). Food items lost or stolen were also recorded. Foods were weighed before and after supplementation to measure the mass of each food item taken. The perishable food items were refrigerated between supplementation and were replenished when they were spoilt.

5.2.4. Adult focal behavioural observations

Focal observations ('focals') were carried out on colour-ringed adults from experimentally fed nests and colour-ringed controls. Focal data were collected from the date of hatch until the nestlings were blood-sampled. The methods for focal data collection are described in full detail in Stofberg et al., (2019). In brief, I observed colour-ringed adults for 20 minutes at a time, recording behaviours: foraging, perching, preening and others, as well as provisioning rates (number of nest visits). If an individual was lost, it was recorded as "out of sight", and the focal continued until the required 20 minutes were reached once the bird was found again. However, the search for the bird was abandoned after five minutes if I was unsuccessful in relocating it, in which case the focal attempt was stopped. I collected focal data in a balanced manner, ensuring that observations were made during each week of the nestling period for each sex and each treatment group. I also balanced samples between high human presence (weekdays in term time, hereafter 'HHP' days) and low human presence (weekends and vacation days, hereafter 'LHP' days) on campus (*see Table S4.1*).

5.2.5. Adult diurnal body mass change (ΔM_b)

Adult mass data were collected from both supplemented pairs and from colour-ringed control pairs, between the date the nestlings hatched until they were blood-sampled at day 16 ± 1 day. Diurnal body mass of focal individuals was measured twice daily on HHP and LHP days, in the morning between 08h00-11h00 (w_1) and in the late afternoon between 16h00-18h00 (w_2). The average time between the two mass measurements was six hours. Diurnal body mass change (ΔM_b) was calculated as the percentage change between the morning body mass (w_1) and the afternoon body mass (w_2) divided by the time elapsed (Δt) between the morning (t_1) and late afternoon (t_2) measurements using the following equation modified from du Plessis et al. (2012):

$$\Delta M_b = [100 \times \frac{w2 - w1}{w1}] / \frac{t2 - t1}{6}$$

Where t_1= time when weighed in the morning; t_2= time when weighed in the late afternoon; w_1= mass at t_1; w_2= mass at t_2.

5.2.6. Fatty acid extraction for diet treatments and nestling blood plasma

Blood samples were only taken from nestlings sampled in the first year of the study. The extraction of FAs from the blood samples followed the protocol by Andersson et al. (2018), using 5µl of plasma. The lipids were extracted for one hour at room temperature using 50µl chloroform:methanol (2:1 v/v) which contained 1.67µg/µl methyl cis-10-heptadecenoate (>99% pure Aldrich) as an internal standard. The solvent was evaporated using a stream of N_2 before base methanolysis, where the FAs are transformed into FA methyl esters using 100µl KOH/methanol (0.5 mol l−1) at 40°C. After one hour the samples were neutralized and the reaction was terminated using 100µl HCl/methanol (0.5 mol l−1) and resulting FA methyl esters were extracted by adding 300µl re-distilled n-hexane. The samples were cleaned and dried by washing with deionized H_2O and using anhydrous sodium sulphate respectively. The final samples were analysed using an Agilent 6890 GC equipped with an HP-88 capillary column ([88% cyanopropyl] aryl-polysiloxane; 30m, 0.25mm id, df 0.25µm; Agilent) and an Agilent 5975 mass spectrometry detector. The carrier gas used was helium (flow: 1ml min^{-1}) and the temperature programme was 80°C for 1 min which was increased by 10°C min−1 until reaching the maximum temperature of 230°C and held there for 20 minutes. The chromatograms were quantified in Agilent ChemStation software. The FA methyl esters were identified by comparing retention times and mass spectra of known synthetic standards from Sigma-Aldrich.

A total of 20 FAs were identified and quantified through their methyl ester derivatives. The proportion of each FA per individual was calculated by dividing the peak area with the sum of all FA peak areas. These proportions were then logit transformed (log ($\frac{a1}{1-y}$)) prior to analysis (Warton & Hui, 2011). FAs with a relative percentage of <1% were excluded from further analyses.

5.2.7. Nestling morphology

When nestlings reached 16 ± 1 days old they were ringed with one uniquely numbered metal ring (SAFRING) and one plastic alphanumeric ring, measured head and tail length (to the nearest 1mm), and the length of each tarsus (to the nearest 0.1mm) and each wing (to the nearest 1mm) and weighed them on a top-pan balance (Ohaus, New Jersey 500 x 0.1 g). A blood sample (~ 300 µl) was also taken from the brachial vein using 27-gauge ½-inch needles and heparinized capillary tubes. Directly after blood collection, red blood cells and plasma were separated by centrifuging on site (10,000 rpm/20 min) and samples were stored at -80°C until processing. Nestlings were ringed, measured, weighed and bled approximately between 08h00 and 09h00 near the nest location, just after the nests were supplemented.

5.2.8. Statistical analysis

All analyses were performed using the statistical software R (v.4.1.2, R Core Team 2021). Initial models with all variables of interest were fitted, after which backward-stepwise model selection was performed. Final models included only treatment as the main term of interest and any terms with P <0.05 (supplementary material Table S4.3-S4.21). Where significant results were found in the final model, post-hoc *Tukey* Honestly Significantly Different comparisons were performed to establish pairwise differences between factor levels. Statistical significance was taken as P< 0.05 and data are presented as mean estimates ± standard errors (SE).

Supplementary feeding: amount of supplemented food taken between treatments

To explore if there was a difference in the amount of food taken between treatments, the mass of food taken by the pair (g) during food supplementation was fitted as the response variable in a linear mixed model with a *gaussian* error distribution. The initial model included feeding time (morning or afternoon), day status (HHP versus LHP day) and year category (2018 versus 2019) as fixed terms and the interaction between treatment and nest age (one to four weeks old) and the interaction between treatment and brood size (one to three nestlings). Nest identity was fitted as a random term to control for repeated measures taken on the same pair assigned to different treatments.

Supplementary feeding: amount of supplemented food consumed versus provisioned

To explore if there was a difference in the amount of supplemented food adults in each treatment allocated to nestlings, the number of food items provisioned to the nest versus consumed by each adult during supplementation was fitted with the column bind (*cbind*) syntax as a response variable and with a *binomial* error distribution. The initial model included feeding time, day status and year category as fixed effects and, the interaction between treatment and nest age, the interaction between treatment and brood size and the interaction between treatment and adult sex. Bird identity was fitted as a random term to control for repeated measures taken on the same pair and to control for the same pair being assigned to different treatments between years. To correct for overdispersion, the row number of the data was fitted as a random effect following (Harrison, 2014) and each row contained data for a single individual. The *Bobyga* optimizer model in R-package *lme4* (Bates, et al., 2015) was used to solve convergence issues.

Adult focal behaviour

The length of a focal was taken as the time the observer was able to keep the focal individual in sight. The proportion of the focal spent foraging, perching, and preening were fitted as the response variable in separate models to explore if they differed between treatments. In each model the response was arcsine square-root transformed to improve normality and fitted with a *gaussian* error distribution. Initial models were fitted with adult sex, day status, and year category as fixed effects and the interaction between treatment and nest age. In these models, brood size was not fitted because the analysed data included the control group (i.e., nests were inaccessible and brood sizes were thus unknown). Models included bird identity as a random term to account for repeated measures taken on the same individual and were weighted by the square-root of the duration of the focal (minutes) to account for varying lengths of focals.

Food consumption of adult individuals (the number of beakfuls of food collected per minute focal) was fitted as the response in a model to explore differences in food consumption between treatments. This model was fitted with a *gaussian* error distribution rather than *poisson* because of overdispersion issues with *poisson* and Knief and Forstmeier, (2021) showed that *gaussian* models are more robust to slight violations of non-normality than previously suggested. The model was fitted with day status, year category and adult sex and the interaction between treatment and nest age. The square-root of the focal duration (minutes) was fitted as a weighted term and bird identity was fitted as a random term.

Provisioning rate (number of visits to the nest within a focal) was fitted as the response in a model to explore differences in provisioning rate between treatments, with a *poisson* error distribution and the (log) focal length (minutes) was added as offset term to account for the varying length of focal observations. The model included day status, year category and sex as and the interaction between treatment and nest age fitted as explanatory variables. The square-root of the focal duration (minutes) was fitted as a weighted term and bird identity was fitted as a random term.

Adult daily body mass change (ΔM_b)

To explore differences in ΔM_b between treatments, ΔM_b was fitted as a response variable in a model with a *gaussian* error distribution. The initial model was fitted with day status, year category, adult sex and the interaction between treatment and nest age as explanatory variables. Bird identity was fitted as a random term.

Nestling FA physiology and morphology

I explored whether there were differences in the percentage of total SFAs, total MUFAs, and total ω-6 ω-3 PUFAs, in the blood plasma of nestlings between treatments. The initial models exploring the effects of treatment on nestling FA percentages and morphology respectively, included nestling age and the interaction between treatment and brood size as explanatory variables. Year category was also included as an explanatory variable in the model exploring the effects of treatment on morphology but could not be included in the model exploring FA differences as FA data were only available for 2018. Both models included nest identity as a random term to account for multiple nestlings being sampled from the same nest and in the case of the analysis of nestling morphology, the same nests (traditional nest sites are used repeatedly between years in this species) being assigned to different treatments between years.

5.3. Results

A total of 19 different nests were supplemented across years, 11 were supplemented in the first year (2018) and 13 in the second (2019). Five of the 19 nests included in the experiment were supplemented in both years while the remaining 14 were supplemented either in the first or the second year. In the first year, five nests were assigned to the processed food treatment and six nests to the unprocessed food treatment, and in the second year, six nests were assigned to the processed food treatment and seven to the unprocessed food treatment. Three of the 19 nests were assigned to different treatment between years.

5.3.1. Treatment relative FA percentages

SFAs in the processed food treatment were twice as high as that of the unprocessed food treatment; SFAs made up 66% of the FA profile of processed foods and 33% for natural foods. The percentage of MUFAs in treatments was similar, with MUFAs only slightly lower in the processed food treatment than in the unprocessed food treatment; 30% and 33% respectively. In terms of PUFAs, the percentage of ω-6 PUFAs in processed food was lower than that of the unprocessed food treatment; 4% versus 33% respectively, while in terms of ω-3 PUFAs, the processed treatment had none, and the unprocessed treatment had 1% (Figure 5.1).

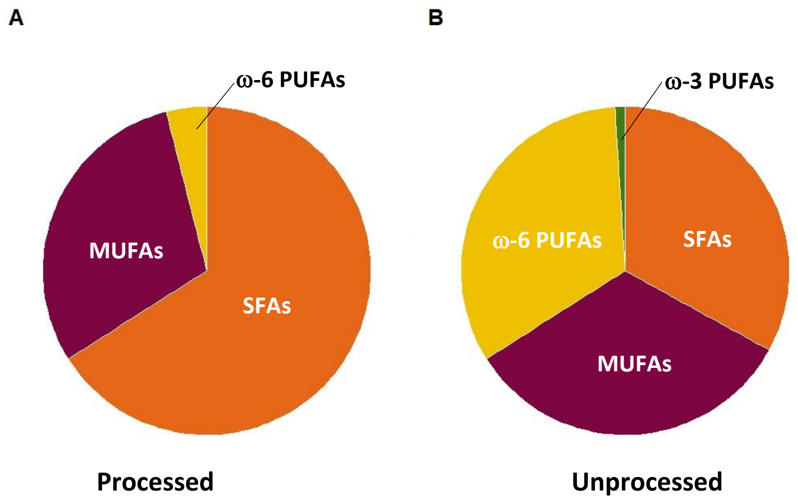

Figure 5.1: The relative % composition of fatty acids in the **(a)** processed food treatment and **(b)** unprocessed food treatment. Processed food consisted of processed cheese and cheese flavoured corn snacks (Nik-Naks brand manufactured by Simba. Unprocessed food consisted of green apples and mealworms (*Tenebrio molitor*).

5.3.2. Supplementary feeding: amount of food supplement taken

A total of 1007 supplementary feedings (supplementing a single nest for 15-minutes) were carried out over the entire experiment. Information on the amount of food taken by pairs was obtained from 892 of these feedings (88% of the supplementary feedings data). Pairs from UF$_{\text{NESTS}}$ took an average of 13.62 ± 0.43g per feeding of supplemented food (9.65 ± 0.34 g mealworms and 3.38 ± 0.27 g of apple) while PF$_{\text{NESTS}}$ took half that amount; 6.83 ± 0.22g per feeding of supplemented food (3.49 ± 0.20 g cheese and 2.76 ± 0.45 g of corn snacks).

There was a significant interaction between treatment and nest age on the amount of supplemented food taken by pairs (Table 5.1a; Figure 5.2). Pairs from PF$_{\text{NESTS}}$ took similar amounts of food throughout the nestling period (i.e., independent of nest age), while the amount of food taken by pairs from UF$_{\text{NESTS}}$ increased as nestlings aged. Pairs took significantly more food during afternoon feedings: taking an average of 11.28 ± 0.52g of supplemented food during afternoon feedings and an average of 9.86 ± 0.52g in the morning. Pairs took significantly more of supplemented food on LHP days than they did on HHP days (Table 5.1a): taking an average of 11.70 ± 0.60g on LHP days and 9.44 ± 0.470g on HHP days. There were also significant differences in the amount of food pairs took across years (Table 5.1a): in the first year of the study, they took 11.87 ± 0.58g but this amount decreased in the second year to 9.27 ± 0.56g.

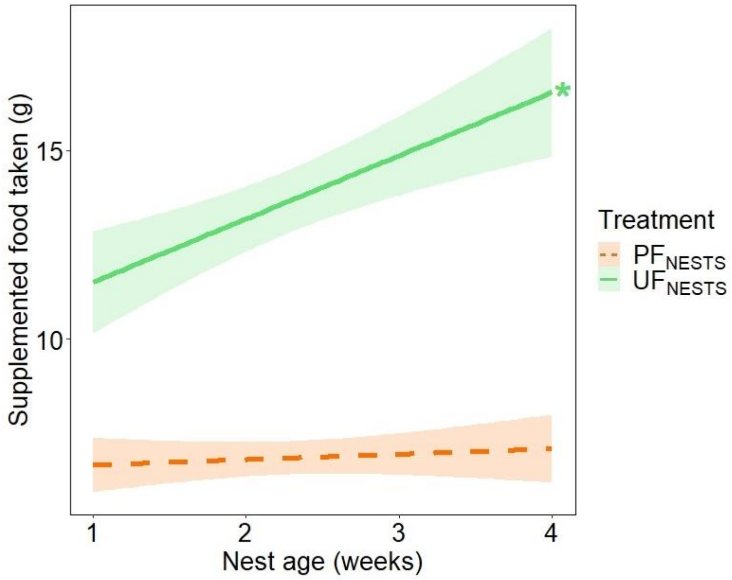

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Figure 5.2: The mass of supplemented food (g) taken in relation to nestlings' age by pairs from PF$_{NESTS}$ (dashed, orange line) and UF$_{NESTS}$ (solid, green line) during week 1-4 of the nestling period. Trend lines with 96% CI's were generated from GLMMs. The interaction between the mass of supplemented food taken by pairs and nest age on the amount of supplemented food taken by pairs was statistically significant (Table 5.1a). Data were derived from 892 feedings carried out in 5 PF$_{NESTS}$ and 6 UF$_{NESTS}$ in 2018 and 6 PF$_{NESTS}$, and 7 UF$_{NESTS}$ in 2019. The asterisk indicates a significant relationship.

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5.3.3. Supplementary feeding: amount of the supplement allocated to nestlings

I had information on adult allocation of the supplementary food between themselves and their nestlings from 719 feedings (71% of the supplementary feedings data). In all weeks regardless of nest age, the proportion of supplemented food pairs fed to nestlings was higher for those from UF_{NESTS} than for those from PF_{NESTS} (Table 5.1b; Figure 5.3a). The proportion of supplemented food allocated to nestlings increased significantly with nestling age in PF_{NESTS} whereas this change was not significant for UF_{NESTS}. There was also a significant interaction between treatment and brood size on the amount of supplemented food pairs allocated to nestlings (Table 5.1b; Figure 5.3b) such that the amount of supplemented food allocated to nestlings increased significantly with brood size for PF_{NESTS}, but not for UF_{NESTS}. Females allocated a greater amount of supplemented food to nestlings than males. Pairs also allocated more supplemented food to nestlings on LHP days and in the first year of the study period (2018) (Table 5.1b).

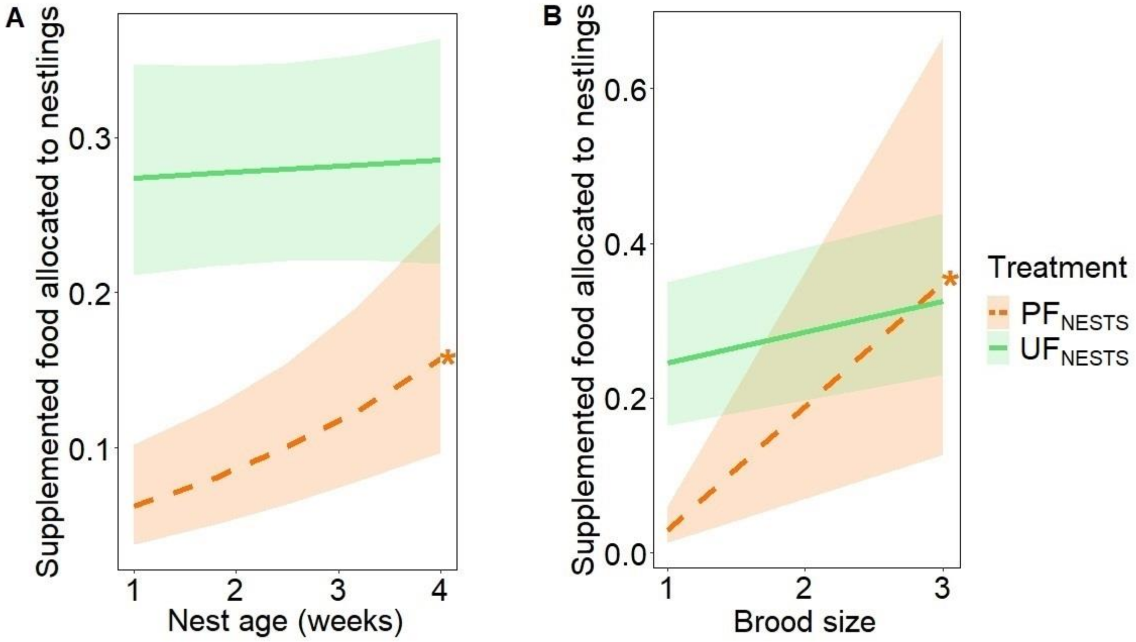

Figure 5.3: The proportion of supplemented food allocated to nestlings with **(a)** nest age (weeks) and with **(b)** brood size by pairs supplemented with natural (solid, green line) and anthropogenic (dashed, orange line) food. Trend lines with 95% CI's were generated from GLMMs. The interactive effect of nestling age and brood size with treatment respectively on the ratio of food allocated to nestlings were both significant (Table 5.1b). Data were derived from 892 of 1007 feedings carried out in 6 nests supplemented with processed food and 5 nests with unprocessed food in 2018, and 6 nests supplemented with processed food and 7 nests with unprocessed food in 2019. The asterisk indicates a significant relationship.

Table 5.1: Results from (a) LMMs performed on the mass (g) of food taken by supplemented pairs and (b) and the GLMMS performed on the proportion of supplemented food taken by pairs which they allocated to their nestlings during supplementary feeding. Data for each model were derived from 892 and 719 feedings for (a) and (b) respectively. Model (a) included nest ID as a random term and model (b) included individual ID as a random term. I provide the estimates relative to the UF_{NESTS} Treatment, the year 2018, HHP days, morning feedings and female sex as the reference category. Significant predictors are indicated in bold.

Response variable	**Explanatory variable**	χ^2	**df**	***P***	**Factor level**	**Estimate ± S.E.**	**df**	***P***
(a) Mass of supplemented food taken	**Treatment**	**81.94**	**1**	**<0.001**	**PF_{NESTS}**	-4.25 ± 1.34	**522.7**	**<0.001**
	Nest age	**7.89**	**1**	**0.004**	**Nest age**	**1.21 ± 0.35**	**880.9**	**<0.01**
	Feeding time	**8.27**	**1**	**0.004**	**Afternoon**	**1.42 ± 0.49**	**863.8**	**<0.01**
	Day status	**16.79**	**1**	**<0.001**	**LHP**	**2.60 ± 0.65**	**866.3**	**<0.001**
	Year	**15.79**	**1**	**<0.001**	**2019**	**-1.08 ± 0.52**	**884.72**	**0.04**
	Treatment*nest age	**4.32**	**1**	**0.04**	**PF_{NESTS}*nest age**	**1.09 ± 0.54**	**779.0**	**0.04**
(b) Proportion of supplement pairs allocated to nestlings	**Treatment**	**18.58**	**1**	**<0.001**	**PF_{NESTS}**	**-4.40 ± 1.02**		**<0.001**
	Nest age	**20.15**	**1**	**<0.001**	**Nest age**	**0.02 ± 0.05**		**<0.001**
	Year	**244.48**	**1**	**<0.001**	**2019**	**-3.40 ± 0.22**		**<0.001**
	Brood size	**9.38**	**1**	**0.002**	**Brood size**	**0.20 ± 0.20**		**<0.01**
	Sex	**10.45**	**1**	**<0.001**	**Male**	**-0.78 ± 0.24**		**<0.01**
	Day status	**5.11**	**1**	**0.02**	**LHP**	**0.19 ± 0.09**		**0.02**
	Treatment*nest age	**12.71**	**1**	**<0.001**	**PF_{NESTS}*nest age**	**0.32 ± 0.091**		**<0.001**
	Treatment*brood size	**5.47**	**1**	**0.02**	**PF_{NESTS}*brood size**	**1.26 ± 0.54**		**0.02**

5.3.4. Adult focal behaviour

A total of 149 focals were collected from 49 unique individuals, 25 males and 24 females. 52 focals were collected on individuals assigned to the UF_{NESTS} and from 12 nests, 50 focals on individuals assigned to the PF_{NESTS} and from ten nests, and 47 focals on individuals assigned as $CTRL_{NESTS}$ and from eight nests. Between years, 69 focals were carried out during the first year of the experiment and 80 focals in the second.

There was no significant difference in the behaviour of adults between treatments (Table 5.2a-e, Figure 5.3a-e). Provisioning rates during focals decreased significantly with nest age (Table 5.2a), from an average frequency of 1.6 nest visits per minute focal during the first week of the nestling period declining to less than one visit (0.8 nest visits per minute focal) during the fourth week. Provisioning rates during focals also differed significantly between years (Table 5.2a) with adults provisioning twice as much in 2018 as they did in 2019; 0.11 ± 0.01 and 0.05 ± 0.01 nest visits per minute focal respectively. Foraging effort also differed significantly between years (Table 5.2b) with adults spending on average 22.1% ± 2.42% the focal foraging in 2018 to 30.0% ± 2.24% in 2019.

5.3.5. Adult ΔM_b

A total of 428 diurnal ΔM_b records was collected from 32 unique colour-ringed individuals, 17 males and 16 females. 175 out of 428 total measurements were from individuals assigned to the UF_{NESTS} treatment and from ten unique nests, 170 individuals assigned to the PF_{NESTS} and from nine unique nests, and 83 assigned as $CTRL_{NESTS}$ and from 6 unique nests. Between years, 238 mass records were taken in 2018 and 190 in 2019.

The difference in ΔM_b between treatments was marginally non-significant (Table 5.2f; Figure 5.3f). Adult starlings did however weigh significantly more in year 2018 than they did in 2019 (Table 5.2f); gaining an average of 2.75 ± 0.24g between morning and evening measurements in 2018 and an average of 1.94 ± 0.25 in 2019.

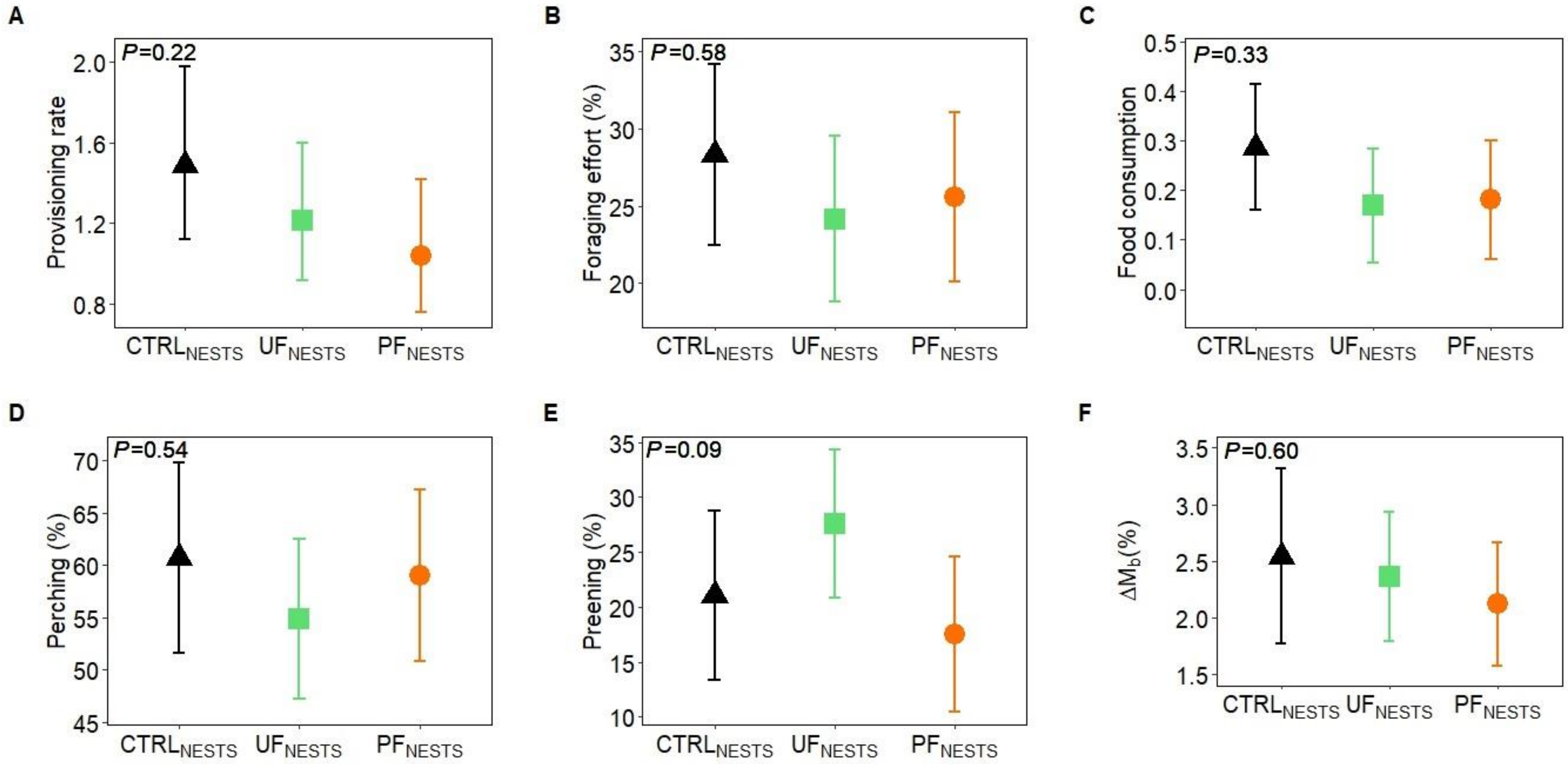

Figure 5.3: The behaviour of adult individuals during focal observations showing the average (a) provisioning rate (number of nest visits per minute focal), (b) foraging effort, (c) food consumption (the number of beakfuls of food collected per minute focal), (d) time spent perching, (e) time spent preening and (f) the diurnal ΔM_b of individuals assigned to PF_{NESTS} (orange triangles), UF_{NESTS} (green squares) and $CTRL_{NESTS}$ (black circles). Means and standard error bars were generated from LMMs. Data for a-e were derived from 149, 20-minute focals: 50 focals from individuals assigned to PF_{NESTS}, 52 from individuals assigned to UF_{NESTS}, and 47 from individuals assigned as $CTRL_{NESTS}$ which comprised 49 unique individuals (25 males and 24 females). Data for (f) were derived from 428 ΔM_b records: 175 UF_{NESTS} records, 170 PF_{NESTS} and 83 $CRTL_{NESTS}$ and which comprised 32 individuals (17 males and 16 female).

Table 5.2: Results from LMMs performed on the (a) provisioning rate, (b) foraging effort, (c) food consumption, (d) time spent perching and (e) time spent preening of adult starlings. Data were collected from 149, 20-minute focals carried out on 49 unique individuals: 52 focals for the $\mathrm{UF}_{\mathrm{NESTS}}$ treatment, 50 focals for the $\mathrm{PF}_{\mathrm{NESTS}}$, and 47 focals on $\mathrm{CTRL}_{\mathrm{NESTS}}$. Results from LMMs performed on (f) the ΔM_b of adult birds. The data were collected from 428 ΔM_b records (175 $\mathrm{UF}_{\mathrm{NESTS}}$, 170 $\mathrm{PF}_{\mathrm{NESTS}}$, 83 $\mathrm{CTRL}_{\mathrm{NESTS}}$) which constituted 32 unique colour-ringed individuals (17 males and 16 female). I provide the estimates relative to the $\mathrm{CTRL}_{\mathrm{NESTS}}$ Treatment and the year 2018 as the reference category. Significant p-values are indicated in bold.

Response variable	**Explanatory variable**	**χ^2**	**df**	***P***	**Factor level**	**Estimate ± S.E.**	**df**	***P***
(a) Provisioning rate	Treatment	3.04	2	0.22	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.36 ± 0.21		0.08
					$\mathrm{UF}_{\mathrm{NESTS}}$	-0.21 ± 0.20		0.29
	Nest age	**9.45**	**1**	**0.002**	**Nest age**	**-0.22 ± 0.07**		**0.002**
	Year	**19.25**	**1**	**<0.001**	**2019**	**-0.76 ± 0.16**		**<0.001**
(b) Foraging	Treatment	1.09	2	0.58	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.03 ± 0.04	145.0	0.50
					$\mathrm{UF}_{\mathrm{NESTS}}$	-0.01 ± 0.04	145.0	0.71
	Year	**5.73**	**1**	**0.02**	**2019**	**0.08 ± 0.03**	**145.0**	**0.02**
(c) Food consumption	Treatment	2.23	2	0.33	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.11 ± 0.09	37.48	0.23
					$\mathrm{UF}_{\mathrm{NESTS}}$	-0.12 ± 0.09	47.89	0.17
(d) Perching	Treatment	1.24	2	0.54	$\mathrm{PF}_{\mathrm{NESTS}}$	0.02 ± 0.06	39.93	0.79
					$\mathrm{UF}_{\mathrm{NESTS}}$	-0.06 ± 0.06	57.84	0.31
(e) Preening	Treatment	4.72	2	0.09	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.04 ± 0.05	28.42	0.50
					$\mathrm{UF}_{\mathrm{NESTS}}$	0.07 ± 0.05	40.29	0.20

(f) ΔM_b	Treatment	1.02	2	0.60	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.42 ± 0.44	55.74	0.35
					$\mathrm{UF}_{\mathrm{NESTS}}$	-0.18 ± 0.44	54.73	0.49
	Year	**7.29**	**1**	**<0.001**	**2019**	**-0.81 ± 0.30**	170.21	**0.01**

5.3.6. Relative percentages of FAs in the blood plasma of nestlings

The relative percentages of four different FAs (i.e., total SFAs, total MUFAs, total ω-3 PUFAs, and total ω-6 PUFAs), as well as the total $\frac{\omega-6}{\omega-3}$ PUFA were obtained from 23 nestlings and from 14 unique nests: 11 nestlings from UF_{NESTS} from five unique nests, 8 nestlings from PF_{NESTS} from 6 unique nests, and four nestlings from $CTRL_{NESTS}$ from 3 unique nests. Nestlings were 16 ± 1 days old, and the average brood size of nestlings was 2 ± 1 nestlings per nest. Significant differences were found in the FA percentages between treatments for SFAs and ω-6 PUFAs but not for MUFAs, ω-3 PUFAs and $\frac{\omega-6}{\omega-3}$ PUFA however, differences in MUFAs and the $\frac{\omega-6}{\omega-3}$ PUFA were marginally non-significant between treatments (Table 5.3a-e, Figure 5.4a-e).

SFAs had the highest percentage in the blood plasma of nestlings across all other FAs of interest (Figure 5.4a). Nestlings from PF_{NESTS} had the highest % of SFAs with an average of 43.6% ± 0.97, nestlings from $CTRL_{NESTS}$ had the second highest % with an average of 41.4% ± 1.39% SFAs and nestlings from UF_{NESTS} had the lowest %SFAs at 36.3% ± 0.86%. SFAs were not significantly different between nestlings from PF_{NESTS} and $CTRL_{NESTS}$ but these treatments SFA levels were both significantly higher than that of nestlings from $CTRL_{NESTS}$ (Table 5.3a; Figure 5.4a; *see Table S4.2a for pairwise comparisons*).

In terms of PUFAs, nestlings from UF_{NESTS} had the highest average % ω-6 PUFAs at 29.8% ± 1.41%, followed by nestlings from $CTRL_{NESTS}$ with the second highest % at 24.3% ± 2.12% while nestlings from PF_{NESTS} had the lowest % of 23.4% ± 1.56% (Figure 5.4c). ω-6 PUFAs were significantly different between treatments whereby the %s differed between nestlings from supplemented nests but not between nestlings from supplemented nests and $CTRL_{NESTS}$ (Table 5.3c; Figure 5.4c; *see Table S24.b for pairwise comparisons)*. When comparing the $\frac{\omega-6}{\omega-3}$ PUFAs, nestlings UF_{NESTS} had significantly higher ratios at 6.01 compared with PF_{NESTS} with a ratio of 4.11 but did not differ significantly from $CTRL_{NESTS}$ (Table 5.3d, *see Table S24.c for pairwise comparisons*). I also found a significant effect of brood size (Table 5.3e) whereby the ratio decreased from 6.32 ± 0.59 in nests with a single nestling to 3.68 ± 0.82 in nests with three nestlings (Table 5.3e).

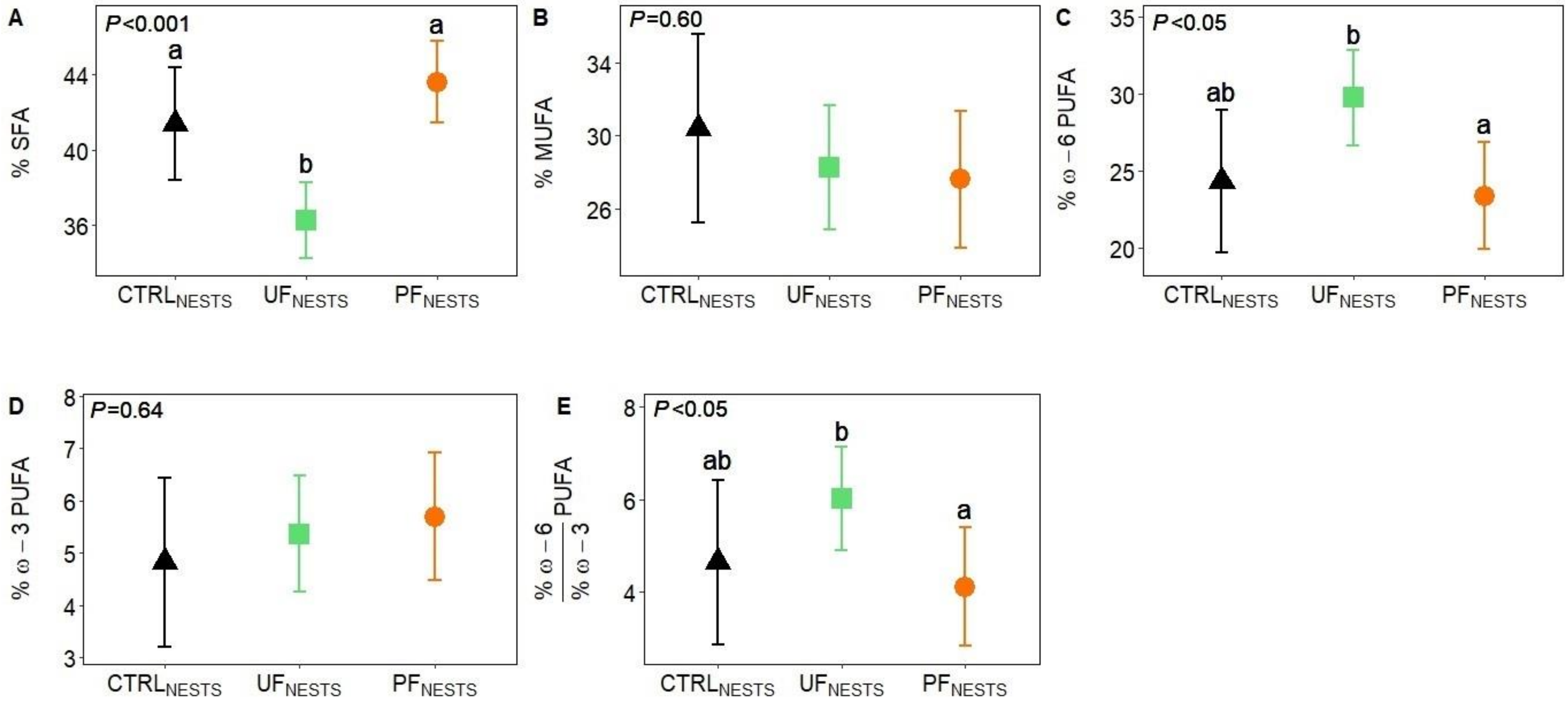

Figure 5.4: The relative percentages of (a) SFAs, (b) MUFAs, (c) ω-6 PUFAs, (d) ω-3 PUFAs, and (e) the $\frac{\omega-6}{\omega-3}$ PUFAs in the blood plasma of nestlings assigned to PF_{NESTS} (orange triangles), UF_{NESTS} (green squares) and $CTRL_{NESTS}$ (black circles). Means and standard error bars were generated from LMMs. Data were derived from the blood plasma of 23, 16.74 ± 0.18-day old nestlings: eight nestlings from PF_{NESTS}, 11 from UF_{NESTS} and four from $CTRL_{NESTS}$ sampled in 2018. For FAs which were significantly different between treatments, means sharing the same letter are not significantly different in pairwise comparisons.

Table 5.3: Results from LMMs performed on the relative percentage of (a) SFAs, (b) MUFAs, (c) ω-6 PUFAs, (d) ω-3 PUFAs, and (e) $\frac{\omega-6}{\omega-3}$ PUFA in the blood plasma of nestlings. Models correspond with data collected from 23 nestlings: 11 from $\mathrm{UF}_{\mathrm{NESTS}}$, eight from $\mathrm{PF}_{\mathrm{NESTS}}$, and 4 from $\mathrm{CTRL}_{\mathrm{NESTS}}$. Nestlings were all aged 16 ± 1 day old and were sampled from nests with an average of 2 ± 1 nestlings per nest. Models included nest identity as a random term. I provide the estimates relative to the $\mathrm{CTRL}_{\mathrm{NESTS}}$ Treatment. Significant p-values are indicated in bold.

Response variable	**Explanatory variable**	χ^2	**df**	***P***	**Factor level**	**Estimate ± S.E.**	**df**	***P***
(a) SFAs	**Treatment**	**36.25**	**2**	**<0.001**	$\mathrm{PF}_{\mathrm{NESTS}}$	2.21 ± 1.65	20	0.20
					$\mathbf{UF}_{\mathbf{NESTS}}$	**-5.13 ± 1.57**	**20**	**<0.001**
(b) MUFAs	Treatment	1.03	2	0.60	$\mathrm{PF}_{\mathrm{NESTS}}$	-2.81 ± 2.80	12.60	0.33
					$\mathrm{UF}_{\mathrm{NESTS}}$	-2.19 ± 2.83	13.24	0.45
	Nestling age	**7.78**	**1**	**<0.001**	**Nestling age**	**3.16 ± 1.13**	**18.82**	**0.01**
(c) ω-6 PUFAs	**Treatment**	**10.04**	**2**	**0.01**	$\mathrm{PF}_{\mathrm{NESTS}}$	0.95 ± 2.57	11.63	0.72
					$\mathbf{UF}_{\mathbf{NESTS}}$	**5.42 ± 2.56**	**12.37**	**0.05**
	Nestling age	**6.26**	**1**	**0.01**	**Nestling age**	**-2.20 ± 0.88**	**17.78**	**0.02**
(d) ω-3 PUFAs	Treatment	0.90	2	0.64	$\mathrm{PF}_{\mathrm{NESTS}}$	0.87 ± 0.92	12.69	0.36
					$\mathrm{UF}_{\mathrm{NESTS}}$	0.55 ± 0.88	12.33	0.55
(e) ω-6 /ω-3 PUFA	**Treatment**	**6.11**	**2**	**0.05**	$\mathrm{PF}_{\mathrm{NESTS}}$	-0.53 ± 0.92	11.63	0.72
					$\mathbf{UF}_{\mathbf{NESTS}}$	**5.43 ± 2.57**	**12.37**	**0.05**
	Brood size	**4.54**	**1**	**0.03**	**Brood size**	**-1.32 ± 0.62**	**9.75**	**0.06**

5.3.7. Nestling morphology

Morphometric data were obtained from 56 nestlings in total, 25 nestlings from UF_{NESTS} and from 12 unique nests, 20 nestlings from PF_{NESTS} and from 11 unique nests, and 12 nestlings from $CRTL_{NEST}$ from eight unique nests. Between years, data were obtained from 22 nestlings in 2018 and 34 in 2019.

None of the nestling morphometric measures differed significantly with treatment (Table 5.4a-e; Figure 5.5a-e). There was a significant decrease in nestling body mass and tail length between years (Table 5.4a, e) with mass decreasing from 92.2g ± 4.31g in 2018 to 82.7g ± 3.72g in 2019, and tail length decreasing from 31.4mm ± 2.21mm in 2018 to 25.8mm ± 1.81mm in 2019.

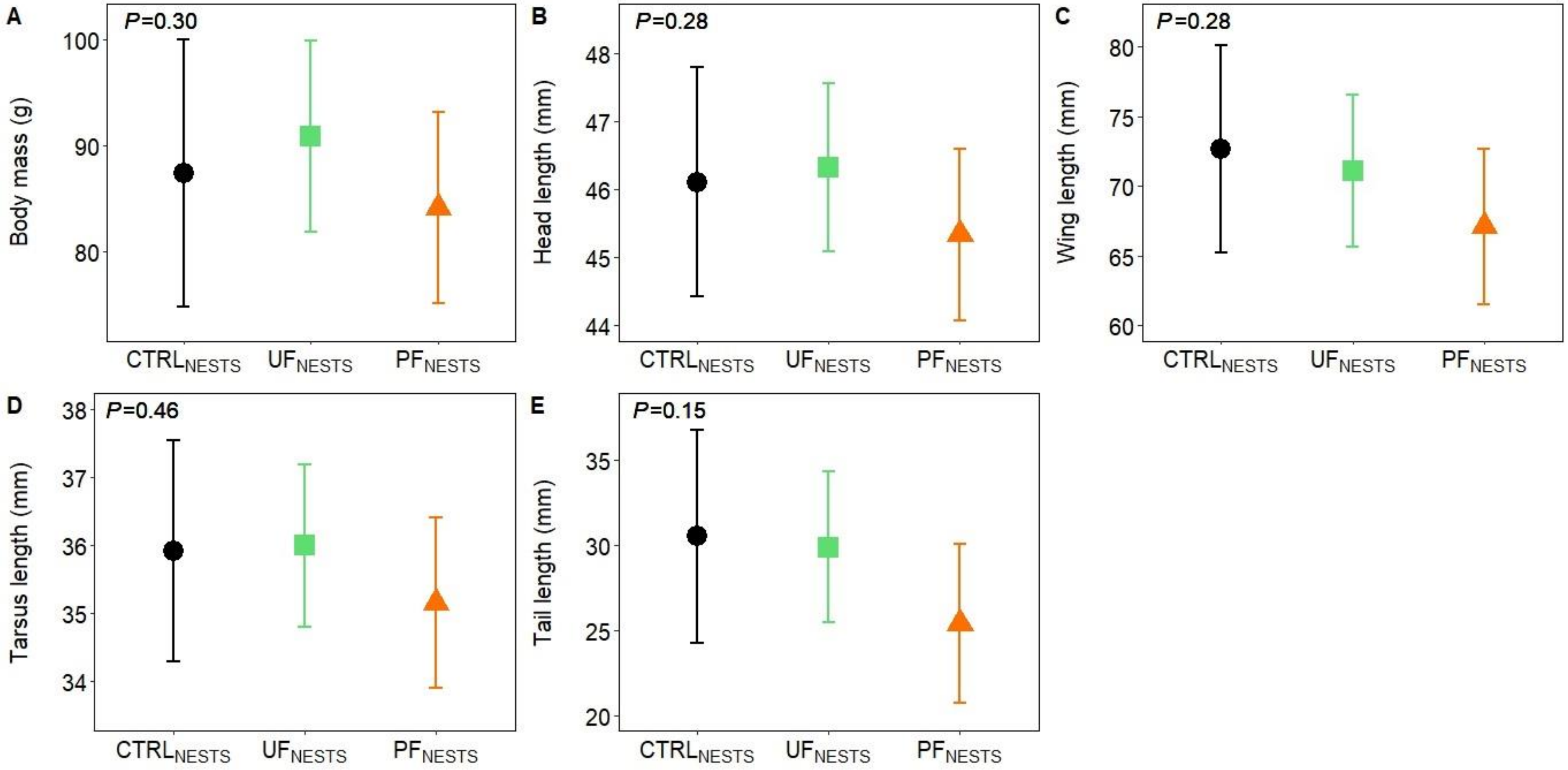

Figure 5.5: The average (a) body mass, (b) head length, (c) wing length, (d) tarsus length and (e) tail length of nestlings assigned to $\mathrm{PF}_{\mathrm{NESTS}}$ (orange triangles), $\mathrm{UF}_{\mathrm{NESTS}}$ (green squares) and $\mathrm{CTRL}_{\mathrm{NESTS}}$ (black circles). Means and standard error bars were generated from LMMs. Data were derived from the blood plasma of 57, 16.74 ± 0.18-day nestlings: 20 nestlings from $\mathrm{PF}_{\mathrm{NESTS}}$, 25 from $\mathrm{UF}_{\mathrm{NESTS}}$ and 12 from $\mathrm{CTRL}_{\mathrm{NESTS}}$ collected in 2018 and 2019.

Table 5.4: Results from LMMs performed on the (a) body mass, (b) head length, (c) wing length, (d) tarsus length and (e) tail length of nestlings. Models correspond with data collected from 57 nestlings. Models included nest identity as a random term. I provide the estimates relative to the CTRL$_{NESTS}$ Treatment and the year 2018 as the reference category. Significant p-values are indicated in bold.

Response variable	**Explanatory variable**	χ^2	**df**	***P***	**Factor level**	**Estimate ± S.E.**	**df**	***P***
(a) Body mass	Treatment	2.40	2	0.30	PF$_{NESTS}$	-3.22 ± 6.86	45.92	0.64
					UF$_{NESTS}$	3.52 ± 7.39	39.47	0.64
	Year	**5.71**	**1**	**0.02**	**Year**	**-9.50 ± 3.98**	**49.26**	**0.02**
(b) Head length	Treatment	2.15	2	0.28	PF$_{NESTS}$	-0.77 ± 0.97	44.64	0.43
					UF$_{NESTS}$	0.22 ± 0.99	39.79	0.83
(c) Wing length	Treatment	2.55	2	0.28	PF$_{NESTS}$	-5.55 ± 4.33	43.41	0.21
					UF$_{NESTS}$	-1.56 ± 4.39	38.10	0.73
(d) Tarsus length	Treatment	1.54	2	0.46	PF$_{NESTS}$	-0.76 ± 0.97	43.27	0.43
					UF$_{NESTS}$	0.08 ± 0.97	37.81	0.94
(e) Tail length	Treatment	3.81	2	0.15	PF$_{NESTS}$	-5.09 ± 3.58	41.80	0.16
					UF$_{NESTS}$	-0.63 ± 3.69	33.66	0.87
	Year	**5.75**	**1**	**0.02**	**Year**	**-5.63 ± 2.35**	**52.92**	**0.02**

5.4. Discussion

Few studies have investigated the implications of anthropogenic food consumption on urban wildlife. Using a food supplementation experiment, I tested the hypothesis that processed food is advantageous for breeding adults but detrimental for their nestlings. My results do not support this hypothesis as I did not observe significant differences in adult behaviour or body mass across different treatments (predictions 2-5). For nestlings, I demonstrated notable differences in the plasma fatty acid compositions of nestling, attributable to their respective treatments, Specifically, nestlings assigned to PF_{NESTS} exhibited elevated levels of SFAs and reduced levels of PUFAs in their blood plasma compared to UF_{NESTS} and $CTRL_{NESTS}$ (prediction 6). However, there was no discernible adverse impacts on the nestling morphology resulting from these differences (prediction 7).

5.4.1. Allocation of supplement to nestlings during food supplementation

When supplemented with unprocessed food, pairs allocated more of the supplement to nestlings compared to when supplemented with processed food. Adults therefore appear to behave in such a way that suggests they have the ability to differentiate between high- and low-quality foods and appear to prioritize feeding high-quality food to their nestlings which has also been observed in other experiment studies on other urban birds passerines (Cowie & Hinsley, 1988; Mennechez & Clergeau, 2006; Støstad, et al., 2017; Sauter, et al., 2006). Alternatively, the higher proportion of food allocated to nestlings observed in UF_{NESTS} compared to PF_{NESTS} may be influenced by variations in the calorie content of the supplemented foods. It's possible that unprocessed foods are less satiating, thus necessitating larger quantities compared to processed foods.

However, I also found an effect of age and brood size on the proportion of the supplement that pairs allocated to nestlings. Experimental evidence has shown that the proportion of food allocated to nestlings generally increases as they got older, whether the supplement is of high quality (e.g., Seress, et al., 2020) or not (e.g., Cowie & Hinsley, 1988) and also increases when when the brood demand is high (Sauter, et al., 2006). Being less discriminatory with respect to food quality as nestlings get older as well as when provisioning larger broods could have saved parents valuable foraging time. These trends were only observed for PF_{NESTS} whereas the increased allocation of food to nestlings as they grew older and were from increasingly larger broods was non-significant for UF_{NESTS} pairs.

This was unanticipated from $UF_{NESTS,}$ considering that nestlings require an increased food supply as they grow which necessitates greater parental effort (Royama, 1966). This result was also unexpected since they were being provided with a high-quality food to nourish nestlings, which should theoretically reduce the heightened effort required by birds in urban areas to find such food sources for feeding nestlings (Jarrett, et al., 2020). Given that UF_{NESTS} received both live and dead mealworms and were observed spending more effort repeatedly beating mealworms on the ground, presumably to kill them or to remove their exoskeleton, it is plausible that this increased handling time might have limited their ability to increase the food allocated to nestlings. In contrast, PF_{NESTS} only broke down processed food items into manageable pieces and accomplished this more swiftly.

5.4.2. Adult behaviour during focals and ΔMb

The lack of an impact from food supplementation on adult behaviour was unexpected, considering that reduced foraging effort as a result of access to extra food has been demonstrated in other studies (Goldenberg, et al., 2016; Soriano-Redondo, et al., 2021; Cucco & Malacarne, 1997). Access to extra food has resulted in a reduction in the time that parents need to invest in foraging for themselves regardless of the food quality (Lill & Geraldene, 2016; Seress, et al., 2020) and has resulted in high body condition (when supplemented with unprocessed food) (Seress, et al., 2020). Whereas other studies have found that processed food had a significant negative effect on the body condition of non-breeding adult passerines (Bernat-Ponce, et al., 2023).

My result likely reflects limitations in both the quality and the quantity of the supplement provided to adults during feeding sessions. Despite attempts to offer starlings ad libitum food, 15-minute sessions might not have been long enough to constitute a substantial portion of their daily diet, thus limiting the effect on their behaviour and body mass. Additionally, the treatment effect may have been further diminished by adults allocating a portion of the supplement to nestlings. Conducting this study outside of the breeding season and supplementing a portion that constitutes a more significant portion of their daily diets would provide a better assessment of the effects of anthropogenic food on adult birds in urban environments.

However, starlings in this study site have demonstrated multiple times their ability to maintain behaviour and body mass in spite of stark contrasts in the consumption of anthropogenic food both during the breeding and non-breeding season in this population (Catto, et al., 2021; Stofberg, et al., 2019; Risi, et al., 2021). For example, while previous studies on this study population have reported significant variations in anthropogenic food consumption between weekends and weekdays (Catto, et al., 2021; Stofberg, et al., 2019; Risi, et al., 2021), Jensen et al. (2019) observed no significant differences in the circulating plasma fatty acids in their blood plasma between day types. His findings indicate that the significant variations in the amount of anthropogenic food consumed between weekends and weekdays, and consequently differences in diet quality between day types, may not have a substantial physiological significance for urban starlings. This lack of significance could be even more pronounced when considering the smaller-scale diet quality differences of my study. Furthermore, because starlings still have access to a wide variety of natural food in this environment (Stofberg et al., 2019), they could include these to consume a more balanced diet thereby mitigating potential positive or negative effects of anthropogenic food on their physiology and body condition.

5.4.3. Nestling FA percentages

The FA percentages in the blood plasma of nestlings largely mirror those found in their respective diets, showing elevated levels of SFAs and lower levels of ω-6 PUFAs than those fed unprocessed foods. Although SFAs can be synthesized *de novo,* the observed differences between nestlings were more likely dietary-induced. However, the implications of elevated plasma SFAs on the health and fitness has rarely been investigated in the literature. Although studies stem mostly from ectotherms, evidence suggests that lower proportions of SFAs in plasma are preferred given that increased saturation decreases membrane fluidity (Hazel, 1995; Hazel & Williams, 1990), which suggests that processed foods typically high in SFAs could be costly for cell function.

Much like processed food's capacity to elevated plasma ω-6 PUFAs PUFA levels (Herrera-Duenas, 2018), my study demonstrates that similar effects can be observed in urban birds consuming unprocessed foods. Elevated ω-6 PUFAs levels and low ω-3 PUFAs in plasma resulted in significantly higher levels of $\frac{\omega-6}{\omega-3}$ PUFA in the blood plasma of nestlings fed unprocessed food. This higher percentage of plasma ω-6 PUFAs observed for nestlings fed unprocessed foods found in my study is concerning given their implications on oxidative balance and inflammation. More specifically, elevated levels of ω-6 PUFAs relative to ω-3 PUFAs in plasma increases the risk of oxidative stress in birds (Hulbert, et al., 2007; Gaschler & Stockwell, 2017) which is associated with disease, tissue and DNA damage, cellular dysfunction, ageing, and lowered survival (Hulbert, 2005; Isaksson, 2015; Bize, et al., 2008; Costantini & Verhulst, 2009). Elevated levels of ω-6 PUFA relative ω-3 PUFAs in plasma are also associated with increased sensitivity to antigens by promoting inflammatory responses (Simopoulos, 2002; Calder, 2007; Romieu, et al., 2008).

Furthermore, it's been shown that urban birds may be particularly vulnerable to the adverse effects of elected plasma ω-6 PUFAs as they may lack the capacity to regulate plasma FA levels compared to their conspecifics in rural environments. Additionally, oxidative stress can be exacerbated in urban birds because in urban birds they can be dietary-induced but also brought on by other environmental stressors in urban environments such as pollution (Herrera-Dueñas, et al., 2018; Isaksson, 2015).

5.4.4. Nestling morphology

Despite differences in FA composition in the blood plasma of nestlings assigned to different treatments, I found no evidence that processed food consumption impairs the development of nestlings. This contrasts with several suggestions that anthropogenic food may be detrimental for the growth and development of nestlings. A recent experiment investigated the impact of processed food on the physical body condition of sparrows and found that the lower-quality of processed food was physiologically reflected in the birds' poorer physical condition (Bernat-Ponce, et al., 2023). However, they attribute this effect to the high carbohydrate and low protein content of their processed food treatment, which likely differs in my study. Unlike their study, the processed food items in my experiment, namely nik-naks and cheese, are typically high in carbohydrates and protein respectively. This protein content may have helped mitigate the potential negative effects of processed food on body condition, as observed in Bernat-Ponce et al.'s (2023) study.

Furthermore, the absence of a significant difference in nestling morphology between treatments might have been influenced by the non-significant difference in ω-3 PUFAs in between treatment groups as ω-3 PUFAs have been shown to be a strong positive predictors of the growth and development of nestlings (Twining, et al., 2016; Twining, et al., 2018). My results are supported by that of Herrera-Dueñas et al. (2018) who found no deleterious effects on the physical condition of urban sparrows (*Passer domesticus L.*) supplemented with processed food.

Alternatively, these findings may highlight that the development of some morphological measurements may be strategically prioritized through resource allocation irrespective of food limitations in quality or quantity in order to mitigate any negative fitness costs incurred during post-fledging (Schew & Ricklefs, 1998). This has been more prominently observed for skeletal growth of nestlings faced with acute or chronic food restrictions (Killpack & Karasov, 2012; Negro, et al., 1994; Lepczyk & Karasov, 2000; Moe, et al., 2004). For example, food-limitation experiments on House sparrows (*Passer domesticus*) have shown that although food-restricted nestlings had lower body mass, they had similar skeletal growth compared to controls of similar age (Killpack & Karasov, 2012). Additionally, the absence of distinctions in morphological measurements among nestlings assigned to different treatments could reflect the importance of distinct individual growth strategies that vary in response to their physiological condition. For example, recent research on development trajectories suggests that they may adopt personalized growth strategies, with some prioritizing mass gain while other focus on structural growth. These individual growth strategies may be more reliable predictors of their physiological condition compared to solely considering their absolute growth measurements at fledging age alone (Allen, et al., 2022).

The absence of a significant difference in nestling morphology, particularly when considering that nestlings assigned to PF_{NESTS} had an average mass six grams lower than those from $UF_{NESTS,}$ was unexpected. Other experimental evidence has shown that feeding on human snacks significantly reduced the body condition of adult sparrows (Bernat-Ponce, et al., 2023). However, it's important to note that while these effect sizes were reasonable and the observations taken over two years, the sample sizes in the dataset might have weakened the statistical power to detect such differences. Likewise, the significant differences observed in nestling plasma fatty acid levels between treatments, which also had reasonable effect sizes but were based on only one year of data, should also be interpreted with caution due to limit sample sizes.

During the first year of the experiment, the Western Cape region experienced a three-year stretch of below-average rainfall from 2015 to 2018, which coincided with the first year of my study. By 2018, the total water shortage for Cape Town and surrounding areas had decreased to below 30%. This drought was highly publicized and became so severe that city officials imposed strict water use restrictions, limiting residents of Cape Town to only 50 litres of per day in an effort to manage the remaining water supply (City of Cape Town, 2018). The drought likely impacts breeding starlings' ability to locate natural food and water, both for themselves and their nestlings. This situation likely explains why adults worked harder during 2018 compared to 2019, exhibiting significantly higher provisioning rates while also suffering lower body mass during the drought year. Despite their efforts to provide an adequate amount of food, the nestlings also suffered from reduced body mass and tail length during that same year.

Conclusion

This study did not find supporting evidence for the idea that processed food may benefit adult birds and can be detrimental for the nestlings in urban environments. There was no observed negative impact of processed food consumption on the behaviour and body mass of adult birds, not on the morphology of nestlings. The most notable finding was that unprocessed intake led to higher plasma $\frac{\omega-6}{\omega-3}$ PUFAs, while processed food consumption resulted in elevated plasma SFA levels in nestlings. There are some suggestions that SFA-rich diets may negatively impact cell-membrane fluidity and ultimately cell function (Hazel, 1995; Hazel & Williams, 1990) however the implications of such changes are is still largely unknown as most of the research have focused on the role of unsaturated FAs in the physiology and development of birds. My study shows that birds feeding on unprocessed food might also be at risk of elevated oxidative stress (Hulbert, et al., 2007; Gaschler & Stockwell, 2017) and proinflammatory responses (Simopoulos, 2002; Calder, 2007; Romieu, et al., 2008) associated with elevated levels of plasma $\frac{\omega-6}{\omega-3}$ PUFAs.

The contrasting findings of the effects of processed food between my study and that of others demonstrate that anthropogenic food quality in urban area may differ im multiple ways, some of which may benefit starlings, some that may be detrimental and other that may have no effect. I suggest further investigation into the effects or processed food on various aspects of avain physiology and development. Given that these FA levels have been shown to vary over time after processed food consumption (Herrera-Duenas, 2018) future research should investigate the consequences of elevated processed food consumption beyond the nestling period. Furthermore, considering that the diversity urban stressors, including the quality and quantity of anthropogenic food and the differential capacity to regulate plasma FA levels all differ along the urban gradient (Isaksson, 2015; Herrera-Duenas, 2018; Townsend, et al., 2019), I recommend further research to investigate the effects of processed food across this urban gradient to enhance our understanding of processed food consumption's impact in wildlife.

5.5. Acknowledgements

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5.7. Supplementary material

Table S4.1: The total number of focals collected on males and female Red-winged starlings from PF$_{\text{NESTS}}$ and UF$_{\text{NESTS}}$, for each week of the nestling period and on HHP and LHP days.

Nest age (weeks)	**Day status**	**Sex**	**UF$_{\text{NESTS}}$**	**PF$_{\text{NESTS}}$**	**CTRL$_{\text{NESTS}}$**	**Subtotal**
1	**HHP**	**Female**	4	7	2	13
		Male	3	3	5	11
	LHP	**Female**	3	2	4	9
		Male	3	3	3	9
2	**HHP**	**Female**	3	4	3	10
		Male	2	3	3	8
	LHP	**Female**	3	2	3	8
		Male	5	2	3	10
3	**HHP**	**Female**	3	2	2	7
		Male	6	3	3	12
	LHP	**Female**	2	4	3	9
		Male	2	3	3	8
4	**HHP**	**Female**	3	3	3	9
		Male	3	3	3	9
	LHP	**Female**	4	3	2	9
		Male	3	3	2	8
Total			**47**	**50**	**52**	**149**

Table S4.2: The pairwise comparisons of the average relative percentages of (a) SFAs and (b) ω-6 PUFAs in the blood plasma of nestlings. Linear contrasts between groups were calculated from GLMM's. Statistically significant are highlighted in bold.

Explanatory variable	**Predictor variable**	**Estimate**	**df**	**t ratio**	**p value**
(a) SFAs	PF$_{\text{NESTS}}$ - CTRL$_{\text{NESTS}}$	2.21 ± 1.70	12.38	1.30	0.42
	PF$_{\text{NESTS}}$ – UF$_{\text{NESTS}}$	**7.33 ± 1.30**	**8.77**	**5.66**	**<0.001**
	CTRL$_{\text{NESTS}}$ - UF$_{\text{NESTS}}$	**5.13 ± 1.63**	**11.41**	**3.14**	**<0.05**
(b) ω-6 PUFAs	PF$_{\text{NESTS}}$ - CTRL$_{\text{NESTS}}$	-0.95 ± 2.58	11.1	-0.37	0.93
	PF$_{\text{NESTS}}$ – UF$_{\text{NESTS}}$	**-6.38 ± 2.13**	**10.6**	**-2.99**	**<0.05**
	CTRL$_{\text{NESTS}}$ - UF$_{\text{NESTS}}$	-5.43 ± 2.59	11.8	-2.09	0.13
(c) $\frac{\omega-6}{\omega-3}$ PUFAs	PF$_{\text{NESTS}}$ - CTRL$_{\text{NESTS}}$	-0.53 ± 0.92		-0.58	0.83
	PF$_{\text{NESTS}}$ – UF$_{\text{NESTS}}$	**1.89 ± 0.77**		**2.45**	**0.04**
	CTRL$_{\text{NESTS}}$ - UF$_{\text{NESTS}}$	1.36 ± 0.96		1.41	0.33

Table S4.3: Backward reduced random-effect table for the GLMM exploring differences in the amount (g) of supplemented food taken by each nest. Significant variables are highlighted in bold.

Global model: supplement taken (g) ~ treatment*nest age + treatment*brood size + day status + feeding time + year + (1|nest ID)

	eliminated	*F*	ndf	ddf	*P*
Treatment*brood	1	0.42	1	21.04	0.52
Brood size	2	1.81	1	24.25	0.19
Day status	**0**	**16.45**	**1**	**866.32**	**<0.001**
Year	**0**	**14.23**	**1**	**45.68**	**<0.001**
Feeding time	**0**	**8.22**	**1**	**863.79**	**<0.001**
Treatment*nest age	**0**	**4.15**	**1**	**779.04**	**0.04**

Minimum adequate model: supplement taken (g) ~ treatment*nest age + day status + feeding time + year + (1|nest ID)

Table S4.4: Backward reduced random-effect table for the GLMM exploring differences in the ratio of supplemented food allocated to nestlings versus eaten. Significant variables are highlighted in bold.

Global model: cbind (items loaded, items eaten) ~ treatment*nest age + treatment*brood size + treatment*sex + feeding time + day status + year + (1|bird ID) + (1|residuals)

	eliminated	$\chi2$	ndf	ddf	*P*
Feeding time	1	1.47	1	-	0.23
Treatment*sex	2	1.76	1	-	0.18
Treatment*nest age	**0**	**12.71**	**1**	**-**	**<0.001**
Treatment	**0**	**18.58**	**1**	**-**	**<0.001**
Nest age	**0**	**20.15**	**1**	**-**	**<0.001**
Year	**0**	**244.48**	**1**	**-**	**<0.001**
Sex	**0**	**10.45**	**1**	**-**	**<0.001**
Brood size	**0**	**9.38**	**1**	**-**	**<0.001**
Day status	**0**	**5.11**	**1**	**-**	**0.02**
Treatment*brood size	**0**	**5.47**	**1**	**-**	**0.02**

Minimum adequate model: amount of food taken ~ treatment*nest age + treatment*brood size + sex + day status + (1|nest ID) + (1|residuals)

Table S4.5: Backward reduced random-effect table of the GLMM exploring provisioning rate of adult starlings. Significant variables are highlighted in bold.

Global model: provisioning rate ~ treatment*nest age + sex + day status + year + (1|bird ID)					
	eliminated	χ^2	*ndf*	*ddf*	*P*
Day status	1	0.43	1	-	0.51
Sex	2	2.73	1	-	0.10
Treatment*nest age	3	5.28	2	-	0.07
Treatment	0	3.04	2	-	0.22
Year	**0**	**19.25**	**1**	**-**	**<0.001**
Nest age	**0**	**9.45**	**1**	**-**	**<0.001**
Minimum adequate model: provisioning rate ~ treatment + nest age + year + (1|bird ID)					

Table S4.6: Backward reduced random-effect table of the LMM exploring foraging effort of adult starlings.

Global model: time spent foraging ~ treatment*nest age + sex + day status + (1|year/bird ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Sex	1	0.01	1	24.65	0.94
Treatment*nest age	2	0.03	2	141.0	0.92
Nest age	3	0.03	1	143.0	0.85
Day status	4	0.26	1	144.0	0.61
Treatment	0	0.54	2	145.0	0.58
Year	0	5.73	1	145.0	0.02
Minimum adequate model: time spent foraging ~ treatment + year + (1|bird ID)					

Table S4.7: Backward reduced random-effect table of the GLMM exploring food collection rate of adult starlings. Significant variables are highlighted in bold.

Global model: food collection rate ~ treatment*nest age + sex + day status + year + (1|bird ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Treatment*nest age	1	0.50	2	125.04	0.61
Nest age	2	0.12	1	141.64	0.73
Day status	3	0.28	1	132.99	0.60
Sex	4	2.22	1	28.89	0.15
Year	5	2.52	1	120.37	0.11
Treatment	0	1.12	2	48.50	0.34
Minimum adequate model: food collection rate ~ treatment + (1|bird ID)					

Table S4.8: Backward reduced random-effect table of the LMM exploring time spent perching of adult starlings. Significant variables are highlighted in bold.

Global model: time spent perching ~ treatment*nest age + sex + day status + year + (1|bird ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Sex	1	0.00	1	27.71	0.97
Treatment*nest age	2	0.21	2	131.1	0.81
Nest age	3	0.27	1	136.59	0.60
Year	4	1.33	1	137.96	0.25
Day status	5	2.28	1	117.12	0.13
Treatment	0	0.62	2	56.77	0.54
Minimum adequate model: time spent perching ~ treatment + (1|bird ID)					

Table S4.9: Backward reduced random-effect table of the LMM exploring time spent preening of adult starlings. Significant variables are highlighted in bold.

Global model: time spent preening ~ treatment*nest age + sex + day status + year + (1|bird ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Year	1	0.26	1	127.84	0.61
Treatment*nest age	2	0.66	2	124.67	0.52
Nest age	3	0.16	1	143.0	0.69
Day status	4	0.44	1	118.95	0.51
Sex	5	1.11	1	21.86	0.30
Treatment	0	2.36	2	40.43	0.11
Minimum adequate model: time spent preening ~ treatment + (1|bird ID)					

Table S4.10: Backward reduced random-effect table of the LMM exploring body mass change (ΔM_b) of adult starlings. Significant variables are highlighted in bold.

Global model: ΔM_b ~ treatment*nest age + sex + day status + (1|bird ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Sex	1	0.22	1	44.59	0.64
Treatment*nest age	2	1.11	2	418.48	0.33
Day status	3	1.29	1	407.62	0.26
Nest age	4	1.95	1	419.51	0.16
Treatment	0	0.51	2	59.77	0.60
Year	**0**	**7.29**	**2**	**170.21**	**<0.001**
Minimum adequate model: ΔM_b ~ treatment + year + (1|bird ID)					

Table S4.11: Backward reduced random-effect table for the LMM exploring % SFAs in nestling blood plasma. Significant variables are highlighted in bold.

Global model: SFAs ~ treatment*brood size + nestling age + (1|nest ID)					
	eliminated	*F*	ndf	ddf	*P*
Nestling age	1	0.14	1	16	0.72
Treatment*brood size	2	2.25	2	17	0.14
Brood size	3	0.26	1	19	0.61
Treatment	**0**	**18.12**	**2**	**20**	**<0.001**
Minimum adequate model: SFAs ~ treatment + (1|nest ID)					

Table S4.12: Backward reduced random-effect table for the LMM exploring % MUFAs in nestling blood plasma. Significant variables are highlighted in bold.

Global model: MUFAs ~ treatment*brood size + nestling age + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Treatment*brood size	1	0.05	2	8.70	0.95
Brood size	2	0.0	1	10.96	0.99
Treatment	0	0.51	2	12.39	0.61
Nestling age	**0**	**7.78**	**1**	**18.82**	**0.01**
Minimum adequate model: MUFAs ~ treatment + nestling age + (1|nest ID)					

Table S4.13: Backward reduced random-effect table for the LMM exploring % ω-6 PUFAs in nestling blood plasma. Significant variables are highlighted in bold.

Global model: ω-6 PUFAs ~ treatment*brood size + nestling age + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Treatment*brood size	1	0.23	2	8.12	0.80
Brood size	2	1.14	1	10.37	0.31
Treatment	**0**	**5.02**	**2**	**11.65**	**0.03**
Nestling age	**0**	**6.26**	**1**	**17.78**	**0.02**
Minimum adequate model: ω-6 PUFAs ~ treatment + nestling age + (1|nest ID)					

Table S4.14: Backward reduced random-effect table for the LMM exploring % ω-3 PUFAs in nestling blood plasma.

Global model: ω-3 PUFAs ~ treatment*brood size + nestling age + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Treatment*brood size	1	0.15	2	7.61	0.86
Nestling age	2	0.27	1	19.95	0.61
Brood size	3	1.50	1	10.12	0.25
Treatment	0	0.45	2	11.67	0.65
Minimum adequate model: ω-3 PUFAs ~ treatment + (1|nest ID)					

Table S4.15: Backward reduced random-effect table for the LMM exploring $\frac{\omega-6}{\omega-3}$ PUFA in nestling blood plasma.

Global model: ω-6/ω-3 PUFA ~ treatment*brood size + nestling age + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Treatment*brood size	1	0.02	2	7.46	0.98
Nestling age	2	0.23	1	17.14	0.64
Treatment	0	3.06	2	9.86	0.09
Brood size	0	4.54	1	9.75	0.06
Minimum adequate model: ω-6/ω-3 PUFA ~ treatment + brood size + (1|nest ID)					

Table S4.16: Backward reduced random-effect table for the LMM exploring nestling body mass (g). Significant variables are highlighted in bold.

Global model: nestling body mass ~ treatment*brood size + nestling age + year + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Nestling age	1	0.51	1	47.58	0.48
Treatment*Brood size	2	0.85	2	41.76	0.44
Brood size	3	0.60	1	46.70	0.44
Treatment	0	1.20	2	50.79	0.31
Year	**0**	**5.71**	**1**	**49.26**	**0.02**
Minimum adequate model: nestling body mass ~ treatment + year + (1|nest ID)					

Table S4.17: Backward reduced random-effect table for the LMM exploring nestling head length.

Global model: head length ~ treatment*brood size + nestling age + year + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Nestling age	1	0.01	1	46.47	0.94
Treatment*brood size	2	0.10	2	40.16	0.91
Brood size	3	0.41	1	42.30	0.53
Year	4	2.55	1	51.77	0.12
Treatment	0	1.26	2	42.44	0.30
Minimum adequate model: head length ~ treatment + (1|nest ID)					

Table S4.18: Backward reduced random-effect table for the LMM exploring nestling wing length.

Global model: wing length ~ treatment*brood size + nestling age + year + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Nestling age	1	0.04	1	44.60	0.83
Treatment*brood size	2	0.61	2	37.90	0.55
Brood size	3	0.02	1	39.32	0.90
Year	4	2.40	1	52.86	0.13
Treatment	0	1.27	2	42.55	0.29
Minimum adequate model: wing length ~ treatment + year + (1|nest ID)					

Table S4.19: Backward reduced random-effect table for the LMM exploring nestling tarsus length.

Global model: tarsus length ~ treatment*brood size + nestling age + year + (1|nest ID)					
	eliminated	*F*	*ndf*	*ddf*	*P*
Nestling age	1	0.75	1	42.23	0.39
Treatment*brood size	2	1.52	2	35.45	0.23
Year	3	0.88	1	51.96	0.35
Brood size	4	1.16	1	37.36	0.29
Treatment	0	0.77	2	43.24	0.47
Minimum adequate model: tarsus length ~ treatment + (1|nest ID)					

Table S4.20: Backward reduced random-effect table for the LMM exploring nestling tail length. Significant variables are highlighted in bold.

<table>
<tr><td colspan="6">Global model: tail length ~ treatment*brood size + nestling age + year + (1|nest ID)</td></tr>
<tr><td></td><td>eliminated</td><td><i>F</i></td><td><i>ndf</i></td><td><i>ddf</i></td><td><i>P</i></td></tr>
<tr><td>Nestling age</td><td>1</td><td>0.32</td><td>1</td><td>43.89</td><td>0.57</td></tr>
<tr><td>Treatment*brood size</td><td>2</td><td>1.23</td><td>2</td><td>36.51</td><td>0.30</td></tr>
<tr><td>Brood size</td><td>3</td><td>0.10</td><td>1</td><td>38.50</td><td>0.75</td></tr>
<tr><td>Treatment</td><td>4</td><td>1.91</td><td>2</td><td>47.41</td><td>0.16</td></tr>
<tr><td>Year</td><td>0</td><td>5.75</td><td>1</td><td>52.92</td><td>0.02</td></tr>
<tr><td colspan="6">Minimum adequate model: tail length ~ treatment + year + (1|nest ID)</td></tr>
</table>

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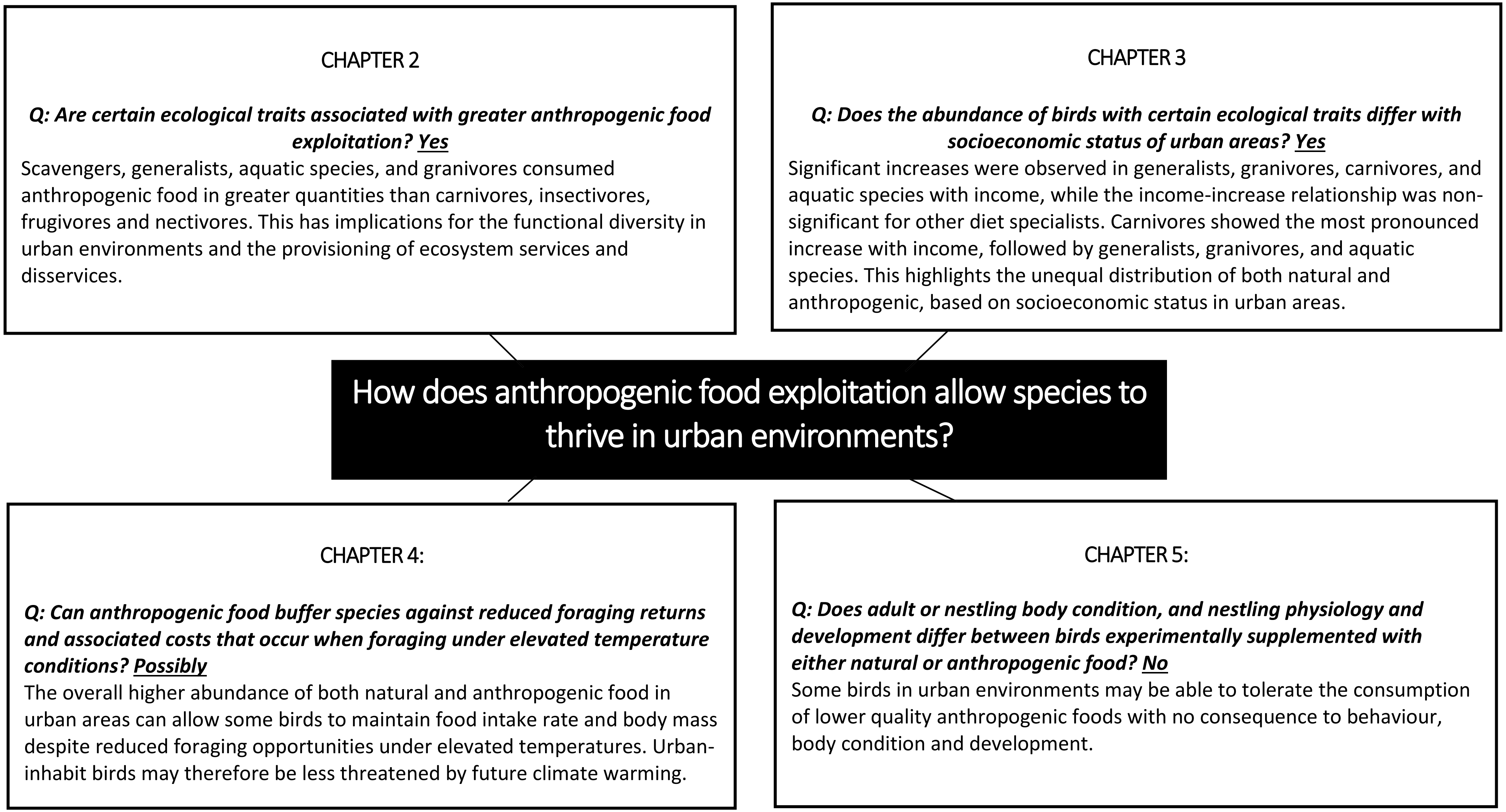
CHAPTER 6

General discussion and synthesis

Anthropogenic food has been recognized as an important trophic input in urban systems (Jones & Reynolds, 2008; Jones, 2011; Oro, et al., 2013) and likely a major driver of the colonization of urban areas by animals (Shochat, 2004; Anderies, et al., 2007; Marzluff, et al., 2001). As a result, a wide range of taxa have shifted to incorporate anthropogenic food into their diet (McKinney, 2002) with birds being one of the best examples of these. However, the extent of use of anthropogenic food across different species has never been quantified and the effects on aspects of their biology are still poorly understood. As urbanization continues to increase rapidly, anthropogenic food sources are likely to become more widespread in the diet of different species. This argues for the need to better understand the predictors and effects of anthropogenic food exploitation in urban environments.

In this thesis I aimed to understand how anthropogenic food allows birds to exploit urban environments by (i) exploring the extent of use of anthropogenic food in birds inhabiting urban environments and belonging to different foraging guilds (and other ecological traits). Thereafter (ii) I explored the responses of birds belonging to different foraging guilds (and other ecological traits) to the gradient of household income of urban areas of South Africa to understand how variation in urban food resources associated with the income might affect their likelihood of occurrence in urban areas. In the final two chapters I explored the benefits and costs associated with anthropogenic food exploitation: more specifically, (iii) I explore whether access to anthropogenic food in urban environments can mitigate the costs associated with foraging under elevated temperature conditions. Finally (iv) I investigate the potential costs of anthropogenic food exploitation on behaviour, physiology and morphology in an urban-inhabiting passerine. Here I summarize the main findings of my research, outline their significance, and propose considerations for managing birds in an increasingly urbanized world.



CHAPTER 2

Q: Are certain ecological traits associated with greater anthropogenic food exploitation? Yes

Scavengers, generalists, aquatic species, and granivores consumed anthropogenic food in greater quantities than carnivores, insectivores, frugivores and nectivores. This has implications for the functional diversity in urban environments and the provisioning of ecosystem services and disservices.

CHAPTER 3

Q: Does the abundance of birds with certain ecological traits differ with socioeconomic status of urban areas? Yes

Significant increases were observed in generalists, granivores, carnivores, and aquatic species with income, while the income-increase relationship was non-significant for other diet specialists. Carnivores showed the most pronounced increase with income, followed by generalists, granivores, and aquatic species. This highlights the unequal distribution of both natural and anthropogenic, based on socioeconomic status in urban areas.

How does anthropogenic food exploitation allow species to thrive in urban environments?

CHAPTER 4:

Q: Can anthropogenic food buffer species against reduced foraging returns and associated costs that occur when foraging under elevated temperature conditions? Possibly

The overall higher abundance of both natural and anthropogenic food in urban areas can allow some birds to maintain food intake rate and body mass despite reduced foraging opportunities under elevated temperatures. Urban-inhabit birds may therefore be less threatened by future climate warming.

CHAPTER 5:

Q: Does adult or nestling body condition, and nestling physiology and development differ between birds experimentally supplemented with either natural or anthropogenic food? No

Some birds in urban environments may be able to tolerate the consumption of lower quality anthropogenic foods with no consequence to behaviour, body condition and development.

Figure 6.1: Schematic representation of the research questions and key findings of each chapter which set the framework for this thesis.

6.1. Anthropogenic food exploitation: A facilitator, not a prerequisite for urban living

Urbanization tends to select against dietary specialists such as insectivores, frugivores, carnivores and nectivores while scavengers, generalists and granivores exhibit greater urban tolerance (Chace & Walsh, 2006; Kark, et al., 2007; Evans, et al., 2011; Patankar, et al., 2021; Croci, et al., 2008; Callaghan, et al., 2019). The evidence for this is unequivocal and has been attributed to the presumed benefits these dietary groups derive from anthropogenic food in urban areas (Fuller, et al., 2008; Jokimäki, et al., 2002). I build upon this work and my findings offer supporting evidence for these suggestions as the same species which exhibit greater urban tolerance also exhibit greater exploitation of anthropogenic food sources. Using a trait-based approach, (Chapter 2) to explore the degree of anthropogenic food exploitation in urban-dwelling birds, I found that scavengers, aquatic species, generalists and granivores consumed anthropogenic food to a greater extent than other dietary guilds. Diet is a strong determinant of where birds can be found (Kark, et al., 2007; Newton, 1980) but dietary breadth specifically is one the most important traits influencing species success in urban environments (Evans, et al., 2011; Kark, et al., 2007), it's not surprising that the species which incorporate a greater proportion of anthropogenic food into their diets namely scavengers, generalists, aquatic species ad granivores, are also the same diet groups which exhibit greater adaptability in urban environments (Chace & Walsh, 2006; Kark, et al., 2007; Evans, et al., 2011; Patankar, et al., 2021; Croci, et al., 2008; Callaghan, et al., 2019).

Given that I found no phylogenetic relationship between species and their level of exploitation of anthropogenic food, that is that closely related urban-dwelling species (species with similar ecological traits) show stark differences in their degree of anthropogenic food exploitation, it seems evident that greater anthropogenic food exploitation can facilitate urban living but is not a key determinant of being successful in urban environments. Some of the species which show heighted urban adaptability include, for example, Common starlings (*Sturnus vulgaris*), House sparrows (*Passer domesticus*) and Feral pigeons (*Columba livia domestica*) all of which exhibit minimal exploitation of anthropogenic food. In additional to having broader diets, urban exploiters are also more social, more sedentary and more likely to nest on buildings than urban adapter (Kark, et al., 2007; Leveau, 2013; Leveau & Ibáñez, 2022; Croci, et al., 2008).

The lack of a phylogenetic signal between closely related species and their level of anthropogenic food exploitation also suggests that within dietary guild different strategies independent of evolutionary linkages might be important for greater anthropogenic food exploitation. For example, behavioural factors not explicitly explored in my study such as behavioural flexibility, increased boldness and reduced neophobia may also enable a greater exploitation of anthropogenic food resources (Ducatez, et al., 2017; Biondi, et al., 2020). For example, some gull species can fine-tune their daily foraging schedules to match specific times of greater human activity, such as during school break times and peak operating times of waste disposal facilities, in order to maximize foraging opportunities (Spelt, et al., 2021; Parra-Torres, et al., 2020). Similarly, the ability to innovate different foraging techniques and reduced neophobia could facilitate greater anthropogenic food exploitation and may be successful for urban colonisation (Sol, et al., 2011; Lill & Hales, 2015; Griffin & Guez, 2014). This kind of behavioural flexibility may be important to maximize anthropogenic food exploitation in urban environments and some studies have suggested that these behavioural traits may be species specific rather than a function of specific diet groups (Griffin & Guez, 2014).

6.2. Anthropogenic food exploitation: A driver of avian functional diversity in urban environments

My findings certainly support suggestions that anthropogenic food exploitation can be a key driver of changes in avian functional diversity in urban environments (Amrhein, 2013). The same species which exhibit greater anthropogenic food exploitation are also those that occupy urban areas in higher numbers. For example, crows and gulls are amongst the most abundant and proficient exploiters of urban environments throughout the world (Marzluff, et al., 2001; Blair, 1996) and the expansion of their populations has been attributed to the exploitation of anthropogenic food sources (Marzluff & Neatherlin, 2006; Webb, et al., 2011). This has implications for the provisioning of ecosystem services and disservices in urban areas.

Birds play a very important role in urban ecosystems, contributing to all four types of ecosystem services namely provisioning, regulatory, supporting and cultural (Whelan, et al., 2008). Scavengers provide regulatory services such waste-disposal services and disease mitigation when they feed on decaying matter (DeVault, et al., 2016; O’Bryan, et al., 2018). Carnivores also provide regulatory services such as acting as pest control agents when they prey on rodent populations. Granivores, nectivores and frugivores can provide provisioning services by acting as seed dispersers and pollinators respectively (Goodness, et al., 2016). The stability of these services may be threatened if those responsible for maintaining choose to swich to consuming more anthropogenic food or if natural food sources for dietary specialists are not maintained in urban environments. Additionally, if the consumption of anthropogenic food leads to large aggregations of scavenger, generalists and aquatic species in urban environments this might also lead to increased ecosystem-disservices, such as increased disease transmission (Monaghan, et al., 1985), negative impacts on soil and vegetation, issues with sanitation (Soh, et al., 2002; Belant, 1997) and increased human-wildlife conflict (Soulsbury & White., 2015).

6.3. Anthropogenic food availability: A driver of urban biodiversity inequality

In Chapter 3, using citizen science data, I broaden our understanding of the luxury effect observed among urban birds in South Africa's urban areas by investigating whether birds with certain ecological traits exhibit a more pronounced increase with income than others. In keeping with other studies, I find evidence of the luxury effect for bird species across the urban landscape of South Africa for urban areas below a threshold of 43% urbanised. My key findings showed that species responses to improving socioeconomic conditions were dependent on their diet and habitat type. In terms of diet, carnivores, generalists, granivores and aquatic species showed the most pronounced increases with income, while the relationship with income was non-significant for frugivores, nectivores, scavengers, herbivores and insectivores. In terms of habitats type, species associated with forest/woodland, desert/rock and aquatic habitats showed more pronounced increases with income, whereas species associated with grassland, shrubland and human-dominated habitat were not significantly influenced by income. Overall, these findings likely reflect the differences in the ecological attributes that likely exist along socioeconomic gradients of South African urban areas consistent with other studies in urban areas across the world (Chamberlain, et al., 2020; Leong, et al., 2018; Mahan, et al., 2000; Hope, et al., 2003) with improving socioeconomic conditions. Consequently, I expect a loss of ecosystem services in communities already disadvantaged by inadequate infrastructural, economic, and social services.

The robust increase in specific diet groups, particularly generalists, granivores and aquatic species, as evidenced in Chapter 3, along with their prominent presence among the high exploiters of anthropogenic food sources highlighted in Chapter 2, lends strong support to the idea that avian functional diversity in urban environments is influenced by both natural and human-provided food resources. Although I don’t measure anthropogenic food subsidies directly, the parallels between Chapter2 and Chapter 3 provides support for the idea of anthropogenic food abundance as a driver of the luxury effect seen in urban areas (Leong, et al., 2018; Fuller, et al., 2008). It also provides additional support for suggestions that already unequal distribution of avian diversity with socioeconomic background could be exacerbated by increased provisioning of anthropogenic food opportunities present in wealthier neighbourhoods (van Heezik & Hight, 2017). Alternatively, it also highlights the opportunities of food provisioning to support diverse avian communities and increase wildlife encounters for the benefit of all urban residents.

Similarly, those dietary guilds which exhibited minimal exploitation of anthropogenic food in Chapter 2 showed no evidence of a luxury effect in Chapter 3 specifically herbivores, insectivores, frugivores and nectivores. The absence of a luxury effect observed for frugivores and nectivores was surprising as I expected a similar increase in nectar feeders, fruiting trees and flowerbeds with income observed in other cities (Walther, et al., 2018; Rigacci, et al., 2021) to be evident in urban areas of South Africa. For example, previous studies have shown that high-income neighbourhoods in medium-sized towns in the Eastern Cape of South Africa, support more frugivore and nectivore communities, likely due to increased investment in the maintenance of flowering and fruit-bearing trees (Tricam, 2020). In contrast, the findings in Lubbe et al., (2010) showed a higher abundance of frugivores in low-income neighbourhoods of the city of Tlokwe, South Africa, suggesting that people in poorer communities grew more fruit trees. Additionally, a study on bird species diversity in urban green spaces of the city of Johannesburg, South Africa found no evidence of a luxury effect; and suggested that the luxury effect response may have been buffered by historical urban spatial planning decisions, specifically the use of water bodies to separate racial groups, likely buffered low-income neighbourhoods from reduced avian diversity (Howes & Reynolds, 2021). Overall, the disparities between existing literature and mine show that there may be differences in how the socioeconomic factors and urban management protocols of different cities drive species diversity that may not be detected when using a multi-city/nation-wide approach (Howes & Reynolds, 2021). Furthermore, this also highlights that the relationship between socioeconomic conditions and anthropogenic and natural food opportunities may not be straightforward.

My results also suggest that avian functional diversity may respond differently between the Northern and Southern Hemisphere as reflected by the observed differences in the of anthropogenic food exploitation between the two hemispheres likely brought about by differences in the intensity of provisioning between the two hemispheres. For example, studies exploring urban tolerance show different responses between the two hemispheres with granivores (Chace & Walsh, 2006; Kark, et al., 2007; Evans, et al., 2011) being more urban tolerant in European whereas this pattern is absent in the Southern Hemisphere (Callaghan, et al., 2019) and attributed to the fact that bird feeding is thought to be more established in European cities in comparison to cities in the Southern Hemisphere (Fuller, et al., 2008; Reynolds, et al., 2017; Jones, 2018). Additionally, the selection of dietary guild may also differ with prevailing climate which likely impacts reliance on anthropogenic food sources. For example, generalists may have a particular advantage in temperate regions where the availability of natural food sources are limited during the winter as they can adapt to a broader range of food options. In contrast, the advantage of having a broader diet might not be as pronounced as in Mediterranean regions which have milder winters and seasonal rainfall, which provides a more consistent access to natural food sources (Kark, et al., 2007; Lim & Sodhi, 2004).

6.4. Urban food and water sources potentially mitigate effects of temperature

Chapter 4 explored the heat dissipation behaviour of an urban-adapted passerine, the Red-winged starling, and investigated whether the consumption of anthropogenic food could mitigate the costs of thermoregulation at elevated temperatures, thus affecting the ability to maintain body mass. My findings showed that starlings increased panting with temperature, while foraging effort declined concurrently, as expected. Despite reduced foraging effort, starlings maintained foraging efficiency and did not incur any costs to mass gain. Moreover, there were no significant differences observed in the behavioural thermoregulatory patterns and their associated costs between days characterized by high anthropogenic food availability (workweek days) and days marked by lower anthropogenic food availability (weekends). Therefore, I cannot present any evidence that supports the idea that anthropogenic food resources can alleviate the effects of elevated temperatures on urban birds. Instead, these findings may highlight that the overall availability of food and water in this urban environment did not demonstrate significant differences between workweek and weekends. This observation might have limited my ability to thoroughly investigate whether abundant anthropogenic food can offset thermoregulatory costs, as birds have the option to seek out natural food sources when anthropogenic food is limiting. Perhaps a better way to explore the possibility of anthropogenic food and its mitigation effects would be by comparing the responses of starling between rural and natural environments or by supplementing rural starlings with anthropogenic versus natural foods and exploring their thermoregulatory responses.

Evaporative heat dissipation is physiologically costly in terms of water use (Dawson, 1954; Speakman & Król, 2010). Nevertheless, my findings suggest that urban birds may benefit from the plethora of surface water sources in urban environments such as drains, water features, taps, pipes and gutters as well as and anthropogenic items with higher water content, such as fruits. Consequently, the risk of dehydration may be considerably reduced for those who can exploit these resources, allowing them to employ evaporative heat dissipation methods at an earlier stage. I observed starlings panting at a relatively low temperature of 25°C, in contrast to other passerines studied in natural environments, where birds began panting at ambient temperatures in the mid-30s°C (du Plessis, et al., 2012; Cunningham, et al., 2015; Smit, et al., 2016). My results find support in the only other known study that explored the thermoregulatory reactions of an urban-dwelling bird to higher temperatures. This study similarly found that Western Australian magpies (*Cracticus tibicen dorsalis*) started panting at a temperature of 27°C, which was also relatively lower than what is typically observed in natural ecosystems (Edwards, et al., 2015).

Whether anthropogenic food consumption does provide benefits and can mitigate the effects of elevated temperature is likely to dependent on the level of anthropogenic food exploitation/the level diet specialisation and the type of anthropogenic food consumed. This is because natural food is more susceptible to the effects of temperature in comparison of anthropogenic food. For example, specialist species such as insectivores may suffer reduced intake rates on hotter days because activity and distribution of arthropod prey may be reduced under hot weather conditions (du Plessis, et al., 2012; Van de Ven, et al., 2019). Specialists might, therefore, experience more pronounced trade-offs between foraging and thermoregulation under elevated temperatures. This is because their efficiency is reduced, both due to the inability to forage effectively under higher temperatures and decreased natural food abundance. For species which exploit anthropogenic food sources, the latter would not necessarily be expected as anthropogenic foods may be equally abundant regardless of temperature. Alternatively, there is also the possibility that anthropogenic foods may be less beneficial due to their likely lower water content and that therefore might pose a greater risk in terms of dehydration due compared to natural food sources.

Moreover, the varying responses observed in birds inhabiting mesic environments, as compared to those in arid environments, highlight that these responses may depend on the prevailing local temperatures. Consequently, we can anticipate different degrees of trade-offs between foraging and thermoregulation under various levels of urban cover. This anticipation stems from the influence of factors such as the urban heat island effect and surface temperature, which may vary across different urban cover levels (Oke, 1982; Oke, 1973). All of which may be further complicated and exacerbated by the effects of climate change and urbanization.

6.5. Urban birds and broad physiological tolerance to processed food

In Chapter 5, using a food, I tested the hypothesis that processed anthropogenic food is advantageous for breeding adults but detrimental for their nestlings. My findings don't provide support for this hypothesis as I did not observe significant differences in adult behaviour or body mass across different treatments. Neither did I observe any differences in the development of nestlings, despite differences in the composition of their plasma fatty acids. Notably, those fed processed food had higher levels of saturated fatty acids in their blood plasma compared to nestlings fed unprocessed food, while nestlings fed unprocessed food had significantly more omega-six polyunsaturated fatty acids. My findings, therefore, offer limited support for the junk-food hypothesis for urban nestlings, a topic that has rarely been studied within the context of urban avian populations.

Despite previous studies showing the remarkable ability of starlings at this study site to maintain behaviour and body mass in response to varying levels of anthropogenic food consumption, both during breeding and non-breeding seasons (Catto, et al., 2021; Stofberg, et al., 2019; Risi, et al., 2021), the absence of an effect from food supplementation on adult behaviour was unexpected. This result may suggest that the quantity of the diet supplemented to adult starlings was too small to significantly impact their behaviour and body mass, as it might not have constituted a significant portion of their daily food intake. Additionally, my findings for the effect of anthropogenic food on nestling morphology contrasts with several suggestions that anthropogenic food may be detrimental for the growth and development of nestlings (Bernat-Ponce, et al., 2023; Mennechez & Clergeau, 2006; Liker, et al., 2008). While I attribute this result to the ability of some species to strategically prioritize the development of specific morphological measurements through resource allocation, regardless of food limitations in quality or quantity (Schew & Ricklefs, 1998) it's worth considering that the sample sizes in the dataset might have reduced the statistical power to detect these differences.

Overall, these results are perhaps also indicative of the broad environmental tolerance of urban birds (Bonier et al., 2007) which allows them to tolerate a broad array of conditions possibly including phycological conditions brought about by the consumption of anthropogenic food and that would otherwise be stressful in rural birds. Research into the physiological responses of urban birds has only recently gained attention, revealing the remarkable ability of certain species to thrive on relatively lower quality anthropogenic food and resist detrimental effects. This adaptation contributes to their increased success in urban environments. For example, studies on stress physiology in urban nestlings birds have shown that after hand-raising nestlings born in urban environment and their conspecifics born in rural environments under identical conditions that urban nestlings had lower acute stress responses compared to rural nestlings and these stress responses were persisted at ages five, eight, and 11 months. Suggesting that the coping styles of urban birds have shifted to the extent that they possess genetic preadaptations for resisting acute stress and exhibit inherently reduced reactivity to stress (Partecke, et al., 2006).

Patankar et al. 's (2021) review on the traits influencing responses to urbanization also proposed that inconsistencies in physiological responses and body mass among urban birds that exploit anthropogenic food likely stem from the physiological plasticity of specific species in urban habitats. This implies that not all urban-dwelling species can equally adapt to the challenges presented by urban environments, including the availability of anthropogenic food. Particularly, species with diverse diets may exhibit contrasting trends in physiology and body mass. The varying physiological responses observed among urban birds may suggest that only those species with sufficient physiological adaptability to cope with urban conditions, including the incorporation of anthropogenic foods, can thrive, achieve high population densities, and dominate urban avian communities.

For a comprehensive understanding of physiological responses in urban birds, future research should focus on species-specific reactions, characterizing the specific types of anthropogenic food consumed, and investigating how different nutritional aspects of this food impact avian health and fitness. Other urban stresses such as pollution and pathogen exposure should also be accounted considering that anthropogenic food can potentially offset some of these negative aspects that urbanization (Wilcoxen, et al., 2015; Townsend, et al., 2019).

Conclusion

This thesis has significantly deepened our understanding of how urban avian species interact with anthropogenic food resources. It underscores the pivotal role of anthropogenic sustenance in shaping both the functional diversity and population abundance of urban ecosystems. This interplay is strongly influenced by the varying levels of tolerance displayed by species with different ecological traits toward these anthropogenic food sources. It also sheds light on how the accessibility and abundance of anthropogenic food can differ based on the socioeconomic factors of urban areas, with provisioning being greater in wealthier neighbourhoods than in low-income communities.

Moreover, it expands on why certain species, namely generalists, scavengers, granivores, and aquatic species, prosper while others face challenges in their survival in urban environments. These insights have far-reaching implications, particularly in terms of the services and disservices provided by urban avian communities to ecosystems. They underscore the necessity of regulating access to both anthropogenic and natural food to prevent the dominance of specific avian groups, cater to dietary specialists, and mitigate potential costs associated with thermoregulation under elevated temperatures.

Additionally, it delves into the positive and negative aspects of consuming processed anthropogenic food, highlighting that these effects may be species-specific, further emphasizing that some species may be more tolerant of urban-adapted than others. Future research should focus on more species-specific investigations while considering the role that other urban factors, such as natural food abundance, pollution, pathogens, and diseases, may play in influencing the effect of anthropogenic food on species. Ultimately, these findings hold significant relevance for urban management practices, especially in the context of mounting urbanization and the challenges posed by climate change.

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