

Street-wise: does prey abundance buffer Black Sparrowhawks (*Accipiter melanoleucus*) from the negative health impacts of urbanisation?



Jessleena Suri¹

e-mail: jessleena.suri@gmail.com

Supervisors:

Arjun Amar¹, Petra Sumasgutner¹, Eléonore Hellard¹

¹*Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, Department of Biological Sciences, University of Cape Town, Rondebosch, South Africa*

Minor dissertation presented in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology in the Department of Biological Science



12 February 2016



The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Plagiarism Declaration

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.
2. Each contribution to and quotation in this assignment from the work(s) of other people has been attributed, cited and referenced.
3. I acknowledge that copying someone else's assignment or essay, or part thereof, is wrong and that this assignment is my own.
4. I have not allowed, and will not allow anyone to copy my work with the intention of passing it off as his or her own work.

Signature:

Signed by candidate
Signature Removed

Jessleena Suri

Date: 12 February 2016

Acknowledgements

I would firstly like to thank my supervisors Dr. Arjun Amar, Dr. Petra Sumasgutner and Dr. Eléonore Hellard for proposing this project to me and giving me the opportunity to pursue my interests and study an urban raptor, for providing so much guidance and for training me in new skills along the way.

Secondly, I am massively grateful to Ann and Johan Koeslag for all the work they do in monitoring this Black Sparrowhawk population and for carrying out such valuable fieldwork and data collection over the years. Thank you for inducting me into the Black Sparrowhawk project, teaching me and providing unforgettable field experiences. Several photos in this thesis were also taken by Ann Koeslag. Many thanks must also go to the rest of the Black Sparrowhawk research team, including Mark Cowen, Gareth Tate, Margaret Maciver and Sharon Pryce.

Denise Hamerton and Jofred Opperman from the Iziko National Museum of Natural History arranged access to the avian osteology collections and provided comparative material for the identification of prey remains. Bruce Baigrie identified samples from 2012 and 2013 and Dr. Graham Avery assisted with identification of samples.

Petra Müller and Chevonne Reynolds provided us with the necessary microscope equipment, and Gabriella Leighton, Michelle Maritz and Elelwani Musekwa helped with analysing blood slides and compiling the parasite and leucocyte database. Juan Millán assisted with compilation of the GIS database and Nicholas Lindenberg assisted with GIS analysis.

Marie-Sophie Garcia-Heras, Caroline Isaksson, Susie Cunningham and Peter Ryan provided valuable input during the planning stages of this project, and Anthea Links and Gonzalo Aguilar were vital in administrative assistance and for providing necessary field and laboratory equipment. Thanks also to Hank Chalmers at Eagle Encounters for facilitating training in blood collection and for the rehabilitation of our urban raptors.

Finally, thank you to my family for always supporting me and encouraging my interests and to Nick Fordyce, for constant support and for assistance in the field, and to my friends and to the Conservation Biology class of 2015, for all the moral support and laughter throughout the year.

Table of Contents

Abstract.....	1
Introduction	3
Urbanisation and biodiversity.....	3
Towards understanding the individual level impacts of urbanisation.....	4
Urban impacts on raptors	6
Black Sparrowhawks on the Cape Peninsula, South Africa.....	8
Aims and objectives	9
Methods.....	11
Study Area.....	11
Data Collection.....	13
Field sampling	13
Estimation of health status	13
Diet estimation.....	14
Ethical note	18
Data Analysis.....	19
Defining the urban gradient.....	19
Statistical analyses	19
Results.....	21
Black Sparrowhawk territories on the urban gradient	21
Health and blood parasite infection along the urban gradient	23
Diet composition along the urban gradient.....	25
Prey abundance across habitats	26
Discussion.....	29
Urbanisation does not impose apparent negative health impacts on Black Sparrowhawks	29

A stable diet along the urban gradient: a potential buffer to the stress of city-life?	30
Limitations and future directions.....	33
Conclusions: Black Sparrowhawks as urban-adapters.....	34
Glossary.....	36
References	37
Appendix A.....	48
Appendix B	49
Appendix C	51

Abstract

As trends in urbanisation continue globally, there is a growing need to understand the impacts of urban development on wildlife. Whilst urban impacts on patterns of diversity and abundance of species have been well-studied, there remains a distinct lack of understanding around the impacts on ecological interactions. Different species have different levels of tolerance to urban disturbance, some species even appear to thrive in urban areas and make use of human-subsidised resources; but the physiological costs and trade-offs faced by urban-dwelling species are poorly understood.

Given that their range in South Africa has only recently expanded into the human-dominated landscapes of the Western Cape, the Black Sparrowhawk (*Accipiter melanoleucus*) provides an excellent opportunity to explore some of these questions. In this study we explored how urbanisation may affect the health of this raptor on the Cape Peninsula, South Africa. If the health of this species is negatively influenced by levels of urbanisation, this might be driven by differences in diet and prey availability across the urban spectrum. Thus, we explored this potential mechanism by examining diet composition and assessing prey abundance within different territories and habitat types.

The health of nestling Black Sparrowhawks was evaluated through their immune response (Heterophil/Lymphocyte ratio in white blood cell counts), body condition (based on morphometric measurements) and blood parasite infection (presence and abundance of *Haemoproteus* and *Leucocytozoon*). Trends in diet composition along a gradient of urban cover were determined through the analysis of prey remains collected in the immediate nest surroundings and differences in prey abundance were determined through point counts in different habitat types.

Contrary to our expectations, we found no negative effect of urbanisation on the health of the nestlings. We found no significant effect of urbanisation on the Heterophil/Lymphocyte ratio, body condition, or the risk and intensity of infection by *Haemoproteus*. For the other blood parasite investigated, *Leucocytozoon*, we found that the risk and intensity of infection actually decreased with increasing urban cover. This could be because highly urbanised areas contain less suitable habitat for the vectors of this parasite, the black fly, which requires moving fresh water. Finally, we found no change in diet breadth or composition with increasing urban cover. Overall abundance of prey species was higher in urban and open intensive (golf courses, lawns) habitats, though some species were more abundant in more natural habitats. Between all major prey species of the Black Sparrowhawk, all habitat types investigated contained ample prey, with

the exception of forests and gardens. This may mask the effect of an urban gradient on diet composition and on health parameters.

The abundance of food resources and resulting lack of nutritional stress may explain why Black Sparrowhawks are seemingly free of the negative health impacts expected to arise from urbanisation. These findings may help to understand the success of the species in its newly colonised area and suggest that for urban-dwelling, bird-eating raptors, the abundance of prey in cities may override potential negative impacts of urbanisation on health due to disturbance or other sources of stress.

Keywords: urban ecology, raptor, diet, blood parasite, body condition, *Leucocytozoon*, *Haemoproteus*, Heterophil/Lymphocyte ratio

Introduction

Urbanisation and biodiversity

As the earth's natural areas are rapidly being transformed into cities and the majority of the world's population now lives in urban areas, increasing emphasis is being placed on biological research and conservation within cities (Grimm et al., 2008; Kowarik, 2011). The impacts of urbanisation on global biodiversity have been extensive, leading to the loss of indigenous species and spread of alien-invasive species, habitat loss and fragmentation, altered biogeochemical cycles and the introduction of novel stressors such as traffic, noise, disease, pollution and introduced predators such as domestic pets (Brearley et al., 2012; Goddard et al., 2009; Grimm et al., 2008; Marzluff, 2001; McKinney, 2006). In terms of its effects on biotic communities, urbanisation generally leads to a complete rearrangement of assemblages whereby natural habitats and species are replaced with human-dominated landscapes containing novel species compositions and interactions (McDonald et al., 2008; Miller and Hobbs, 2002; Ortega-Alvarez and Macgregor-Fors, 2009). In addition, through a process known as biotic homogenisation, urbanisation creates a uniform physical environment by replacing natural ecosystems with a built-up environment where urban-tolerant species become widespread, diluting the diversity of urban flora and fauna (Crocì et al., 2008; McKinney, 2006; Ortega-Alvarez and Macgregor-Fors, 2009; van Rensburg et al., 2009).

Birds are often studied as indicators of ecosystem health, including in an urban context, because their ecology is well-understood and they respond rapidly to environmental changes (Alberti, 2005; Breuste et al., 2008; Fontana et al., 2011; Vandewalle et al., 2010; Wenny et al., 2011; Whelan et al., 2008). Birds are affected by urbanisation "directly through changes in ecosystem processes, habitat, and food supply" or "indirectly through changes in predation, interspecific competition and diseases" (Alberti, 2005, p.179). The best-studied effects of urbanisation on birds are its effects on species composition, filtering species according to their levels of tolerance to urban disturbance. In line with this, birds (and other urban species) can be split into three groups – 'urban avoiders', 'urban adapters' and 'urban exploiters' (Blair, 1999; McKinney, 2002). The term urban exploiters refers to a number of mainly non-native species such as pigeons (*Columbia livia*) or Common Starlings (*Sturnus vulgaris*), whose success in urban areas is related to their ability to exploit anthropogenic resources such as garbage dumps, feeders or nest boxes, which they are largely dependent on (McKinney, 2002). Urban-adapting species make use of both natural resources and those subsidised by humans, and are thus more flexible in their lifestyles (McKinney, 2002). Urban-avoiding species are those that are highly sensitive to stressors and have very specific habitat and

resource requirements, therefore tending not to occur in cities (McKinney, 2002). As a result of this ecological filtering, overall avian diversity usually decreases in cities, but the sheer abundance of birds may increase due to a greater volume of urban exploiters (Blair, 1996; Croci et al., 2008; Faeth et al., 2011; Marzluff, 2001; McKinney, 2002; Ortega-Alvarez and Macgregor-Fors, 2009).

An urban-exploiting or adaptable species may be able to make use of abundant resources in the short term, but other costs of urban-living may undermine its long-term health and persistence in an urban environment. In other words, cities may act as ‘ecological traps’ – habitats which appear attractive due to abundant food and nest-sites and an overall decrease in predators, but are in fact unsuitable due to novel threats, disturbance, disease or low food quality (Mannan and Boal, 2004; Rutz, 2006; Rutz, 2008; Sumasgutner et al., 2014a).

Towards understanding the individual level impacts of urbanisation

Much research has concentrated on changes in biodiversity and species composition as a result of urbanisation (Blair, 1999; Clergeau et al., 1998; Kowarik, 2011; McDonald et al., 2008; McKinney, 2002; Ramalho and Hobbs, 2012), but our understanding of smaller-scale impacts on species ecology and physiology remains shallow (Almasi et al., 2015; Giraudeau et al., 2014; Hahs and Evans, 2015; Isaksson, 2015). In spite of a growing body of literature on urban ecology, there remains a distinct lack of research on smaller-scale impacts on species ecology and physiology, and the mechanisms by which urbanisation affects ecological interactions and evolutionary processes (Delgado and French, 2012; Jacquin et al., 2013; Liker et al., 2008; Shochat, 2004). There can be both positive and negative effects of urbanisation and these effects differ at the individual, population and community levels (Almasi et al., 2015). Therefore, an appreciation of how these conflicting impacts interact to affect the short and long-term survival and fitness of species remains a major gap in our understanding.

At the individual level, urban disturbances can have significant impacts on physiology, behaviour and fitness (e.g. Almasi et al., 2015; Giraudeau et al., 2014; Isaksson, 2015). Direct and indirect disturbances in urban areas can include noise (Slabbekoorn and Ripmeester, 2008), diet imbalances (Andersson et al., 2015; Faeth et al., 2005; Shochat, 2004), changes in predation pressure (Fischer et al., 2012; Møller, 2008, 2009, 2012), urban heat island effects (Yow, 2007), collision with cars and windows (Ortega-Alvarez and MacGregor-Fors, 2009), electrocution (Palomino and Carrascal, 2007) and chemical pollution (Giraudeau et al., 2014). These disturbances can elicit responses at different levels, leading for instance, to oxidative

stress, altered immune defences or changes in levels of aggression or foraging behaviour (Almasi et al., 2015; Ditchkoff et al., 2006; Isaksson 2015; Lowry et al., 2013). Such responses at the physiological or behavioural level usually have short-term impacts, though some disturbances may have consequences for individual fitness, usually with medium-term consequences on breeding performance or individual survival and sometimes long-term consequences on species and population dynamics (Almasi et al., 2015).

Due to its impacts on habitats, community composition, behaviour and physiology, urbanisation is also likely to alter interactions between hosts and pathogens. The increased densities and contact between humans, domestic and wildlife species, and sometimes the abundance of favourable environments for parasite vectors, can increase the transmission of infectious diseases or favour the (re)emergence of pathogens in urban environments (Brearley et al., 2012; Ditchkoff et al., 2006). In addition, the higher level of physiological stress faced by animals in cities can compromise their immune ability and increase their susceptibility to pathogens (Bradley and Altizer, 2007; Brearley et al., 2012; Giraudeau et al., 2014). However, studies on parasite prevalence in urban areas have found mixed results. In some cases, parasite infection increases with urbanisation, whereas in other cases it decreases (Delgado and French, 2012; Okanga et al., 2013). The lack of a single trend is likely due to the diversity of hosts and of pathogens and their modes of transmission (Brearley et al., 2012; Delgado and French, 2012).

Urbanisation can further alter interspecific interactions by disrupting trophic interactions in complex multi-species networks, changing distribution patterns of predators, prey and competitors or shifting phenologies, thus producing trophic mismatches and food shortages (Fischer et al., 2012). On the other hand, urban habitats can provide an artificially enhanced diversity of anthropogenic food and nesting resources, for example due to the cultivation of flowering plants in parks and gardens (Fischer et al., 2012; McKinney, 2002; Zhou and Chu, 2012). Urban impacts on species interactions can further interact with existing impacts on health or host-parasite interactions and exacerbate their effects (Ditchkoff et al., 2006). For example, competition or food shortages may be a cause of both physiological stress and increased densities, which may facilitate the transmission of pathogens, due to both increased susceptibility and exposure.

Again, birds make good study species for examining these finer scale impacts of urbanisation on individual species. Because of their high mobility and exposure to several environments, birds may be exposed to a number of pathogens and stressors which occur in urban environments, potentially placing them under greater threat. Certain groups of birds may offer additional research interest in this regard, due to their ecological roles or conservation status, such as raptors (Carrete et al., 2009). Most studies that have

addressed the impacts of urbanisation on the ecology and physiology of birds have focused on smaller passerines (e.g. Bonnington et al., 2013; Dominoni et al., 2013; Giraudeau et al., 2014; Meillière et al., 2015) but few have been conducted on raptors and many of these have been restricted to urban raptors in the developed world (e.g. Coleman et al., 2002; Mannan and Boal, 2000; Parker, 1996; Rosenfield et al., 1995; Rutz, 2006; Sodhi et al., 1992; Sumasgutner et al., 2014a).

Urban impacts on raptors

Raptors form an important group of species to study in an urban context and are of particular conservation concern since they are often considered apex predators and umbrella species in urban environments, their loss often having cascading effects on food webs (Lyly et al., 2015; Mueller et al., 2016; Palomino and Carrascal, 2007, Sekercioglu, 2006). They are also charismatic species which attract interest and stewardship amongst urban residents and they can be flagship species for urban conservation (Mannan and Boal, 2004; Palomino and Carrascal, 2007). In addition, each species may perform distinct ecological functions, filling unique trophic or habitat niches, and the presence of several raptor species in an urban area may be indicative of a healthy, well-functioning ecosystem (Burgas et al., 2014; Carrete et al., 2009; Palomino and Carrascal, 2007; Sekercioglu, 2006; Sorace and Gustin, 2009). However, raptors are often vulnerable to a wide range of threats since their success is dependent on relatively large tracts of good habitat and a stable supply of prey (Newton, 1979; Ontiveros and Pleguezuelos, 2000; Reeves and Boshoff, 2015; Widén, 1994). Studying the dynamics of raptor populations and the mechanisms of their persistence or peril in urban areas can therefore be informative for urban biodiversity conservation (Rutz, 2008).

Several raptor species seem to actively seek out urban areas. Over 25 species are known to live and breed in cities (Love and Bird, 2000; Rutz, 2008; Sumasgutner et al., 2014b), including the Mississippi Kite (*Ictinia mississippiensis*; Parker, 1996), Merlin (*Falco columbarius*; Sodhi et al., 1992), Cooper's Hawk (*Accipiter cooperii*; Boal and Mannan, 1998; Rosenfield et al., 1995), Sharp-shinned Hawk (*Accipiter striatus*; Coleman et al., 2002), Eurasian Kestrel (*Falco tinnunculus*; Sumasgutner et al., 2014b) and Eastern Screech Owl (*Megascops asio*; Gehlbach, 1994). These species may sometimes be more common in cities than in natural habitats (Mannan and Boal 2004). The most famous example is the Peregrine Falcon (*Falco peregrinus*; Cade and Bird, 1990; McKinney, 2002), a species that in many regions is actually best recognised as a metropolitan, city-dwelling raptor. Species such as these tend to thrive in urban areas because they are free from natural predators and persecution and enjoy an abundant supply of food and

habitat (Chace and Walsh, 2006; Gehlbach, 1994; Mannan and Boal, 2004; Shochat, 2004). Their prey species, such as rodents or pigeons, are abundant in urban landscapes, and cities often contain structures that mimic their natural habitats (Mannan and Boal, 2004). For example, concrete buildings resemble the natural cliffs and crags that Peregrine Falcons and kestrels nest in (Faeth et al., 2011; McKinney, 2002; Sumasgutner et al., 2014b) Similarly, exotic tree plantations substitute for the natural tropical, montane and riparian woodlands which Cooper's Hawks and several other congeners tend to nest in (Mannan and Boal, 2004; Tarboton and Allan, 1984). As a result, the trend of raptors colonising urban areas is on the rise, with more and more cases being reported, like the Crested Goshawk (*Accipiter trivirgatus*; Lin et al., 2015), Crowned Eagle (*Stephanoaetus coronatus*; McPherson et al., 2015; Reeves and Boshoff, 2015), Northern Goshawk (*Accipiter gentilis*; Rutz, 2006), Eurasian Sparrowhawk (*Accipiter nisus*; Rutz, 2006; Rutz, 2008) and the focus of this study, the Black Sparrowhawk (*Accipiter melanoleucus*; Martin et al., 2014b).

In contrast, many other raptors are vulnerable to the impacts of urbanisation (Mannan and Boal, 2004) and are expected to decline (Carrete et al., 2009; Møller, 2011), due to collisions with windows or traffic, electrocution, predation by domestic animals, shortages of suitable prey or habitat, persecution and poisoning (Mannan and Boal 2004). Cities may also pose more subtle physiological risks to raptors, even to those species which appear to do well in urban areas. Careful investigation is therefore required before it is assumed that these raptors are faring successfully in urban areas without consequences. For example, Eurasian Kestrels may benefit from buildings which serve as prime nesting sites, but may be forced to travel further distances to find suitable prey, or attempt (less successfully) to exploit new prey items, resulting in decreased breeding success (Sumasgutner et al., 2014a). Examining the mechanisms behind the perceived success of raptors in urban areas can thus help to establish whether these species are falling into ecological traps or whether they are genuine urban-adapters. In this study, we explore some of these questions in the Black Sparrowhawk, an African raptor that has recently colonised predominantly urban areas in south-western South Africa, and determine whether it may be suffering from hidden consequences of urban living.

Black Sparrowhawks on the Cape Peninsula, South Africa

The Black Sparrowhawk is the largest of all African *Accipiter* species (Brown and Brown, 1979) and occurs in the forested areas of East, West and southern Africa. In South Africa, it has experienced a dramatic and rapid range expansion in recent years, which has seen its distribution extend south and westwards (Hockey and Midgley, 2009). On the Cape Peninsula, Black Sparrowhawks were once described as uncommon residents, with early records of the species in the Cape dating back to the 1970s (Curtis, 1998). Since then, they have rapidly colonised the Cape and become common breeding residents, with almost 50 pairs believed to be currently breeding on the Cape Peninsula (Curtis, 1998; Martin et al., 2014b). This range expansion has increasingly brought Black Sparrowhawks into contact with urban and human-dominated landscapes (Sumasgutner et al., under review). As a result, there is growing interest in how Black Sparrowhawks are responding to anthropogenic activities (Curtis, 1998).

The success of the Black Sparrowhawk in South Africa has largely been attributed to the spread of exotic trees such as pines, eucalypts and poplars in plantations, gardens, farms and parks (Malan and Robinson, 1999). While the spread of these trees has largely had negative impacts on biodiversity in South Africa, Black Sparrowhawks and other tree-nesting raptors have greatly benefitted from the prime nesting sites which they provide (Malan and Robinson, 2001). In addition, Black Sparrowhawks are bird-eating raptors, favouring mainly *Columbidae* (pigeons and doves) and gamebirds such as francolin and guineafowl (Brown and Brown, 1979; Malan and Robinson 1999). Pigeons and doves tend to proliferate in urban areas, potentially providing Black Sparrowhawks with a rich prey resource which may further contribute to their success in urbanised areas (Malan and Robinson, 1999).

While human-altered environments are believed to have provided resources that have been central to the success of Black Sparrowhawks on the Cape Peninsula, it is unknown whether exposure to urban environments may be having negative consequences on individual birds. There may be impacts on the physiological stress, condition and infection risk of individuals. Thus, while Black Sparrowhawks appear to be very successful in the human-dominated landscapes of the Cape Peninsula, are there any costs that come with this urban living? Addressing these questions in the Black Sparrowhawks could help in understanding and predicting the impacts of urbanisation on other similar species, whilst also shedding light on the mechanisms behind their success on the Cape Peninsula.

Aims and objectives

Taking advantage of the long-term study of the Black Sparrowhawk population on the Cape Peninsula carried out since 2000 (Amar et al., 2014; Curtis, 1998; Lei et al., 2013), we aimed to determine the impacts of urbanisation on the health and diet of this species. We firstly examined whether the degree of urbanisation alters the health of nestlings by analysing various indices of condition, immune response and blood parasite infection along a gradient of increasing urban cover. We secondly assessed the composition of birds' diet and the abundance of prey in habitats of various degrees of urbanisation to determine whether a potential impact of urbanisation on their diet may explain impacts on their health. Understanding these processes will help us to understand the costs and benefits that these raptors might face in an urban environment. For example, urbanisation might provide excellent nesting sites and opportunities to access abundant prey for bird-eating raptors, but it may come at a higher physiological cost.

There are several ways of measuring physiological stress and health status in birds. In this study we focused on body condition, leucocyte profiles and parasite loads. Body condition is a measure of the fat content or nutrient reserves in an animal, and can be a useful indicator of chronic disturbance and nutritional stress (Almasi et al., 2015; Labocha and Hayes, 2012). It is classically estimated by extracting the residuals of a regression run between at least two morphometric measurements (Labocha and Hayes, 2012), accounting for the sex of individuals in size dimorphic species. In urban areas, birds such as House Sparrows (*Passer domesticus*), have been found to be in lower condition than their rural counterparts (Liker et al., 2008; Shochat, 2004). Possible mechanisms include prolonged periods of nutritional stress (due to decrease in quantity or quality of food), illness or high levels of pollution or disturbance. We therefore expect Black Sparrowhawk nestlings to be in lower condition in more urban areas.

Leucocyte profiles, obtained by counting the relative numbers of the different types of leucocytes (white blood cells) in a blood smear, can reveal much about the immune condition and stress of an animal (Davis et al., 2008). Different leucocytes perform different functions and their relative frequencies fluctuate depending on an animal's physiological condition. Heterophils are produced in response to infections, inflammation and stress, whereas lymphocytes produce immunoglobulin (Davis et al., 2008). The ratio of Heterophils/Lymphocytes (H/L ratio) has been shown to be a reliable measure of physiological stress in birds and other vertebrates, since it correlates with the level of glucocorticoids (stress hormones; Davis et al., 2008), while not increasing rapidly when birds are stressed from capture and handling (Cirule et al., 2012). Under conditions of physiological stress, illness or pollution, the secretion of glucocorticoids leads

to an elevation in the number of heterophils in the blood and a decrease in the number of lymphocytes, and thus an increase in the H/L ratio (Davis et al., 2008). Studies have shown that the H/L ratio is sensitive to environmental stressors (Muller et al., 2011) and human-induced habitat changes (Banbura et al., 2013). We thus predict that disturbance and increased immune stress due to pollutants or parasites in more urbanised environments will lead to an elevated H/L ratio in Black Sparrowhawk nestlings.

Potential changes in host-parasite interactions along the urban gradient were investigated using the infection risk and infection intensity by blood parasites. The infection risk measures the probability that an individual is infected by a parasite, as a result of both its exposure to it and its susceptibility to it once exposed. The infection intensity, or parasite load is the degree of parasitemia within infected individuals and should be correlated to individuals' susceptibility to the parasite. Black Sparrowhawks are known to become infected with the avian malarial blood parasites *Haemoproteus nisi* and *Leucocytozoon toddi*; both of which are present in the study population (Lei et al., 2013). They are both vector-borne parasites, transmitted respectively by biting midges and black flies (Valkiunas, 2005). The exposure of the birds to the parasites therefore depends strongly on the abundance of their vectors. Since the effects of urbanisation on these insects are not known, it is difficult to predict an effect on the infection risk. We however predict that a higher susceptibility (due to a compromised immune system or low body condition in the face of physiological stress, disturbance and pollutants) in more urban nestlings may increase their parasite load (Bradley and Altizer, 2007; Brearley et al., 2012; Giraudeau et al., 2014).

Finally, if the health status of Black Sparrowhawks is compromised within urban habitats, one of the mechanisms for this might be due to changes in diet composition, as a result of differences in the abundance of the prey within urban habitats. Alternatively, if there are no negative health impacts of urbanisation, this might be due to urban habitats providing similar or more prey resources compared with less urban areas. We explored this issue by first exploring whether diet composition and diet breadth vary along an urban gradient, by analysing prey remains collected from different nest sites. We then looked at how the abundance of the key prey species varies in different habitats that occur within our Cape Peninsula population and whether this might explain why the species is seemingly thriving within urban environments.

Methods

Study Area

This study was conducted on the resident breeding population of Black Sparrowhawks on the Cape Peninsula, South Africa. The study area falls within the boundaries of the City of Cape Town, which contains a matrix of various habitats and covers an area of 2460km² (Rebelo et al., 2011). The study area are comprises of heavily urbanised areas, suburbia, patches of indigenous Afromontane forest and Fynbos vegetation, wetlands and several artificial habitats like gardens, golf courses, exotic tree stands and vineyards. The Cape Peninsula experiences a Mediterranean climate and receives winter rainfall (mean annual rainfall: ca.1250mm; average monthly temperatures: 12-21°C) (Cowling, MacDonald and Simmons, 1996).

Within the Cape Peninsula, Black Sparrowhawk nests have been monitored since 2000. Currently, the territories of about 50 individual breeding pairs are known and systematically monitored (Figure 1).

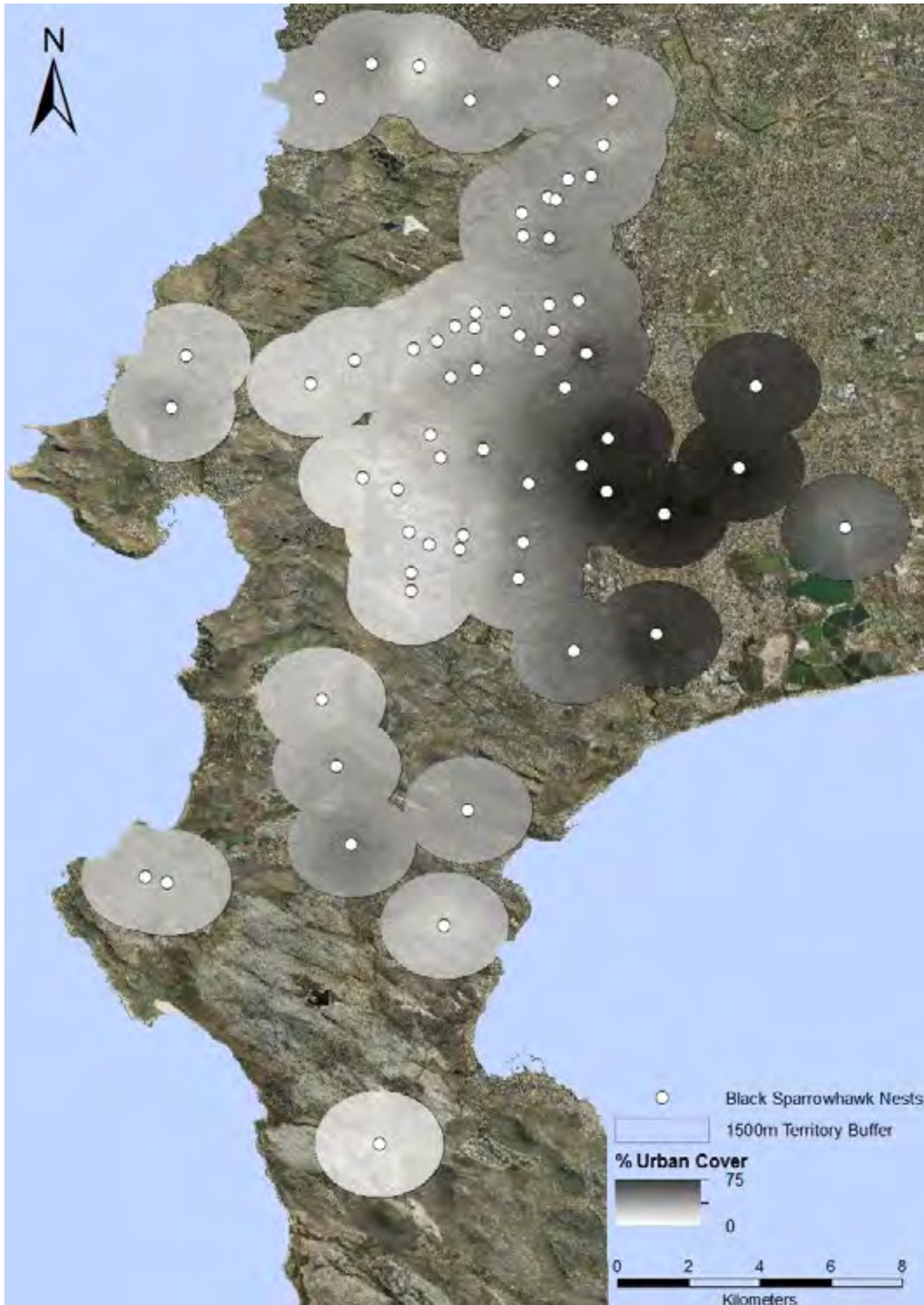


Figure 1: Map of Black Sparrowhawk nest sites (N = 64 territories) used in this study showing the degree of urbanisation within a 1500 m buffer around each nest. Multiple active or abandoned nest sites may occur within a single territory but in this case only the nests most often occupied have been mapped, and those for which we had samples for this study.

Data Collection

Field sampling

During the breeding season (March-November) of each year since 2000, all known Black Sparrowhawk nests on the Cape Peninsula have been monitored to determine whether or not breeding has taken place successfully. Active nests are located by surveying suitable stands of trees and known nesting sites and searching for sparrowhawks, prey remains, whitewash or nesting structures (Martin et al., 2014a). At sites where birds are believed to be attempting to breed, nests are visited repeatedly throughout the season until breeding behaviour is observed (Martin et al., 2014a). At the age of 3-5 weeks, chicks from successful nests are brought down from their nests by a professional tree climber. At this age, nestlings are old enough to be sexed and young enough to be safely handled without the risk of them jumping from the nest. All nestlings are individually colour-ringed and several morphometric measurements are taken. Among them, the body mass and tarsus length (length of the tarsometatarsal bone from the “knee” to the “ball” of the foot, with the foot held at a right angle to the tibia, measured with vernier callipers) of the birds were used in this study to assess their body condition. In most instances, blood samples have also been collected from the brachial vein. The skin over the vein was first sterilised with an alcohol swab and then punctured either with a 21 gauge insulin needle and syringe into which 1ml of blood was drawn, or pierced with a 21 gauge insulin needle and the blood then collected in a 75 µl heparinised capillary tube via capillary action. Blood smears were prepared and air-dried directly in the field. Only data from nestlings were analysed in this study as we did not have a large enough sample size of data from adults. Data from a total of 343 nestlings were used, although the sample size varies depending on the parameter considered (body condition vs. blood parameters) as detailed in the results section.

Estimation of health status

All blood smears prepared in the field were brought back to the lab, where they were fixed with methanol, stained with Giemsa’s stain following the standard protocol by Hemacolor® Rapid staining of blood smear kit (Merck, Darmstadt, Germany) and allowed to set for at least 24 hours. These slides were then analysed under a binocular compound microscope with oil immersion lenses in order to determine relative leucocyte counts as well as infection by blood parasites.

Each slide was scanned for 20 minutes at 40x magnification to determine the presence or absence of each type of blood parasite. The intensity of infection in each individual was determined by scanning each slide

at 1000x magnification and counting the number of parasites seen within 10,000 erythrocytes. In order to do this, we first counted the number of erythrocytes observed in one field of view and then scanned as many fields as necessary to reach roughly 10,000 erythrocytes (usually 30-100 fields). This is generally done in a straight line from one end of the slide to the other in order to compensate for differences in the thickness of the blood smear. Similarly, each slide was scanned at a magnification of 1000x to determine the relative number of each type of leucocyte (heterophil, lymphocyte, basophil, eosinophil and monocyte) within 10,000 erythrocytes. The number of each type of leucocyte within 100 leucocytes was then calculated and this was used to calculate the H/L ratio.

Since nestlings were not all measured at the exact same age, we followed the method described by Roulin et al. (2007) to derive their body condition index. We first extracted residuals from a second-order curve of body mass on tarsus length. To correct for variation in condition due to sexual dimorphism, we then conducted a two-way ANOVA on these residuals. The residuals of the ANOVA were taken as the body condition index (corrected for gender effects) and these values were used for further analyses.

Diet estimation

Diet composition: prey remains analysis

During the breeding season, nests were visited 4-6 times for monitoring purposes. During these visits, the area underneath and around the nest trees were searched for prey remains. Bird-eating raptors like Black Sparrowhawks will pluck the feathers from their prey and eat the meat off the bone, often leaving discarded remains of their prey below perch sites in close proximity of the nest (Brown and Brown, 1979). These remains can easily be identified to species level by comparing them with known reference samples due to distinct osteological features. The main method used to distinguish different species was the shape and size of the humerus, keel, coracoid and pelvic girdle - the bones most commonly found in prey remains, as well as identification of feathers. In cases where multiple remains were collected from a single location, they were only recorded as separate items if several of the same element could be identified, e.g. multiple keels, pelvic girdles or pairs of humeri. Reference specimens of skeletons of known prey species were obtained from the Iziko Natural History Museum of South Africa and used for comparison purposes. In some case the assistance of an archaeozoologist (Dr. Graham Avery, Iziko Museum) was required in identification. Prey remains collected from nest sites in 2012 and 2013 were already analysed

in a previous study (Baigrie, 2013). Additional samples collected in 2014 and 2015 were analysed in the current study and pooled with the previous records.

In the analysis of prey remains, there may be a bias towards larger species, where it is more likely that remains will be discarded; whereas smaller prey species would more often be eaten whole and leave no identifiable remains (Brown and Brown, 1979; Malan and Robinson, 1999; Rutz, 2003; Sodhi and Oliphant 1993). It has however been suggested that smaller passerines weighing less than 60 g are not significant prey items for Black Sparrowhawks (Brown and Brown 1979). It is also important to note that those prey remains found at the nest site may only represent a portion of what is being eaten by adult Black Sparrowhawks, as other remains may be discarded elsewhere (Drewitt and Dixon, 2008; Rutz, 2003). Furthermore, these may not represent all of the prey brought to a nest, as some samples may be lost due to scavenging, decomposition, weather or cleaning (Drewitt and Dixon, 2008).

Prey abundance: point counts

Bird counts were conducted at 116 sites in order to determine the abundance of prey species in each habitat type (Figure 2). The sites were chosen such that each habitat received similar sampling effort (Table 1).

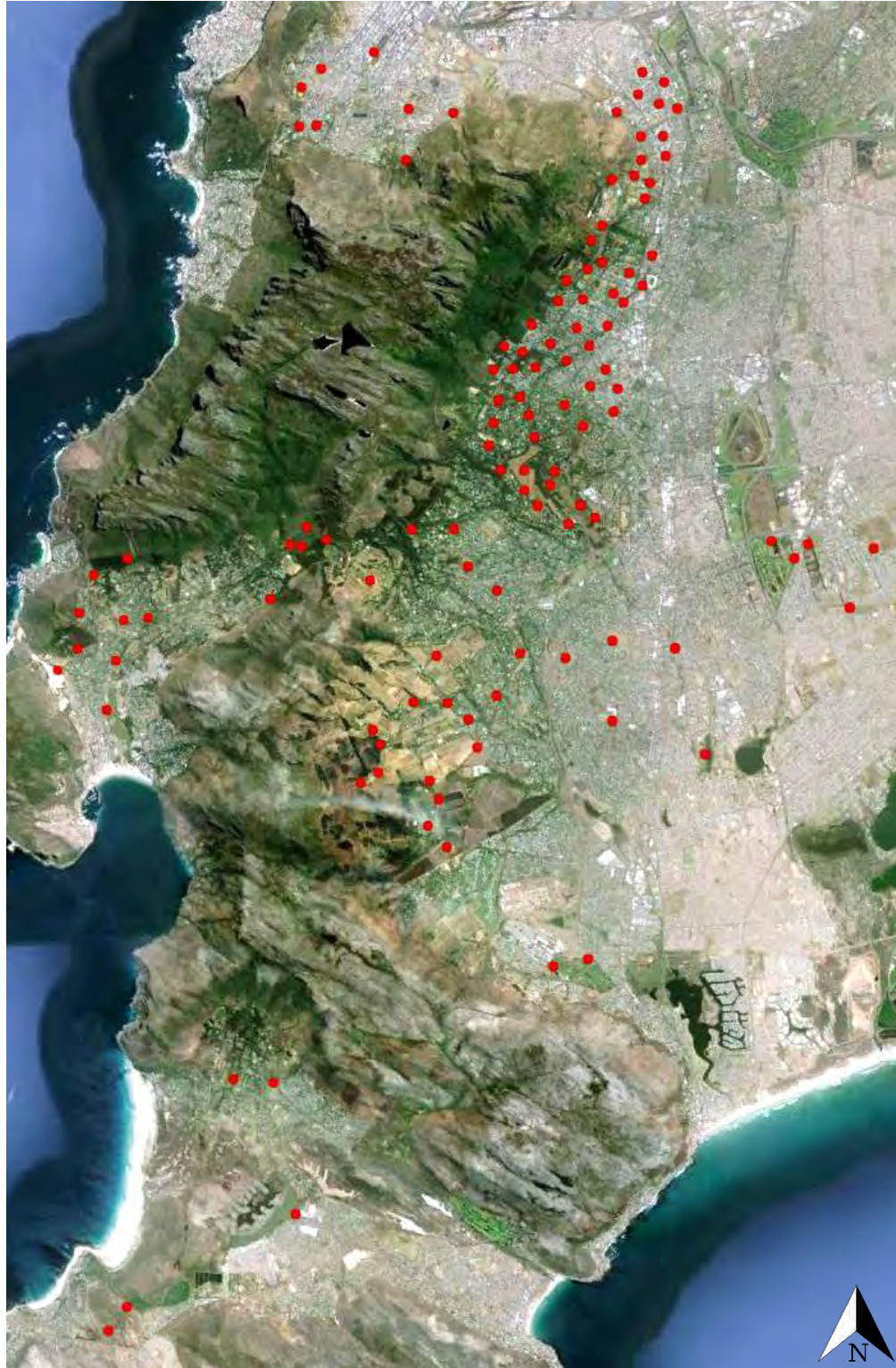


Figure 2: Google Earth image of point count sites (N = 116) covering a range of habitats throughout the Cape Peninsula study area. Each point was surveyed twice either in May and September of 2014 or in October and December of 2015. Point counts lasted 15 minutes and during this time, all birds within 150 m were recorded.

Table 1: Descriptions of habitat types and the number of sites within each of them at which point counts were conducted (*N*).

Habitat Type	Description	N	Picture
Forest	Patches of light-dense forest containing tall trees	17	
Garden	Cultivated, suburban gardens	18	
Open Intensive Landscape	Lawns, sports fields, golf courses	17	
Open Landscape	Natural grassland, fynbos, heathland	17	
Field/Vineyard	Agricultural fields or vineyards	18	
Urban	Roads, pavements, buildings, construction sites, parking lots	20	

Wetland	Natural and semi-natural wetlands, dams, reedbeds, rivers	9	
---------	--	---	---



At each site, all birds seen and heard within a 150 m radius in a 15 minute time period were counted. Two counts were conducted at each site, each count about three months apart, giving a total of 232 individual counts. Of these, 98 counts were conducted in May and August of 2014 and 134 in September/October and December of 2015. Since there was no significant difference in abundance between the different sessions (GLM regressions with negative binomial errors: $p = 0.1$, $z = 1.64$, $dF = 97$ and $p = 0.6$, $z = 0.51$, $dF = 131$, for 2014 and 2015, respectively), the abundance of each species was calculated over all months and years. Of the species recorded in the counts, only those that Black Sparrowhawks are known to prey on (observed in prey remains in this study or documented in other studies; Brown and Brown, 1979; Malan and Robinson, 1999) were included in the analyses.

Ethical note

Ethical clearance was obtained for all procedures required for the long-term study of the Black Sparrowhawk population of the Cape Peninsula and the research was approved by the University of Cape Town's Science Faculty Animal Ethics Committee (permit number: 2012/V37/AA). All procedures were in line with South African legal requirements and the necessary permits for monitoring, capturing and ringing birds were acquired from Cape Nature and South African National Parks.

The amount of blood collected was well within safe limits (below 1% of the body weight; Campbell and Ellis, 2007). No injuries occurred due to these procedures and all personnel that handled sparrowhawks received prior training from a professional veterinarian. All fieldwork procedures were only carried out in daylight hours and never in adverse weather conditions or temperatures exceeding 30°C.

Data Analysis

Defining the urban gradient

A combination of existing spatially explicit geo-layers and a 6.24 cm resolution colour aerial photograph of Cape Town from March 2009 (provided by the University of Cape Town's GIS lab) were used to estimate the percentage of each habitat type within the study area. A 500 x 500 m grid and existing layers (wetland provided by the South African National Biodiversity Institute, and tree cover; Hansen et al., 2013) were overlaid on the aerial image in order to estimate the percentage cover of each habitat type in each grid cell. These data were used to calculate the cover of each habitat type (Table 1) within a 1500 m buffer around each nest. This buffer covers an area of 3 x 3 km squares, i.e. 900 ha, an area slightly larger than the average home range size (95% kernel density) estimated for the species, based on data from four GPS tagged adult birds (breeding season: 644 ha, throughout the year: 677 ha; G. Tate, unpubl. data). The 1500 m buffer around the nest site is hereby referred to as a "territory". A total of 64 territories were covered in this study, though not all of these were included in every component of the analyses. The urbanisation gradient was defined by the percentage of urban land cover within each territory.

Statistical analyses

Effect of urbanisation on health

Each health parameter considered in this study (body condition index, parasite infection risk and intensity for *Haemoproteus* and *Leucocytozoon*, H/L ratio) was analysed as a response variable in a generalised linear mixed model (GLMM) using the degree of urbanisation (% urban cover in each territory) as the explanatory variable. The GLMMs for H/L ratio and body condition followed a Gaussian error structure. Infection risk (presence or absence) for both parasites was analysed with a binomial error structure. Infection intensity was analysed with a negative binomial error structure as these were over-dispersed count data, but only those individuals which were infected were analysed. All analyses were conducted in R (R Core Team, 2015), using the MASS (Venables and Ripley, 2002), lme4 (Bates et al., 2015), effects (Fox, 2003) and car (Fox and Weisberg, 2011) packages. The year, nest site and brood that each nestling was sampled at were included as random terms in each model, in order to account for pseudoreplication due to several individuals coming from the same nest between years or multiple broods within the year, and multiple individuals from the same brood. The quantitative variables were standardised in order to bring

the variables to comparable dimensions. Standardisation was done by centring (subtracting the sample mean) and scaling (dividing by the sample standard deviation) each variable (Schielzeth, 2010).

Effect of urbanisation on diet composition

Data from prey remains collected over multiple years at the same nest were compiled to produce an aggregate description of diet for each territory. Ten prey categories were created, including the nine most common prey items plus another category for all other species (Table 3). We considered all territories for which we had ≥ 7 prey remains, as a rarefaction curve indicated this was enough to describe 90% of the diet of a territory (Appendix A). The diet breadth was calculated for each territory using the standardised Levins index (B_A ; Krebs, 2004):

$$B_A = \frac{B-1}{N-1} \quad (1)$$

where B is the non-standardised Levins index (Levins 1968):

$$B = \frac{1}{\sum p_i^2} \quad (2)$$

where p_i is the proportion of the diet represented by each prey type and N is the number of different prey categories, i.e., 10 in our study. The standardised Levins index, whose values range from 0 to 1, was then analysed against the degree of urbanisation in a generalised linear model (GLM) using a Gaussian error structure. For each species, the proportion they represented within the total prey remains was analysed against the degree of urbanisation with a binomially distributed GLM.

Effect of urbanisation on prey abundance

Point counts were used to calculate the total abundance of each species in each habitat, as well as the average abundance of each prey species observed per point count in each habitat type. For each prey species, we used (1) a Kruskal Wallis test to test whether the prey abundance differed between habitat types and (2) post-hoc Dunn tests (Dunn, 1964) to identify the habitat(s) in which the abundance was(were) significantly different. In step (2), the p-values were corrected using the Bonferroni correction to account for the increased type-I error due to multiple testing. Non-parametric tests were used because

data were non-normal and because we could not find any transformations that enabled us to respect the assumptions of linear models used in the other components of this study.

Results

Black Sparrowhawk territories on the urban gradient

Combining all the territories used in this study (N = 64; Figure 3), open landscape made up the biggest proportion of the study area (34%), followed by forest (28%) and urban areas (27%). Other habitats made up a very small proportion of the study area.

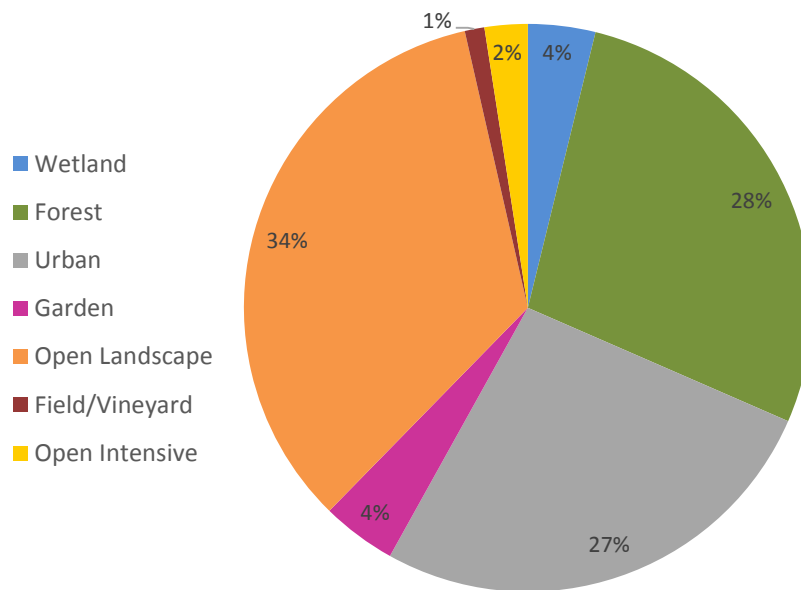


Figure3: Proportion of total area within study area (N = 64 territories pooled) covered by each habitat type.

Of these 64 territories, the degree of urbanisation within them varied from 0.25% to 75%, though most territories experienced relatively low levels of urbanisation (< 40%; Figure 4).

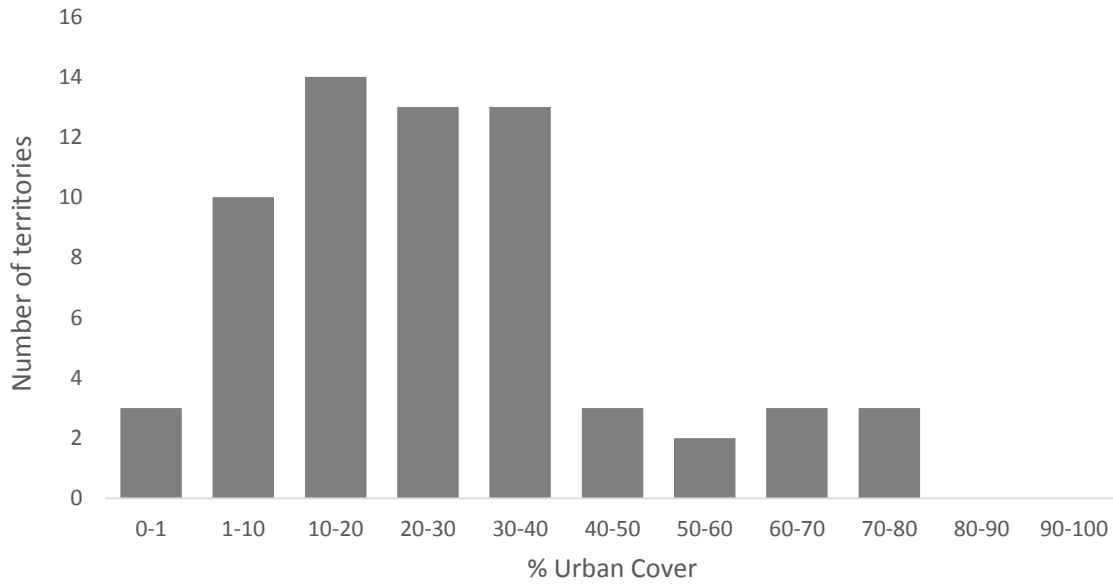


Figure 4: Percentage of urban cover within Black Sparrowhawk territories used in this study (N= 64).

Averaging the 11 territories that were considered highly urbanised (> 40% urban cover; Figure 5a), urban habitat made up the biggest proportion of the area (60%), followed by open landscape (17%). In the 53 territories that were considered less urbanised (< 40%; Figure 5b), the majority of the land cover was made up of open landscape (38%) and forest (32%).

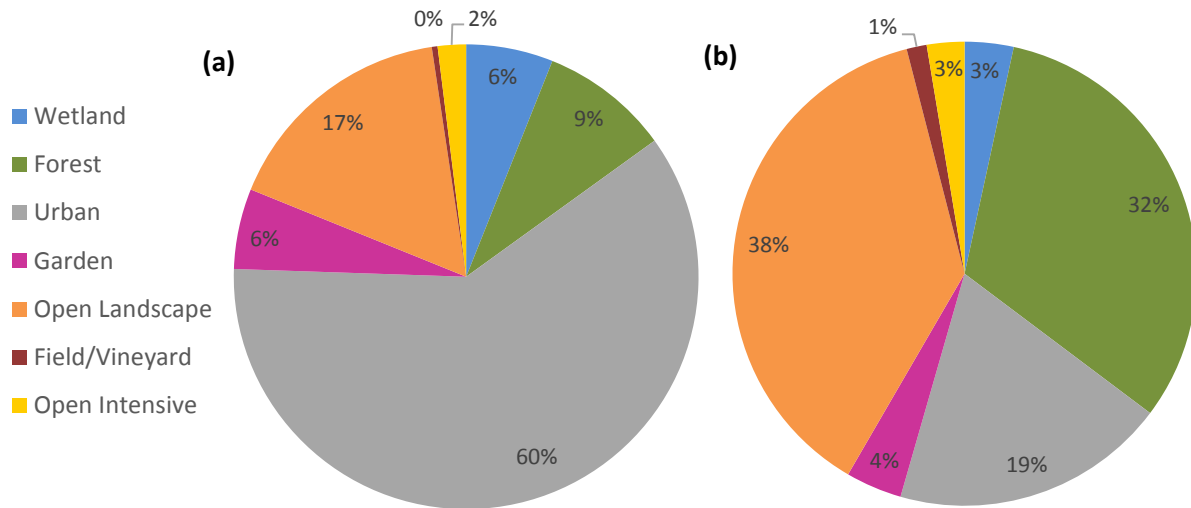


Figure 5: Average proportion of area covered by each habitat type in a) more urban territories (>40% urban cover, N = 11 territories), and b) less urban territories (<40% urban cover, N = 53 territories).

Health and blood parasite infection along the urban gradient

We could estimate the body condition index of 339 nestlings from 55 territories. We found no significant relationship between the degree of urbanisation around their nest and their body condition ($p = 0.79$, $\chi^2 = 0.08$, $ddf = 1178$; Table 2; Figure 6a).

Blood samples were taken from 250 nestlings from 51 territories. The H/L ratio varied considerably among these individuals, ranging between 0.08 and 3.65 (0.83 ± 0.45), but it was not significantly influenced by the degree of urbanisation around the nest ($p = 0.93$, $\chi^2 = 0.007$, $ddf = 132$; Table 2; Figure 6b). Examining the same blood samples for blood parasites, we found that 64 of the 250 nestlings were infected by *Haemoproteus nisi* (26%), with an infection intensity ranging from 1 to 40 parasites per 10,000 erythrocytes. We found no significant relationship between the degree of urbanisation around the nest on either *H. nisi* infection risk ($p = 0.36$, $\chi^2 = 0.83$, $ddf = 132$; Table 2; Figure 6c) or infection intensity ($p = 0.81$, $\chi^2 = 0.06$, $ddf = 41$; Table 2; Figure 6d). For *Leucocytozoon toddi*, 52 of the 250 sampled nestlings were infected (21%), with an infection intensity ranging from 1 to 254 parasites per 10,000 erythrocytes. *L. toddi* infection risk ($p = 0.01$, $\chi^2 = 6.09$, $ddf = 132$; Table 2; Figure 6e) and intensity ($p = 0.009$, $\chi^2 = 7.79$, $ddf = 43$; Table 2; Figure 6f) both decreased significantly with an increasing degree of urbanisation.

Table 2: GLMMs exploring whether nestling health (Heterophil/Lymphocyte ratio, body condition index and blood parasite infection) varies with increasing urban cover within territories.

Variable	Error Structure	N	ddf	Estimate	Std. Error	Chi ²	p-value
Body condition	Gaussian	339	178	-0.06	0.22	0.08	0.79
Heterophil/Lymphocyte ratio	Gaussian	250	132	-0.003	0.04	0.007	0.93
<i>Haemoproteus</i> risk	Binomial	250	132	0.38	0.42	0.83	0.36
<i>Haemoproteus</i> intensity	Negative binomial	64	41	0.02	0.09	0.06	0.80
<i>Leucocytozoon</i> risk	Binomial	250	132	-0.68	0.28	6.09	0.01
<i>Leucocytozoon</i> intensity	Negative binomial	52	43	-0.86	0.31	7.79	0.005

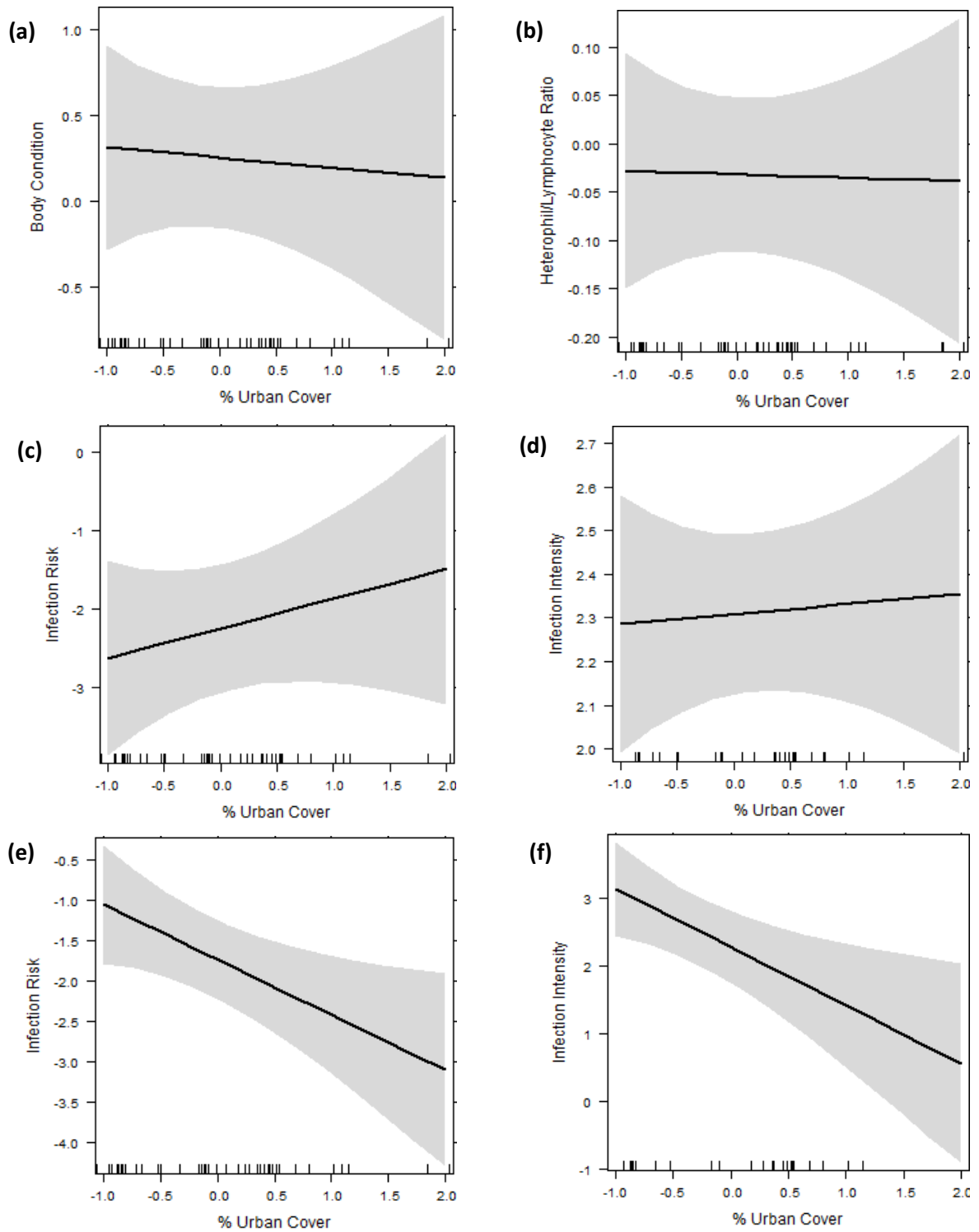


Figure 6: Health parameters of Black Sparrowhawk nestlings against the percentage of urban cover around the nest site: (a) Body condition index, (b) Heterophil/Lymphocyte ratio, (c) *Haemoproteus* infection risk, (d) *Haemoproteus* infection intensity, (e) *Leucocytozoon* infection risk, (f) *Leucocytozoon* infection intensity.

Diet composition along the urban gradient

Doves and pigeons (family *Columbidae*) made up 87.2% (N = 729) of the 836 prey remains collected between 2012 and 2015 from 45 territories (Table 3).

Table 3: Species composition of all prey remains collected from nest sites: number of collected items (N) and their proportion in the prey remains (%).

Species	Latin Name	N	%	Cum. %
Red-eyed Dove	<i>Streptopelia semitorquata</i>	354	42.3%	42.3%
Rock Dove	<i>Columba livia</i>	238	28.5%	70.8%
Speckled Pigeon	<i>Columba guinea</i>	66	7.9%	78.7%
Helmeted Guineafowl	<i>Numida meleagris</i>	47	5.6%	84.3%
Laughing Dove	<i>Streptopelia senegalensis</i>	45	5.4%	89.7%
Cape Turtle Dove	<i>Streptopelia capicola</i>	26	3.1%	92.8%
Spotted Thick-knee	<i>Burhinus capensis</i>	16	1.9%	94.7%
Raptors	<i>Accipiter tachiro</i> , <i>Accipiter rufiventris</i>	11	1.3%	96%
Starlings	<i>Sturnus vulgaris</i> , <i>Onychognathus morio</i>	9	1.1%	97.1%
Other: Domestic chicken, Cape Spurfowl, Blacksmith Lapwing, Olive Thrush, Hadedda Ibis, African Sacred Ibis, Grey Squirrel, Mole Rat spp.		24	2.9%	100%

To test for an effect of urbanisation on the diet at the territory level, we considered the 26 territories for which we had 7 or more prey remain samples, since a rarefaction curve indicated it was sufficient for explaining 90% of the diet composition (Appendix A). This yielded a sample size of 795 prey samples and thus we lost very little of the information (5%) from the full sample of remains (Appendix B).

Diet breadth ranged between 0.03 and 0.61 (mean = 0.26 ± 0.15) and we found no significant trend in diet breadth with the degree of urbanisation ($F = 0.05$, $p = 0.83$; Table 4). We then explored whether the proportion in the diet of the six main prey species (which made up 92.8% of the diet) varied according to the degree of urbanisation. We found no significant relationships between the proportion of any of the prey items and the degree of urbanisation (Table 4).

Table 4: GLMs exploring whether diet breadth or proportion of the six most common prey species varies with the degree of urbanisation surrounding the nest site (F values for models with Gaussian error structure and Chi² values for binomial error structures).

	Error Structure	dF	Estimate	SE	F / Chi²	p
Levins Index	Gaussian	24	< - 0.0001	0.002	0.05	0.83
Red-eyed Dove	Quasibinomial	24	< 0.0001	0.004	33.84	0.99
Rock Dove	Quasibinomial	24	0.003	0.005	47.13	0.52
Speckled Pigeon	Binomial	24	-0.008	0.008	46.35	0.33
Helmeted Guineafowl	Binomial	24	-0.0008	0.009	40.74	0.93
Laughing Dove	Binomial	24	0.003	0.009	48.80	0.76
Cape Turtle Dove	Binomial	24	0.008	0.012	34.49	0.51

Prey abundance across habitats

The abundance of each of the main prey species, except Speckled Pigeon, was significantly different across habitat types (Figure 7). For the Red-eyed Dove, the most important prey species, the Kruskal Wallis tests showed a significant difference across habitats, but after correction for multiple testing, these differences were not picked up in the Dunn tests, therefore this species is abundant in all habitat types. For some species, abundance was clearly higher in more transformed habitats. Post-hoc Dunn tests showed for example that the overall abundance of all 9 species and of Rock Doves was significantly higher in open intensive and urban habitats than the other habitat types (Table 5; Appendix C). Similarly, the abundance of Helmeted Guineafowls was significantly higher in open intensive landscapes. For others, abundance was highest in more natural habitats (e.g. Speckled Pigeon). Some species were abundant in both urban and non-urban landscapes, such as Laughing Doves and Cape Turtle Doves. The habitat types containing the least prey (in terms of total numbers counted) were forests and gardens.

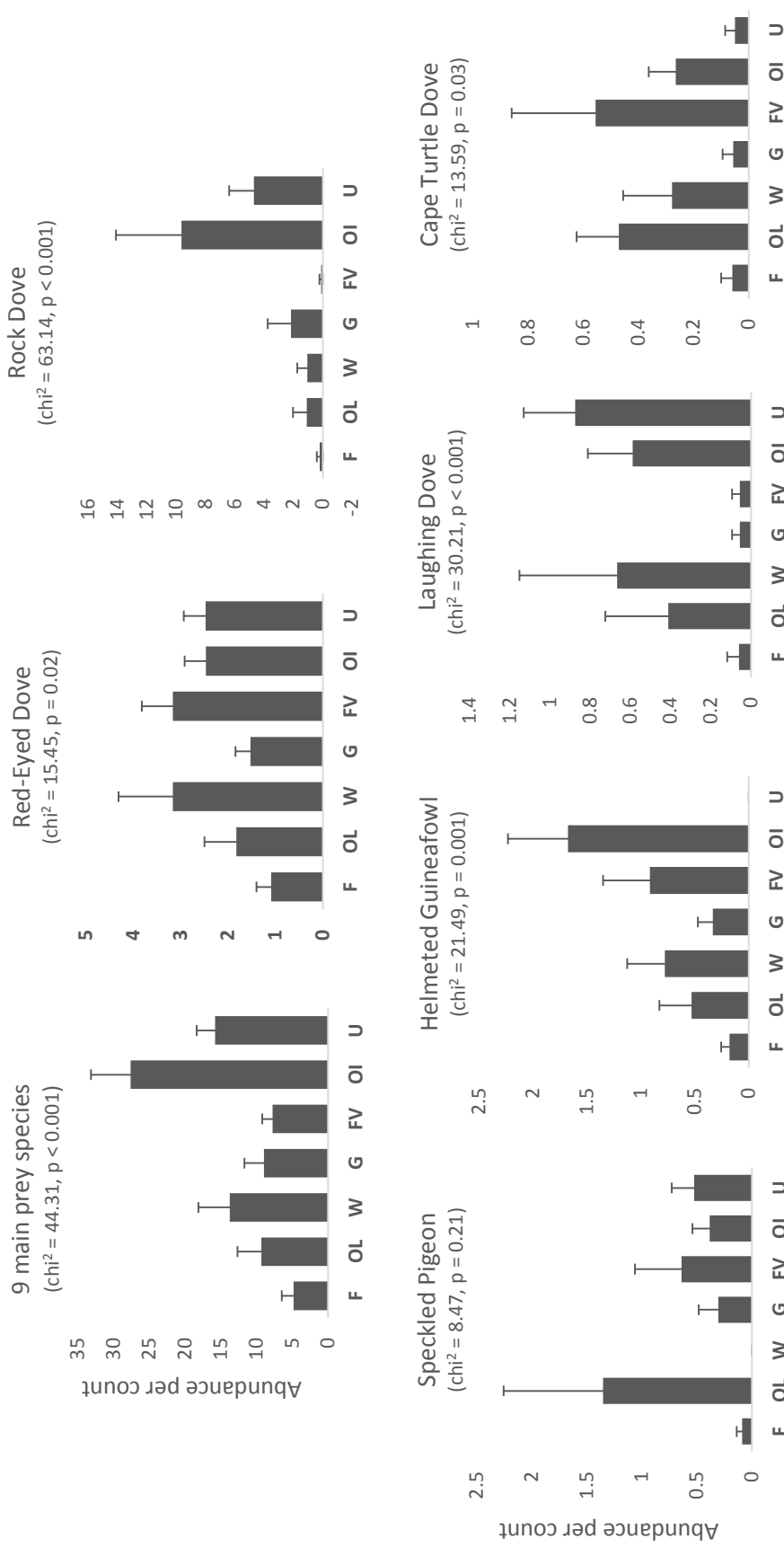


Figure 7: Habitat-specific abundance observed in each count for the bird species most commonly preyed on: Red-eyed Dove (*Streptopelia semitorquata*), Rock Dove (*Columba livia*), Speckled Pigeon (*Columba guinea*), Helmeted Guineafowl (*Numida meleagris*), Laughing Dove (*Streptopelia senegalensis*) and Cape Turtle Dove (*Streptopelia capicola*). The x-axis represents a gradient from the most natural (left) to the most transformed or man-made habitat types (right): F (forest), OL (open landscape), W (wetland), G (garden), FV (field/vineyard), OI (open intensive landscape), U (urban). Results of Kruskal Wallis Chi-squared tests comparing prey abundance across all habitats are also shown (df = 6).

Table 5: Results of the Dunn tests run for each of the main prey species and for the cumulative abundance of the 9 main prey species to test for pairwise differences in abundance between habitats. The value of the z statistic is given and only significant results are shown (*p < 0.05, **p < 0.01, ***p < 0.001).

$y \sim x$	Open Intensive	Urban	Forest	Garden	Open Landscape	Field/ Vineyard
Open Landscape	9 main species (4.27)*** <i>C. livia</i> (4.16)***					
Wetland		<i>C. livia</i> (3.21)* <i>N. meleagris</i> (-2.89)*				
Garden						
Field/Vineyard	9 main species (3.69)** <i>C. livia</i> (4.59)***	<i>C. livia</i> (5.46)*** <i>S. senegalensis</i> (4.02)***				
Open Intensive			9 main species (-5.26)*** <i>C. livia</i> (-4.48)**	9 main species (-4.52)*** <i>C. livia</i> (-4.20)***		
Urban	<i>N. meleagris</i> (4.30)***		9 main species (-4.22)*** <i>C. livia</i> (-5.33)*** <i>S. senegalensis</i> (-4.22)***	9 main species (-3.44)** <i>C. livia</i> (-5.06)*** <i>S. senegalensis</i> (-4.02)***	9 main species (-3.19)* <i>C. livia</i> (-4.99)*** <i>S. senegalensis</i> (-3.78)**	

Discussion

We predicted negative health consequences for Black Sparrowhawk nestlings being reared in heavily urbanised areas. Nestlings are expected to be particularly vulnerable to stressors in urban environments because they are confined to their nests and don't have the option of avoiding any adverse conditions they are exposed to, whilst also being dependent on their parents to provide them with food. Both are part of the early life experiences of an individual, and can be crucial for its fitness (Lindström, 1999). We found no immediate negative health impacts on nestlings, as measured by their body condition, H/L ratio and parasite infections. Instead, we found a significant negative relationship between the infection risk and intensity of one of the blood parasites and the degree of urbanisation around the nest. This lack of negative health impacts, together with the fact that there were no significant trends between the degree of urbanisation and diet composition suggests that Black Sparrowhawks could be categorised as urban-adapters (Blair, 1999; McKinney, 2002; Kark et al., 2007). Our results suggest that they are able to exploit similar food resources across the urban gradient and don't suffer from measured health consequences at the nestling stage.

Urbanisation does not impose apparent negative health impacts on Black Sparrowhawks

There were no significant relationships between urbanisation and body condition or the H/L ratio in Black Sparrowhawk nestlings, suggesting that their health is not impacted by the density of urban structures such as buildings and roads, around the nest. Birds with a higher body condition have been shown to respond and adapt more rapidly to causes of physiological stress than individuals in poorer condition, minimising the physiological impacts of disturbance, pollutants, disease or nutritional stress (Heath and Dufty Jr., 1997). However, the H/L ratio may not always be the appropriate index for detecting impacts of physiological stress, as highlighted by Muller et al. (2011), and should therefore be combined with other indices.

Looking at blood parasite infection, we found no significant effect of urbanisation on the risk or intensity of *Haemoproteus* infection, whereas we found a significant negative one on both parameters for *Leucocytozoon*. Nestlings being reared in more urbanised habitats were less likely to be infected by *Leucocytozoon* and were less intensively infected by this parasite than those reared in less urbanised habitats. We can therefore add to a number of studies (e.g., Delgado and French, 2012) that have found mixed effects of urbanisation on parasite infection and support the observation that the pattern will vary

depending on the host-parasite system under consideration, in particular on the transmission mode of the parasite (Brearley et al., 2012; Giraudeau et al., 2014). When the parasite is transmitted trophically (i.e., by consumption of an infected individual), urban raptors feeding on hyperabundant urban species like pigeons may be more prone to infection than rural ones, as seen in Cooper's Hawks infected with *Trichomonas* (Estes and Mannan, 2003). A number of gastrointestinal parasites transmitted by the faecal-oral transmission of infective oocysts between hosts may also be more easily transmitted in urban environments due to the high density of birds which may share resources such as bird feeders or waste (Giraudeau et al., 2014). In the case of vector-borne parasites, such as the Haemosporidian parasites studied here, the effect of urbanisation on their prevalence will depend on the effect of urbanisation on their vectors. Biting midges can breed in a wide range of habitats (e.g., pools, streams, swamps, tree holes, irrigation pipes) and as long as there is enough water/moisture (Mellor et al. 2000); black flies on the contrary require running water and favour high velocity streams (Rivers-Moore et al. 2007). We therefore hypothesise that black flies are less abundant in highly urbanised areas, potentially explaining why birds are less infected by *Leucocytozoon* in these areas.

This therefore demonstrates that only using a rural-urban gradient approach may be insufficient in explaining the mechanisms behind the health of city-dwelling species, specifically if limited health indices are available. The dynamics of the urban environment in terms of the factors which contribute towards the health of an individual go beyond the degree of urban cover, but consist of a multitude of influences and environmental features (Hahs and Evans, 2015) which maybe be highly specific to habitats and patches (Faeth et al., 2011). For example, there may be additional benefits to living in pine and eucalyptus dominated landscapes which may explain the lack of the expected decline in health and increase in parasite loads in individuals living in more urbanised territories. It has been hypothesised that Black Sparrowhawks line their nests with the leaves of eucalyptus and pine trees which contain volatile chemicals in order to prevent chicks from parasite infestations (Malan et al., 2002; Fleming, 2015), and thus far we have not found any ectoparasites living on nestlings.

A stable diet along the urban gradient: a potential buffer to the stress of city-life?

One mechanism by which urbanisation could negatively affect the health and condition of predatory birds is through their diet, i.e., if urbanisation prevents them from accessing prey in high enough quantities or of good nutritional quality (see e.g., Sternalski et al., 2010; Terraube et al., 2011 for natural systems).

Insufficient prey or prey of insufficient nutritional quality might decrease the condition of the nestlings, or increase physiological stress (due to disturbance, disease, or pollutants), exposing them to a higher risk of parasite infection (Andersson et al., 2015). Our results show that the diet of the Black Sparrowhawk, differs little along the urbanisation gradient, both in terms of diet breadth and in terms of the quantity of preferred preys consumed by the birds. Thus, a similar diet composition along the urban gradient may buffer Black Sparrowhawks from potential negative health impacts of urbanisation.

We attempted to determine whether more urban Black Sparrowhawks had a distinct “urban diet”, dominated for instance by feral pigeons and other doves, and as a result, a decreased diet breadth. This hypothesis was based on foraging theories which predict that diet diversity decreases as the abundance of the most favoured prey items increases (Sodhi and Oliphant, 1993; Stephens and Krebs 1986). Conversely, we expected other prey species that might be less tolerant of urbanisation to feature more in the diet of birds in less urban habitats, resulting in an increase in diet breadth. This has been witnessed in congeners of the Black Sparrowhawk, for example in Cooper’s Hawks, where the diet of urban birds was composed primarily of doves, while rural birds caught a greater variety of prey (Estes and Mannan, 2003). In contrast to these predictions, we observed no trends in diet composition or diet breadth with increasing urbanisation. In terms of prey abundance, all major prey species together and some species in particular, were more abundant in urban habitats (e.g., Rock Doves, Helmeted Guineafowl). However, some species, such as Speckled Pigeons, Laughing Doves and Cape Turtle Doves, were more abundant in less urban habitat types. Therefore, overall, prey abundance was well-spread across all habitat types, particularly that of Red-eyed Doves, the most important prey species of Black Sparrowhawks. This may explain the lack of any trends in diet composition - since prey is abundant in all habitat types considered. These findings lend themselves to the conclusion that Black Sparrowhawks are under little nutritional stress, due to the abundance of prey, but also due to the stability and reliability of this abundance across urban habitats (Mannan and Boal, 2004). This can be a major contributing factor to the persistence of raptors in altered landscapes, as seen with Crowned Eagles in Durban, South Africa, where reliable availability of a variety of prey species allows these birds to withstand the impacts of landscape change (Reeves and Boshoff, 2015).

An additional possibility for why we did not observe an increase in prey species along an urban gradient may be because larger prey items such as pigeons and doves are often eaten and plucked at the site where they were caught, rather than near the nest (Rutz, 2003). This was found in Northern Goshawks, a species very similar to the Black Sparrowhawk in its size and foraging strategies (Brown and Brown, 1979), where

the proportion of pigeons was greatly underestimated in prey remains analyses (Rutz, 2003). To understand diet choice, it is therefore not enough to only look at the abundance of preys in the landscape; it is also important to estimate prey availability and to use diverse methods giving various information (e.g., prey abundance, prey provisioned to the nests, prey availability).

The widespread abundance of prey may not be the only factor contributing to the lack of a clear trend in diet composition with urbanisation. In the case of the Black Sparrowhawk and other congeners with similar hunting and foraging strategies, the sheer availability of food is not the only advantage. Urban habitats may also provide ideal foraging landscapes for these raptors, providing features such as edges, fence lines, perches and tree cover from which to hunt (Bolger, 2001; Rullman and Marzluff, 2014; Rutz, 2006). This has been found for example in Peregrine Falcons in Cape Town (Jenkins and Benn, 1998). Whilst Peregrines clearly benefit from the abundance of prey within urban Cape Town, their capacity to access this rich resource is dependent on the structure of the urban habitat and presence of appropriate structures for hunting successfully (Jenkins and Benn, 1998). Diverse urban and suburban habitats may provide ideal hunting grounds for Black Sparrowhawks, which tend to ambush prey from a hidden perch (Brown and Brown, 1979). This may further explain the lack of a clear trend of urbanisation and habitat type on diet and prey abundance – habitat edges might be more important than the actual habitat type. This is not only relevant for Black Sparrowhawks and their hunting style, but also to prey species which may also favour habitat edges, such as Cape Turtle Doves, which are more abundant in the presence of large habitat mosaics (Malan and Robinson, 1999). This is evident in our results, which show that some species, like Cape Turtle Doves and Helmeted Guineafowl are most abundant in vineyard and open intensive (golf courses, lawns) habitats respectively, in spite of the fact that these habitat types represent a very small proportion of the total study area. To explore these ideas further, we would need to analyse diet in relation to the matrix of habitats and their fragmentation scores (Bolger, 2001; Oliver et al., 2011).

One reason for expecting urbanisation to correlate with poor health and condition was because of the “urban junk food” hypothesis (Shochat, 2004) and because the high density of prey species might cause increased transmission of diseases within prey species, and then from the prey to the predator species (Ditchkoff et al., 2006). Again, this has been observed in Cooper’s Hawks, where nestling mortality increased due to infection by *Trichomonas*, a gastrointestinal parasite largely acquired from their prey, mostly dove species (Estes and Mannan, 2003). Another mechanism through which an urban diet may negatively affect the health of raptors might be through bioaccumulation of contaminants acquired from prey species, as seen in Cooper’s Hawks, Sharp-shinned Hawks (Elliot and Martin, 1994), Barn Owls (*Tyto*

alba), Common Buzzards (*Buteo buteo*) and Tawny Owl (*Strix aluco*; López-López et al., 2001). However, since we were unable to detect any evidence of a distinctly urban diet, nor any signs of adverse health, these predictions do not hold in our study system. Instead, it is plausible that because of the abundance of prey in all habitats, Black Sparrowhawks are not under nutritional stress, which might serve to shield them from the negative impacts of urbanisation.

If this is the case, then we might be able to hypothesise that cities might have a positive effect on bird-eating raptors such as Black Sparrowhawks. This is not surprising, given the number of similar species that have also been seen to thrive in urban areas, such as the Cooper's Hawk (Estes and Mannan, 2003), Red-tailed Hawk (*Buteo jamaicensis*; Stout et al., 2006), Northern Goshawk (Rutz, 2006), Crested Goshawk (Lin et al., 2015) and the Peregrine Falcon (Cade et al., 1996; Rejt, 2001). Bird-eating raptors usually experience decreased hunting success and energy returns from the time they spend foraging (Jenkins and Hockey, 2001; Temeles, 1985) but in urban areas, there is no shortage of hunting opportunities and a potentially higher likelihood of success, potentially freeing them from such restraints. In Barn Owls, human-modified areas with heterogeneous habitat types had a higher and more stable availability of prey, resulting in higher fledgling success (Almasi et al., 2015). These cases lend support to the "predation paradox" observed in urban areas (Shochat, 2004), whereby predator populations increase in urban areas, while overall predation pressure remains lower than in non-urban areas, due to the hyper abundance of prey species in cities (Fischer et al., 2012; McKinney, 2006). Furthermore, given that body condition is often used as an indicator of energy reserves accumulated in the nestling stage (Constantini et al. 2009), there is a good chance that this is what we are observing in the Black Sparrowhawk chicks, and that the lack of a trend in body condition reflects stability in prey abundance across an urban gradient.

Limitations and future directions

One reason we may have not found significant changes in nestling health or diet composition with increasing urbanisation may be because the scale considered in this study is inappropriate – minor changes in urban cover may mean little to a highly mobile Black Sparrowhawk when the city is scattered with patches of suitable habitat, littered with an abundant supply of prey. Thus, the heterogeneous environment in the City of Cape Town may mask the effect of an urban cover gradient. Further research could include areas from outside the core urban area used in this study, encompassing some rural areas in order to represent a wider urbanisation gradient.

In addition, different health/physiological parameters may be incorporated into further studies in order to obtain a well-rounded picture of their physiological responses to urbanisation. During this study, extra blood samples have been collected to look at indices of oxidative stress (Isaksson, 2015), ability to transport oxygen in the blood (haematocrit; Constantini et al., 2009), innate immune function or dietary antioxidants such as plasma carotenoid (Sternalski et al., 2014) and α tocopherol levels – these will be analysed in further studies. This should permit us to gain a deeper understanding of the mechanisms by which birds may deal with urbanisation. For example, small changes in diet can alter innate immune function with negative impacts on survival (Hegemann et al., 2013) and dietary antioxidants can affect the protection against reactive oxygen species (Isaksson, 2015).

If Black Sparrowhawks are able to avoid health and nutritional alterations in urban areas, issues like competition for nest sites with Egyptian Geese (Sumasgutner et al., submitted) or harassment by Pied Crows (A.Koeslag, pers. comm.), two highly abundant species in the area, may be more significant in affecting the long-term success and survival of Black Sparrowhawks in urban environments (Curtis et al. 2007). Furthermore, as with Eurasian kestrels which are affected by the renovation of the buildings in which they nest (Sumasgutner et al. 2014b), the planned removal exotic tree species in urban areas may represent a bigger threat to Black Sparrowhawks since they largely use alien species as nesting sites. Finally, future research in this study system could also incorporate data from adult Black Sparrowhawks in order to determine whether they experience urban living differently to nestlings.

Conclusions: Black Sparrowhawks as urban-adapters

Black Sparrowhawks appear to be very robust to urban stressors, living in the city and avoiding many of the negative health consequences that would be expected to come with urban life. A combination of prime nesting sites and an abundance of food, the two main ingredients for successful establishment of raptors (Rullman and Marzluff, 2014) makes the Black Sparrowhawk thrive in an urban environment.

The findings of this study place Black Sparrowhawks in the category of “urban-adapters”. Urban adapters are most often found in suburban environments (McKinney, 2002) where the diversity of resources provided by humans is vast, but the impacts of urbanisation not as severe, hence their other name ‘suburban adaptables’ (Blair, 2004; Chace and Walsh, 2006; Meffert and Dzioc, 2003). This is evident in the fact that most of the territories of Black Sparrowhawks considered in this study fall in moderately urbanised areas, rather than in the urban cores of Cape Town, despite the availability of potential nesting

trees. As highlighted by Palomino and Carrascal (2007), such areas with moderate levels of urbanisation may in fact favour raptors with opportunistic requirements, like the Black Sparrowhawk. Moreover, urban adapters are often “edge species”, i.e., species adapted to habitat edges such as forests surrounded by open landscape (McKinney, 2002; McKinney, 2006) and forest-dwelling species that nest in high trees (Crocì et al., 2008). Black Sparrowhawks match this definition since they selectively nest in large trees which are sheltered within forest stands but near the edge in order to hunt in adjacent, more open habitats (Malan and Robinson, 2001).

An additional point of interest in the case of the Cape Peninsula Black Sparrowhawks is that this population has been recorded to display a number of unique traits compared with conspecifics elsewhere in their range. For example, Black Sparrowhawks are a polymorphic species, occurring in light and dark morphs. Whilst elsewhere in their range, the light morphs are more common, on the Cape Peninsula, this morph ratio is reversed and the dark morphs are more prevalent (Amar et al., 2014). Furthermore this population is exposed to winter rainfall (Martin et al., 2014b) and experiences two distinct peaks in its breeding season and an overall extension of the breeding period (Martin et al., 2014b). They are also capable of double brooding within one breeding season (Curtis, 2005). These characteristics may illustrate the ability of Black Sparrowhawks to adapt in response to novel anthropogenic conditions, an adaptive capacity that may further explain the lack of apparent negative health impacts observed in this study at the nestling stage. Black Sparrowhawks may quite literally be urban adapters, whereby urban populations contain adaptations that make them more robust to novel conditions in these habitats, which present novel selective pressures (Jacquin et al., 2013). This may be yet another example of how animals in urban areas don't always share life history traits with rural conspecifics, as an adaptation to anthropogenic stressors (Ditchkoff et al., 2006). Future research could incorporate some of the unique characteristics of this population, and address differential responses of light vs. dark morph birds (Jacquin et al., 2013) and early vs. late breeding birds to urbanisation.

Glossary

H/L Ratio	The ratio of Heterophils (Neutrophils in mammals) to Lymphocytes present in a blood sample
Infection risk	Probability that an individual is infected by a parasite, estimated from the presence or absence of parasites in individuals sampled
Infection intensity	Parasite load, or number of parasites observed within the blood sample of an individual
Parasitemia	Similar to infection intensity or parasite load – the quantity of parasites in an infected individual
Prey abundance	Abundance of prey species observed per count
Susceptibility	The probability that an individual becomes infected at a given point when exposed to an infective dose of a pathogen, and shows little resistance to the infection
Territory	In this study, a 1500 m buffer around a Black Sparrowhawk's nest site, corresponding closely to the 95% occupancy determined from GPS tags on four adult birds
Urban-adaptor	Species which make use of both natural and anthropogenic resources, allowing them to be flexible and adapt to urban environments, particularly suburban environments which are rich in resources but not as heavily impacted by urbanisation
Urban-avoider	Species which are highly sensitive to urban stressors and have very specific habitat and resource requirements, therefore avoiding urban environments
Urban-exploiter	Species which are highly successful in urban environments due to their ability to exploit anthropogenic resources, which they are highly dependent on. They are often non-native species.
Urban gradient	A gradient of increasing urbanisation, measured by the percentage of urban cover (area covered by buildings, traffic structures, sealed surfaces and construction sites) within a Black Sparrowhawk's territory

References

- Alberti, M. 2005. The effects of urban patterns on ecosystem function. *International Regional Science Review*, 28(2): 168-192.
- Almasi, B., Beziers, P., Roulin, A. and Jenni, L. 2015. Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. *Oecologia*, doi: 10.1007/s00442-015-3318-2.
- Amar, A., Koeslag, A., Malan, G., Brown, M. and Wrenford, E. 2014. Clinal variation in the morph ratio of a range expanded polymorphic raptor: influence of climate conditions on polymorphism. *Ibis*, doi: 10.1111/ibi.12157.
- Andersson M.N., Wang H.-L., Nord A., Salmon P. and Isaksson C. 2015. Composition of physiologically important fatty acids in great tits differs between urban and rural populations on a seasonal basis. *Frontiers in Ecology and Evolution* 3. doi: 10.3389/fevo.2015.00093.
- Baigrie, B. 2013. *Exploring the breeding diet of the Black Sparrowhawk (Accipiter melanoleucus) on the Cape Peninsula*. Honours Thesis. University of Cape Town, Cape Town.
- Banbura, J., Skwarska, J., Banbura, M., Gladalski, M., Holysz, M., Kalinski, A., Markowski, M., Wawrzyniak, J. and Zielinski, P. 2013. Spatial and temporal variation in heterophil-to-lymphocyte ratios of nestling passerine birds: comparison of Blue Tits and Great Tits. *PLoS ONE*, 8(9): e74226. doi: 10.1371/journal.pone.0074226.
- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1): 1-48.
- Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications*, 6(2): 506-519.
- Blair, R.B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecological Applications*, 9(1): 164-170.
- Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organisation. *Ecology and Society*, 9(5):2.
- Boal, C.W. and Mannan, R.W. 1998. Nest-site selection by Cooper's hawks in an urban environment. *Journal of Wildlife Management*, 62: 864-871.

- Bolger, D. T. 2001. Urban birds: population, community, and landscape approaches. - In: Marzluff, J. M., Bowman, R. and Donnelly, R. (eds.), *Avian Ecology and Conservation in an Urbanizing World*. Springer US, pp. 155-177.
- Bonnington, C., Gaston, K.J. and Evans, K.L. 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *Journal of Applied Ecology*, 50: 15-24.
- Bradley, C.A. and Altizer, S. 2007. Urbanisation and the ecology of wildlife diseases. *Trends in Ecology and Evolution*, 22(2): 95-102.
- Brearley, G., Rhodes, J., Bradley, A., Baxter, G., Seabrook, L., Lunney, D., Liu, Y. and McAlpine, C. 2012. Wildlife disease prevalence in human-modified landscapes. *Biological Reviews*, 88: 427-442.
- Breuste, J., Niemela, J. and Snep, R.P.H. 2008. Applying landscape ecological principles in urban environments. *Landscape Ecology*, 23:1139-1142.
- Brown, L.H. and Brown, B.E. 1979. The behaviour of the Black Sparrowhawk *Accipiter melanoleucus*. *Ardea*, 67: 77-95.
- Burgas, D., Byholm, P. and Parkkima, T. 2014. Raptors as surrogates of biodiversity along a landscape gradient. *Journal of Applied Ecology*, 51(3): 786-794.
- Cade, T.J. and Bird, D.M. 1990. Peregrine falcons, *Falco peregrinus*, nesting in an urban environment: a review. *Canadian Field-Naturalist*, 104: 209-218.
- Cade T.J., Martell M., Redig P., Septon G. and Tordoff H. 1996. Peregrine Falcons in urban North America. In: Bird D.M., Varland D.E., Negro J.J., editors. *Raptors in human landscapes: adaptations to built and cultivated environments*. London: Academic Press.
- Campbell, T.W. and Ellis, C.K. 2007. *Avian and exotic animal hematology cytology*. 3rd ed. Ames, Iowa: Blackwell Publishing.
- Carrete, M., Tella, J.L., Blanco, G. and Bertelotti, M. 2009. Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes. *Biological Conservation*, 142: 2002-2011.
- Constantini, D., Casagrande, S., Carello, L. and Dell’Omo, G. 2009. Body condition variation in kestrel (*Falco tinnunculus*) nestlings in relation to breeding conditions. *Ecological Research*, 24: 1213-1221.
- Chace, J.F. and Walsh, J.J. 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning*, 74: 46-49.

- Cirule, D., Krama, T., Vrublevska, J., Rantala, M.J. and Krams, I. 2012. A rapid effect of handling on counts of white blood cells in a wintering passerine bird: a more practical stress? *Journal of Ornithology*, 153: 161-166.
- Clergeau, P., Savard, J.L., Mennechez, G. and Falardeau, G. 1998. Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. *The Condor*, 100: 413-425.
- Coleman, J.L., Bird, D.M. and Jacobs, E.A. 2002. Habitat use and productivity of Sharp-shinned Hawks nesting in an urban area. *The Wilson Bulletin*, 114(4): 467-473.
- Cowling, R.M., MacDonald, L. and Simmons, M.T. 1996. The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity Conservation*, 5: 527-550.
- Croci, S., Butet, A. and Clergeau, P. 2008. Does urbanisation filter birds on the basis of their biological traits? *The Condor*, 110(2): 223-240.
- Curtis, O. 1998. Natural history of the Black Sparrowhawk on the Cape Peninsula, South Africa. *Journal of African Raptor Biology*, 13:39-41.
- Curtis, O., Malan, G., Jenkins, A. and Myburgh, N. 2005. Multiple-brooding in birds of prey: South African Black Sparrowhawks *Accipiter melanoleucus* extend the boundaries. *Ibis*, 147: 11-16.
- Curtis, O.E., Hockey, P.A.R., Koeslag, A. 2007. Competition with Egyptian Geese *Alopochen aegyptiaca* overrides environmental factors in determining productivity of Black Sparrowhawks *Accipiter melanoleucus*. *Ibis*, 149: 502-508.
- Davis, A. K., Maney, D.L. and Maerz, J.C. 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Functional Ecology*, 22:760-772.
- Delgado, C. A. and French, K. 2012. Parasite–bird interactions in urban areas: Current evidence and emerging questions. *Landscape and Urban Planning*, 105:5-14.
- Ditchkoff, S.S., Saalfield, S.T. and Gibson, C.J. 2006. Animal behaviour in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems*, 9: 5-12.
- Dominoni, D., Goymann, W., Helm, B., Partecke, J. 2013. Urban-like night illumination reduces melatonin release in European blackbirds (*Turdus merula*): implications of city life for biological time-keeping of songbirds. *Frontiers in Zoology*, 10: 60.
- Drewitt, E.J.A. and Dixon, N. 2008. Diet and prey selection of urban-dwelling Peregrine Falcons in southwest England. *British Birds*, 101: 58-67.
- Dunn, O.J. 1964. Multiple comparisons using rank sums. *Technometrics*, 6(3): 241-252.

- Elliott, J.E. and Martin, P.A. 1994. Chlorinated hydrocarbons and shell thinning in eggs of (*Accipiter*) hawks in Ontario, 1986-1989. *Environmental Pollution*, 86(2): 189-200.
- Estes, W.A. and Mannan, R.W. 2003. Feeding behaviour of Cooper's Hawks at urban and rural nests in southeastern Arizona. *The Condor*, 105: 107-116.
- Faeth, S.H., Warren, P.S., Shochat, E. and Marussich, W.A. 2005. Trophic dynamics in urban communities. *BioScience*, 55(5): 399-407.
- Faeth, S.H., Bang, C. and Saari, S. 2011. Urban biodiversity: patterns and mechanisms. *Annals of the New York Academy of Sciences*, 1223: 69-81.
- Fischer, J.D., Cleeton, S.H., Lyons, T.P. and Miller, J.R. 2012. Urbanisation and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *BioScience*, 62(9): 809-818.
- Fleming, C. 2015. *Exploring the function of nest decoration in Black Sparrowhawks (Accipiter melanoleucus)*. Honours Thesis. University of Cape Town, Cape Town.
- Fontana, S., Sattler, T., Bontadina, F. and Moretti, M. 2011. How to manage the urban green to improve bird diversity and community structure. *Landscape and Urban Planning*, 101: 278-285.
- Fox, J. 2003. Effect displays in R for Generalised Linear Models. *Journal of Statistical Software*, 8(15): 1-27.
- Fox, J. and Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks, CA: Sage. URL: <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Gehlbach, F.R. 1994. The eastern screech owl: life history, ecology and behaviour in the suburbs and countryside. Texas A&M University, College Station.
- Giraudeau, M., Mousel, M., Earl, S. and McGraw, K. 2014. Parasites in the city: degree of urbanisation predicts poxvirus and coccidian infections in House Finches (*Haemorhous mexicanus*). *PLoS ONE*, 9(2): e86747. Doi:10.1371/journal.pone.0086747.
- Goddard, M.A., Dougill, A.J. and Benton, T.G. 2009. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, 1175: 1-9.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. and Briggs, J.M. 2008. Global change and the ecology of cities. *Science*, 319(5864): 756-760.
- Hahs, A.K. and Evans, K.L. 2015. Expanding fundamental ecological knowledge by studying urban ecosystems. *Functional Ecology*, 29: 863-867.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. and Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science*, 342: 850-853.

- Heath, J.A. and Dufty Jr., A.M. 1998. Body condition and the adrenal stress response in captive American kestrel juveniles. *Physiological Zoology*, 71(1): 67-73.
- Hegemann, A., Matson, K., Flinks, H. and Tieleman, B. 2013. Offspring pay sooner, parents pay later: Experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. *Frontiers in Zoology*, 10: 77.
- Hockey, P. and Midgley, G. 2009. Avian range changes and climate change: a cautionary tale from the Cape Peninsula. *Ostrich*, 80:29-35.
- Isaksson, C. 2015. Urbanisation, oxidative stress and inflammation: a question of evolving, acclimatising or coping with urban environmental stress. *Functional Ecology*, 29: 913-923.
- Jacquín, L., Récapet, C., Prévot-Julliard, A.-C., Leboucher, G., Lenouvel, P., Erin, N., Corbel, H., Frantz, A. and Gasparini, J. 2013. A potential role for parasites in the maintenance of color polymorphism in urban birds. *Oecologia*, doi: 10.1007/s00442-013-2663-2.
- Jenkins, A.R. and Benn, G.A. 1998. Home range size and habitat requirements of Peregrine Falcons on the Cape Peninsula. *South African Journal of Raptor Research*, 32(2): 90-97.
- Jenkins, A.R. and Hockey, P.A.R. 2001. Prey availability influences habitat tolerance: an explanation for the rarity of Peregrine Falcons in the tropics. *Ecography*, 24(3): 359-367.
- Kark, S., Iwaniuk, A., Schalimtzek, A. and Banker, E. 2007. Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, 34: 638-651.
- Kowarik, I. 2011. Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, 159(8-9): 1974-1983.
- Krebs, C.J. 2004. Ecological methodology, 2nd edition. Menlo Park, California: Benjamin/Cummings.
- Labocha, M.K. and Hayes, J.P. 2012. Morphometric indices of body condition in birds: a review. *Journal of Ornithology*, 153: 1-22.
- Lei, B., Amar, A., Koeslag, A., Gous, T.A. and Tate, G.J. 2013. Differential haemoparasite intensity between Black Sparrowhawk (*Accipiter melanoleucus*) morphs suggests an adaptive function for polymorphism. *PLoS ONE*, 8:e81607.
- Levins, R. 1968. Evolution in changing environments; some theoretical explorations. Princeton, N.J.: Princeton University Press.
- Liker, A., Papp, Z., Bókony, V. and Lendvai, Á.Z. 2008. Lean birds in the city: body size and condition of house sparrows along the urbanisation gradient. *Journal of Animal Ecology*, 77: 789-795.
- Lin, W., Lin, S., Lin, J., Wang, Y. and Tseng, H. 2015. Breeding performance of Crested Goshawk *Accipiter trivirgatus* in urban and rural environments of Taiwan. *Bird Study*, 62(2): 177-184.

- Lindström J, 1999. Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343-348. doi: 10.1016/s0169-5347(99)01639-0.
- López-López, T.J., Alvarez-Piñeiro, M.E., Lage-Yusty, M.A. and Simal-Lozano, J. 2001. PCBs in three predatory birds from Galicia (NW Spain). *Bulletin of Environmental Contamination and Toxicology*, 66(4): 497-503.
- Lowry H., Lill A., Wong B.B.M. 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews*, 88 (3):537–549.
- Love, O.P. and Bird, D.M. 2000. Raptors in urban landscapes: a review and future concerns. In R.D. Chancellor and B. Meyburg (Eds.), *Raptors at risk* (pp. 425-434). Washington, DC: WWGBP/Hancock House.
- Lyly, M.S., Villers, A., Koivisto, E., Helle, P., Ollila, T. and Korpimäki, E. 2015. Avian top predator and the landscape of fear: responses of mammalian mesopredators to risk imposed by the golden eagle. *Ecology and Evolution*, 5:503-514, doi: 10.1002/ece3.1370.
- Malan, G. and Robinson, E.R. 1999. The diet of the Black Sparrowhawk *Accipiter melanoleucus* (Aves: Accipitridae) in South Africa: hunting columbids in man-altered environments. *Durban Museum Novitates*, 24: 43-47.
- Malan, G. and Robinson, E.R. 2001. Nest-site selection by Black Sparrowhawks *Accipiter melanoleucus*: Implications for managing exotic pulpwood and sawlog forests in South Africa. *Environmental Management*, 28(2): 196-205.
- Malan, G., Parasram, W.A. and Marshall, D.J. 2002. Putative functions of green lining in black sparrowhawk nests: mite-repellant role? *South African Journal of Science*, 98: 358-360.
- Mannan, R.W. and Boal, C.W. 2000. Home range characteristics of male Cooper's Hawks in an urban environment. *Wilson Bulletin*, 112: 21-27.
- Mannan, R.W. and Boal, C.W. 2004. Birds of prey in urban landscapes, in Fascione, N., Delach, A. and Smith, M., editors. *People and predators: from conflict to coexistence*. Island Press, pp 105-117.
- Martin, R.O., Koeslag, A., Curtis, O. and Amar, A. 2014a. Fidelity at the frontier: divorce and dispersal in a newly colonised raptor population. *Animal Behaviour*, 93: 59-68.
- Martin, R.O., Sebele, L, Koeslag, A., Curtis, O., Abadi, F. and Amar, A. 2014b. Phenological shifts assist colonisation of a novel environment in a range-expanding raptor. *Oikos*, 123: 1457-1468.
- Marzluff, J.M. 2001. Worldwide urbanisation and its effects on birds. Pages 19-48 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston.

- McDonald, R.I., Kareiva, P. and Forman, R.T.T. 2008. The implications of current and future urbanisation for global protected areas and biodiversity conservation. *Biological Conservation*, 141: 1695-1703.
- McKinney, M.L. 2002. Urbanisation, biodiversity and conservation. *BioScience*, 52(10): 883-890.
- McKinney, M.L. 2006. Urbanisation as a major cause of biotic homogenisation. *Biological Conservation*, 127: 247-260.
- McPherson, S.C., Brown, M. and Downs, C.T. 2015. Diet of the crowned eagle (*Stephanoaetus coronatus*) in an urban landscape: potential for human-wildlife conflict? *Urban Ecosystems*, doi: 10.1007/s11252-015-0500-6.
- Meffert, P.J. and Dziock, F. 2013. The influence of urbanisation on diversity and trait composition of birds. *Landscape Ecology*, 28: 943-957.
- Meillère, A., Brischoux, F., Parenteau, C. and Angelier, F. 2015. Influence of urbanisation on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLoS ONE*, 10(8): e0135685. doi: 10.1371/journal.pone.0135685.
- Mellor, P.S., Boorman, J. and Baylis, M. 2000. Culicoides biting midges: their role as arbovirus vectors. *Annual Review of Entomology*, 45: 307-340.
- Møller, A.P. 2010. Interspecific variation in fear responses predicts urbanisation in birds. *Behavioural Ecology*, 21: 365-371.
- Møller, A.P. 2011. Song post height in relation to predator diversity and urbanisation. *Ethology*, 117: 529-538.
- Møller, A.P. 2012. Urban areas as refuges from predators and flight distance of prey. *Behavioural Ecology*, 23: 1030-1035.
- Mueller, A.-K., Chakarov, N., Hesecker, H. and Krüger, O. 2016. Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. *Journal of Animal Ecology*, doi: 10.1111/1365-2656.12493.
- Muller, C., Jenni-Eiermann and Jenni, L. 2011. Heterophils/Lymphocytes-ratio and circulating corticosterone do not indicate the same stress imposed on Eurasian Kestrel nestlings. *Functional Ecology*, 25: 566-576.
- Newton, I. 1979. Population ecology of raptors. T.&A.D. Poyser, Calton.
- Okanga, S., Cumming, G.S., Hockey, P.A.R. and Peters, J.L. 2013. Landscape structure influences avian malaria ecology in the Western Cape, South Africa. *Landscape Ecology*, 28: 2019-2028.
- Oliver, A. J., Hong-Wa, C., Devonshire, J., Olea, K. R., Rivas, G. F. and Gahl, M. K. 2011. Avifauna richness enhanced in large, isolated urban parks. *Landscape and Urban Planning*, 102: 215-225.

- Ontiveros, D. and Pleguezuelos, J.M. 2000. Influence of prey densities in the distribution and breeding success of Bonelli's eagle (*Hieraetus fasciatus*): management implications. *Biological Conservation*, 93: 19-25.
- Ortega-Alvarez, R. and MacGregor-Fors, I. 2009. Living in the big city: effects of urban land-use on bird community structure, diversity and composition. *Landscape and Urban Planning*, 90: 189-195.
- Palomino, D. and Carrascal, L.M. 2007. Habitat associations of a raptor community in a mosaic landscape of Central Spain under urban development. *Landscape and Urban Planning*, 83: 268-274.
- Parker, J.W. 1996. Urban ecology of the Mississippi kite, in *Raptors in Human Landscapes: adaptations to built and cultivated environments*, ed. D.M. Bird, D.E. Varland, and J.J. Negro, 45-52. Academic Press, San Diego.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Ramalho, C.E. and Hobbs, R.J. 2012. Time for a change: dynamic urban ecology. *Trends in Ecology and Evolution*, 27: 179-188.
- Rebelo, A.G., Holmes, P.M., Dorse, C. and Wood, J. 2011. Impacts of urbanisation in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town. *South African Journal of Botany*, 77: 20-35.
- Reeves, B. and Boshoff, A.F. 2015. Is diet adaptability a reason for the persistence of African Crowned Eagles *Stephanoaetus coronatus* in altered habitats? *Ostrich*, doi: 10.2989/00306525.2015.1108372.
- Rejt L, 2001. Peregrine Falcon and Kestrel in urban environment – the case of Warsaw. In: Gottschalk E, Barkow A, Mühlenberg M, Settele J, editors. *Naturschutz und Verhalten: UFZ-Bericht*. p. 81-85.
- Rivers-Moore, N.A., de Moor, F.C., Morris, C., O'Keeffe, J. 2007. Effect of flow variability modification and hydraulics on invertebrate communities in the Great Fish river (Eastern Cape province, South Africa), with particular reference to critical hydraulic thresholds limiting larval densities of *Simulium chutteri lewis* (Diptera, Simuliidae). *River Research and Applications*, 23: 201-222.
- Rosenfield, R.N., Bielefeldt, J., Affeldt, L. and Bechmann, D.J. 1995. Nesting density, nest area, reoccupancy, and monitoring implications for Cooper's Hawks in Wisconsin. *Journal of Raptor Research*, 29: 1-4.
- Roulin, A. 2007. Melanin pigmentation negatively correlates with plumage preening effort in Barn Owls. *Functional Ecology*, 21(2): 264-271.
- Rullman, S. and Marzluff, J.M. 2014. Raptor presence along an urban-wildland gradient: influences of prey abundance and land-cover. *Journal of Raptor Research*, 48(3): ???

- Rutz, C. 2003. Assessing the breeding season diet of goshawks *Accipiter gentilis*: biases of plucking analysis quantified by means of continuous radio-monitoring. *Journal of the Zoological Society of London*, 259: 209-217.
- Rutz, C. 2006. Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *Ardea*, 94(2): 185-202.
- Rutz, C. 2008. The establishment of an urban bird population. *Journal of Animal Ecology*, 77: 1008-1019.
- Schiegg, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1: 103-113.
- Sekercioglu, C.H. 2006. Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, 21(8): 464-471.
- Sergio, F., Newton, I.A.N., Marchesi, L. and Pedrini, P. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, 43: 1049-1055.
- Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos*, 106: 622-626.
- Slabbekoorn, H. and Ripmeester, E.A.P. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*, 17: 72-83.
- Sodhi, N.S., James, P.C., Warkentin, I.G. and Oliphant, L.W. 1992. Breeding ecology of urban merlins (*Falco columbarius*). *Canadian Journal of Zoology*, 70: 1477-1483.
- Sodhi, N.S. and Oliphant, L.W. 1993. Prey selection by urban-breeding merlins. *The Auk*, 110(4): 727-735.
- Sorace, A. and Gustin, M. 2009. Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning*, 90: 111-118.
- Stephens, D.W. and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.
- Sternalski A, Mougeot F, Eraud C, Gangloff B, Villers A, Bretagnolle V, 2010. Carotenoids in nestling Montagu's harriers: variations according to age, sex, body condition and evidence for diet-related limitations. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 180:33-43. doi: 10.1007/s00360-009-0384-y.
- Stout, W.E., Temple, S.A. and Cary, J.R. 2006. Landscape features of Red-tailed Hawk nesting habitat in an urban/suburban environment. *Journal of Raptor Research*, 40(3): 181-192.
- Sumasgutner P, Millán J, Curtis O, Koelsag A, Amar A (submitted): Is multiple nest building an adequate strategy to cope with inter-species nest usurpation? The case of Black Sparrowhawks (*Accipiter melanoleucus*) and Egyptian Geese (*Alopochen aegyptiaca*). *Animal Behaviour*.

- Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H.W. and Gamauf, A. 2014a. Hard times in the city – attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology*, 11: 48.
- Sumasgutner, P., Schulze, C.H., Krenn, H.W. and Gamauf, A. 2014b. Conservation related conflicts in nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey. *Landscape and Urban Planning*, 127: 94-103.
- Sumasgutner, P., Tate, G., Koeslag, A. and Amar, A. 2015 (under review). Family morph matters: factors determining survival and recruitment in a long-lived polymorphic raptor. *Journal of Animal Ecology*.
- Tarboton, W.R. and Allan, D.G. 1984. The status and conservation of birds of prey in the Transvaal. Pretoria: Transvaal Museum.
- Temeles, E.J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *American Naturalist*, 125: 485-499.
- Terraube J, Arroyo B, Madders M, Mougeot F, 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos* 120:234-244. doi: 10.1111/j.1600-0706.2010.18554.x.
- Valkiunas, G. 2005. Avian malarial parasites and other haemosporidia. CRC Press, Boca Raton, USA.
- Vandewalle, M, de Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., da Silva, P.M., Moretti, M., Niemela, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J. and Woodcock, B.A. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity Conservation*, 19:2921-2947.
- Van Rensburg, B.J., Peacock, D.S. and Robertson, M.P. 2009. Biotic homogenisation and alien bird species along an urban gradient in South Africa. *Landscape and Urban Planning*, 92: 233-241.
- Venables, W.N. and Ripley, B.D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.
- Wenny, D.G., Devault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F. and Whelan, C.J. 2011. The need to quantify ecosystem services provided by birds. *The Auk*, 128(1): 1-14.
- Whelan, C.J., Wenny, D.G. and Marquis, R.J. 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, 1134: 25-60.
- Widén, P. 1994. Habitat quality for raptors: a field experiment. *Journal of Avian Biology*, 25: 219-223.

Yow, D.M. 2007. Urban heat islands: observations, impacts and adaptation. *Geography Compass*, 1(6): 1227-1251.

Zhou, D. and Chu, L.M. 2012. How would size, age, human disturbance, and vegetation structure affect bird communities of urban parks in different seasons? *Journal of Ornithology*, 153: 1101-112.

Appendix A

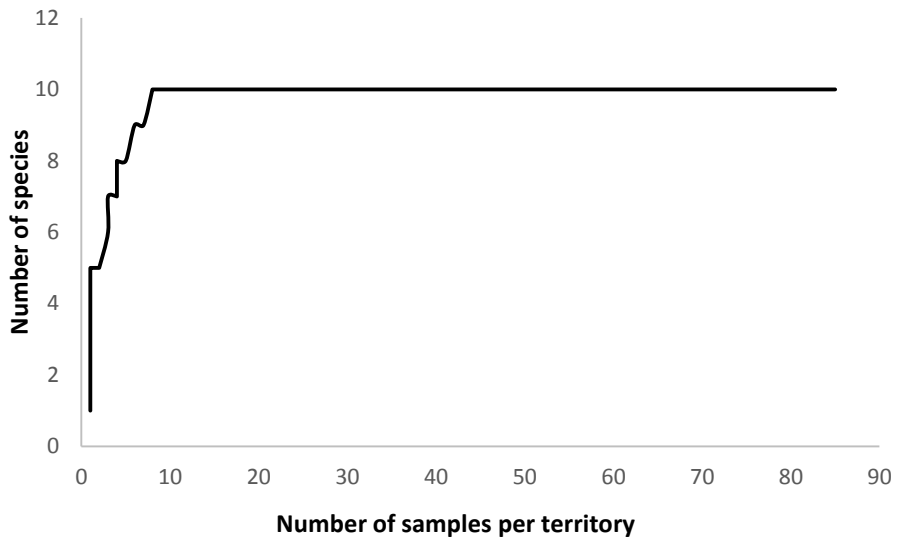


Figure A1: Rarefaction curve (Number of prey species identified in function of the number of samples analysed) to determine the minimum number of samples required to explain 90% of diet composition.

Appendix B

Table B1: Diet composition (number of items of different prey species out of the total prey number of prey remains at each territory (N)), diet breadth and urban cover at 26 Black Sparrowhawk territories.

Territory	Urban		Levins Index	N	Cape		Starlings	Helmeted Guineafowl	Laughing Dove	Red-eyed Dove	Rock Dove	Speckled Pigeon	Spotted Dikkop	Other
	Cover %	Raptor			Turtle Dove									
Alphen Common	45.03	0	0.18	32	0	0	0	1	3	18	7	0	0	Chicken (1), Olive Thrush (2)
Audrey's Nest	11.57	0	0.23	19	0	1	0	2	0	10	3	1	0	Chicken (2)
Bergvliet	74.43	0	0.22	24	0	0	0	2	3	10	9	0	0	
Bishops Court East	34.57	0	0.10	27	0	0	0	2	2	19	4	0	0	
Chart Farm	29.92	0	0.17	85	0	0	3	1	0	38	37	5	0	Budgerigar (1)
Deer Park	28.96	0	0.28	46	0	2	0	1	2	12	18	11	0	
Fernwood	39.26	1	0.13	27	0	0	0	0	0	17	4	5	0	
Glen Dirk	23.17	0	0.25	9	0	0	0	2	0	4	2	0	0	Olive Thrush (1)
Imhoff 1	14.10	1	0.43	11	0	0	0	4	1	2	1	0	1	Chicken (1)
Imhoff 2	14.96	0	0.15	7	0	0	0	0	0	2	4	1	0	
Klein Leeukoppie	24.24	0	0.19	23	0	1	0	1	0	12	7	1	1	
Lower Tokai Forest	33.46	0	0.07	8	0	0	0	0	2	6	0	0	0	
Newlands 1	23.94	4	0.40	54	0	2	0	0	8	18	12	9	0	Rameron Pigeon (1)
Newlands 4	34.04	0	0.03	9	0	0	0	0	0	8	1	0	0	
Newlands Picnic	34.01	0	0.61	20	0	2	1	1	3	5	4	2	1	Squirrel (1)
Oakley Avenue	35.03	0	0.24	26	0	1	0	2	0	9	11	0	1	Cockatiel (1), Hadedda Ibis (1)
Orange Kloof	5.54	2	0.34	36	0	3	0	2	1	11	13	2	0	Squirrel (1), Cockatiel (1)

Ottery	59.78	0.30	60	0	0	2	0	0	6	2	17	25	2	2	Sacred ibis (1), mole rat (2), squirrel (1)
Rhodes Mem	30.61	0.28	9	0	0	0	3	0	0	1	3	0	2	0	
Ruyteplaats	11.82	0.20	29	0	2	0	0	1	1	0	14	10	2	0	
Stone Church	11.36	0.26	56	1	0	0	0	6	1	1	26	14	6	2	
Sunnycroft	37.36	0.60	8	0	1	1	0	1	1	1	2	1	0	1	Lapwing sp. (1)
Tamboerskloof	31.86	0.08	48	0	1	1	1	0	0	6	36	1	2	1	
Tokai Picnic	12.08	0.45	57	1	0	0	0	5	7	7	15	17	4	6	Mole rat (1), chicken (1)
Zonnestraal 2	56.60	0.34	59	0	6	0	0	5	2	2	22	17	6	0	Squirrel (1)
Zonnestraal 3	56.60	0.34	6	1	0	0	0	0	0	0	0	3	2	0	

Appendix C

Table C1: Results of the Dunn test comparing the total abundance of the 9 main prey species of Black Sparrowhawks in each pair of habitat types (*p < 0.05, **p < 0.01, ***p < 0.001).

$y \sim x$		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.81					
	p	1.00					
Open Intensive	z	-5.26	-4.52				
	p	0.000***	0.0001***				
Open Landscape	z	-0.99	-0.20	4.27			
	p	1.00	1.00	0.0002***			
Urban	z	-4.22	-3.44	1.25	-3.19		
	p	0.0003***	0.006**	1.00	0.02*		
Field/Vineyard	z	-1.65	-0.85	3.69	-0.64	2.57	
	p	1.00	1.00	0.002**	1.00	0.11	
Wetland	z	-1.94	-1.29	2.44	-1.11	1.48	-0.59
	p	0.55	1.00	0.16	1.00	1.00	1.00

Table C2: Results of the Dunn test comparing the abundance of Red-Eyed Doves (*Streptopelia semitorquata*) in each pair of habitat types.

y ~ x		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.91					
	p	1.00					
Open Intensive	z	-2.59	-1.72				
	p	0.10	0.90				
Open Landscape	z	-0.09	0.82	2.50			
	p	1.00	1.00	0.13			
Urban	z	-2.45	-1.54	0.24	-2.36		
	p	0.15	1.00	1.00	0.19		
Field/Vineyard	z	-2.51	-1.62	0.12	-2.42	-0.12	
	p	0.13	1.00	1.00	0.16	1.00	
Wetland	z	-1.54	-0.80	0.62	-1.46	0.43	0.52
	p	1.00	1.00	1.00	1.00	1.00	1.00

Table C3: Results of the Dunn test comparing the abundance of Rock Doves (*Columba livia*) in each pair of habitat types (*p < 0.05, **p < 0.01, ***p < 0.001).

y ~ x		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.34					
	p	1.00					
Open Intensive	z	-4.48	-4.21				
	p	0.0001***	0.0003***				
Open Landscape	z	-0.33	0.01	4.16			
	p	1.00	1.00	0.0003***			
Urban	z	-5.33	-5.06	-0.67	-4.99		
	p	0.00***	0.00***	1.00	0.00***		
Field/Vineyard	z	0.04	0.39	4.59	-0.38	5.46	
	p	1.00	1.00	0.00***	1.00	0.00***	
Wetland	z	-1.14	-0.87	2.59	-0.87	3.21	-1.19
	p	1.00	1.00	0.10	1.00	0.014*	1.00

Table C4: Results of the Dunn test comparing the abundance of Speckled Pigeons (*Columba guinea*) in each pair of habitat types.

$y \sim x$		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.36					
	p	1.00					
Open Intensive	z	-1.39	-1.05				
	p	1.00	1.00				
Open Landscape	z	-0.85	-0.50	0.54			
	p	1.00	1.00	1.00			
Urban	z	-1.96	-1.62	-0.52	-1.08		
	p	0.52	1.00	1.00	1.00		
Field/Vineyard	z	-0.99	-0.65	0.42	-0.13	0.96	
	p	1.00	1.00	1.00	1.00	1.00	
Wetland	z	0.78	1.09	1.93	1.49	2.42	1.61
	p	1.00	1.00	0.55	1.00	0.16	1.00

Table C5: Results of the Dunn test comparing the abundance of Helmeted Guineafowl (*Numida meleagris*) in each pair of habitat types (*p < 0.05, **p < 0.01, ***p < 0.001).

y ~ x		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.54					
	p	1.00					
Open Intensive	z	-2.75	-2.25				
	p	0.06	0.26				
Open Landscape	z	-0.89	-0.37	1.86			
	p	1.00	1.00	0.66			
Urban	z	1.44	2.02	4.30	2.37		
	p	1.00	0.46	0.0002***	0.19		
Field/Vineyard	z	-0.75	-0.22	2.04	0.15	-2.24	
	p	1.00	1.00	0.44	1.00	0.26	
Wetland	z	-1.66	-1.23	0.62	-0.92	-2.89	-1.06
	p	1.00	1.00	1.00	1.00	0.04*	1.00

Table C6: Results of the Dunn test comparing the abundance of Laughing Doves (*Streptopelia senegalensis*) in each pair of habitat types (*p < 0.05, **p < 0.01, ***p < 0.001).

y ~ x		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	-0.26					
	p	1.00					
Open Intensive	z	-2.47	-2.24				
	p	0.14	0.26				
Open Landscape	z	-0.43	-0.17	2.04			
	p	1.00	1.00	0.43			
Urban	z	-4.22	-4.02	-1.65	-3.78		
	p	0.0003***	0.0006***	1.00	0.002**		
Field/Vineyard	z	-0.26	0.00	2.24	0.17	4.02	
	p	1.00	1.00	0.26	1.00	0.0006***	
Wetland	z	-0.92	-0.72	1.13	-0.57	2.52	-0.72
	p	1.00	1.00	1.00	1.00	0.12	1.00

Table C7: Results of the Dunn test comparing the abundance of Cape Turtle Doves (*Streptopelia capicola*) in each pair of habitat types.

y ~ x		Forest	Garden	Open Intensive	Open Landscape	Urban	Field/Vineyard
Garden	z	0.04					
	p	1.00					
Open Intensive	z	-1.79	-1.85				
	p	0.77	0.67				
Open Landscape	z	-2.61	-2.69	-0.83			
	p	0.09	0.08	1.00			
Urban	z	0.11	0.07	1.97	2.82		
	p	1.00	1.00	0.52	0.05		
Field/Vineyard	z	-1.11	-1.17	0.70	1.54	-1.27	
	p	1.00	1.00	1.00	1.00	1.00	
Wetland	z	-1.13	-1.17	0.36	1.05	-1.24	-0.22
	p	1.00	1.00	1.00	1.00	1.00	1.00