The ecology of Black Sparrowhawks (Accipiter melanoleucus) in KwaZulu-Natal, South Africa

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ABSTRACT

Black Sparrowhawks (*Accipiter melanoleucus*) are a medium-sized raptor found across much of sub-Saharan Africa. Within South Africa their distribution has historically been across most of the east with no distribution across the west of the country. Recently, however, the Black Sparrowhawks of South Africa appear to have undergone a range shift with their range expanding into the west, and in particular into the Cape Peninsula. Much of their new range appears to be into urban and peri-urban areas. The aim of this thesis was to analyse reproductive characteristics as well as range changes and dynamics of Black Sparrowhawks along a rural urban gradient in KwaZulu-Natal. In particular what influences range changes, reproductive success, nest site selection and home range of Black Sparrowhawks was determined.

Urbanisation is one of the fastest changing and growing land uses worldwide, generally impacting negatively on fauna and flora community composition, species density and species ranges. Despite this the Black Sparrowhawk is one raptor species that appears to be thriving in urban habitats and has seemingly undergone recent range expansion, largely into urban areas. It was investigated whether Black Sparrowhawks have changed their range over recent years in South Africa. This was determined using data from both of the South African Bird Atlas Projects (SABAP1 and 2) and showed a definite shift and increase in the Black Sparrowhawk distribution. Black Sparrowhawk habitat use in terms of indigenous forest, commercial plantations and urban areas in South Africa were compared. Data from the SABAP2 project was analysed together with land cover types using generalized linear models with binomial errors and a logit link function. These results showed a positive relationship between the probability of encountering a Black Sparrowhawk in areas with tree plantations and in urban areas. However, no significant relationship was found between the probabilities of encountering a Black Sparrowhawk in areas of indigenous forest. Black Sparrowhawks appear to be a common urban species, however it seems they are limited to certain land use areas and this could affect their persistence in the future, particularly in urban areas.

Black Sparrowhawks appear to be thriving in urban habitats. Typically known as a shy forest species, they are now frequently seen and heard in urban areas in South Africa during the breeding season. The spatial and environmental factors that influence Black Sparrowhawk nesting sites in urban and peri-urban areas were investigated in KwaZulu-Natal. Our data suggest that Black Sparrowhawks appear to be very selective in nest site selection particularly with respect to nest tree species, tree and nest height, area of
‘greenspace’ surrounding the nest, and associations with water sources, roads and buildings. Black Sparrowhawks show a significant preference for a particular tree height class (20 – 29 m) as well as a significant preference for a specific nest height class (10 – 19 m). Similarly the preference of distance classes to the nearest water sources, buildings and roads all showed a significant selection by Black Sparrowhawks. Nest sites appear to be associated with the alien *Eucalyptus sp*. Due to ever changing urban habitats and human altered landscapes, as well as the removal of alien tree stands within urban areas, the availability of nest sites and foraging habitats may decline. It is therefore important that we understand the specific needs of such a species in order to monitor their success and initiate management programmes where necessary for their persistence.

Black Sparrowhawks appear to be increasing in human altered landscapes, however little is known about their breeding success and characteristics. Consequently their reproductive and resource requirements and trends, as well as overall reproductive success along a rural/peri-urban urban gradient in KwaZulu-Natal were investigated. Over the 2011 and 2012 Black Sparrowhawk breeding seasons the majority of successful nests raised two nestlings. In 2011 Black Sparrowhawk nests had a success rate of 74 % while the success in 2012 was only 41 % which yielded a higher number of unsuccessful breeding attempts, these results were determined by nest observations during the breeding seasons. Nest preparation was done predominantly by the male with incubation then predominantly by the female. An increase in fresh leaf material being brought to the nest as the chick aged suggested that this is more likely due to parasite control rather than showing nest occupancy as has been previously speculated.

There is little known about the movements and home range of Black Sparrowhawks, particularly in an urban environment. Consequently the home ranges of both an adult breeding female and a juvenile male Black Sparrowhawk were determined during the 2012 breeding season in Durban, KwaZulu-Natal. Transmitters were attached to the individuals recording their locations at regular intervals between 6h00 and 18h00. An adult female was trapped and had the transmitter placed approximately a week prior to the chicks fledging the nest. Her breeding season home range remained within close proximity to the nest. A juvenile male from the same nest was trapped approximately two weeks after fledging at the point of starting to learn to hunt independently. The data produced a minimum convex polygon (MCP) for the adult female of 0.0025 km$^2$ while the young male remained within an MCP of 0.4554 km$^2$. This pilot study has allowed us to determine a viable method which can be used to obtain Black Sparrowhawk home range information. This method can now be applied to
numerous pairs within a population to determine home range overlap, territoriality as well as post natal dispersal.

Despite the fact that Black Sparrowhawks appear to be increasing in human altered landscapes and expanding their range, further studies should be built on this pilot study in order to identify the degree of threat this species faces. This will allow for long term management plans to be establish which will facilitate their persistence in South Africa.
PREFACE

The data described in this thesis were collected in the Republic of South Africa from January 2011 to December 2012. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof. Colleen T. Downs and co-supervision of Dr. Mark Brown.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, represents the original work by the author and has not been submitted in any form for any degree or diploma to any university. Where use has been made of the work of others, it is duly acknowledged in the text.

................................................
Erin Paula Wreford
April 2014

I certify that the above statement is correct...

................................................
Professor Colleen T. Downs
Supervisor
April 2014
I, Erin Paula Wreford, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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Erin Paula Wreford
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DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Chapter 2: Publication 1

*Author contributions*
EPW conceived paper with MB and CTD. EPW collected data and analysed data, and wrote the paper. RA and MNR assisted with the data analysis. MB and CTD contributed valuable comments to the manuscript.

Chapter 3: Publication 2

*Author contributions*
EPW conceived paper with MB and CTD. EPW collected data and analysed data, and wrote the paper. MB and CTD contributed valuable comments to the manuscript.

Chapter 4: Publication 3
EP Wreford, M Brown, CT Downs. Reproductive success and breeding characteristics of Black Sparrowhawks (*Accipiter melanoleucus*) in peri-urban and urban areas in KwaZulu-Natal, South Africa.

*Author contributions*
EPW conceived paper with MB and CTD. EPW collected data and analysed data, and wrote the paper. MB and CTD contributed valuable comments to the manuscript.

Chapter 5: Publication 4

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EPW conceived paper with MB and CTD. EPW collected data and analysed data, and wrote the paper. MB and CTD contributed valuable comments to the manuscript. BH assisted with the preparation of the GPS transmitters and data collection.

Appendix 2: Publication 5
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Chapter 1
INTRODUCTION

Urbanisation has been shown to change the behaviour of many wildlife species (Anderson et al. 1990). Urbanisation effects include not only habitat alteration and fragmentation, but also the effects of visual disturbance, noise disturbance and changes in prey abundance as well as prey concealment and a loss of biodiversity (Fairbanks et al. 2002; Bautista et al. 2004; Keough and Conover 2012; Seto et al. 2012). Three general patterns have been noted with avian urbanisation in particular, the first being a change in species composition with urbanisation (Blair 1996). Secondly, the number of avian species declines with increasing urbanisation (Blair 1996; Chase and Walsh 2006). Thirdly, Fairbanks (2004) explains that although human disturbance has negative effects on biodiversity, species richness and abundances however, a positive relationship with richness, especially in bird species has been recorded. Urbanisation results in an increase in artificial mosaic landscaping and thus more artificial water sources and nesting sites, creating an artificial habitat for many opportunistic species (Fairbanks 2004; Keough and Conover 2012). A large number of generalist species are attracted to these artificial habitats where resources are plentiful (Fairbanks 2004). The effects of urbanisation on resources can be seen in both individual bird species and the avian community as a whole (Blair, 1996). Some species considered ‘exploiters’ will reach a maximum density in urbanised areas, whereas other species, ‘avoiders’ will reach their maximum density in undeveloped areas as they are sensitive to development (Anderson et al. 1990; Blair 1996). The exploiters, usually native resident, generalist species often show range expansions of approximately 20% in human altered landscapes (Fairbanks 2004).

The biggest threat to bird populations is urban development, population growth, urbanisation and land transformation, thus resulting in avian habitat loss (Barnes 2000; McKinney 2006) and climate change (Crick 2004; Hockey and Midgley 2009). Urbanised areas are an assortment of industrial, commercial and residential habitats, all of which have a generally high human population density and activity (Grimm et al. 2008; Pautasso et al. 2011). The human population density is constantly growing due to expanding economic and social developments and rapid human population growth rate (Grimm et al. 2008). Red data species are given priority status in conservation as their population numbers and viability are very low. This is largely due to factors that include human overexploitation, manmade structures, poison, alien invasive plant and animal species, afforestation and agriculture
Some research suggests that urban development and increased traffic can negatively affect raptor populations (Berry et al. 1998; Bautista et al. 2004). Fairbanks et al. (2002) used South African Bird Atlas Project (SABAP) data to determine the patterns in avian communities in relation to land use and human land transformation. High levels of human activity act as factors of fragmentation in avian communities (Fairbanks et al. 2002). Fairbanks et al. (2002) found that species diversity showed a positive relationship with highly urbanised areas. Single species dominance does not mean a loss in the numbers of rare species but a marked increase in species whose requirements allow them to thrive in heavily altered landscapes (Fairbanks et al. 2002). Relatively low human disturbance appears to have a negative effect on avian species in the grassland biome but positive effects on species in savannah woodland, Karoo and succulent Karoo biomes (Fairbanks et al. 2002). Urbanisation in drier biomes favours many species as artificial habitats and water sources attract many opportunistic species (Fairbanks et al. 2002). Southern African bird species seem to deviate from the predicted intermediate disturbance hypothesis (Fairbanks et al. 2002). The intermediate disturbance hypothesis predicts that species richness will peak at levels of intermediate disturbance (Fairbanks et al. 2002).

Where development levels are moderate, overall avian species diversity is thought to increase, however when development levels are high native species diversity generally decline (Blair 1996). Urbanisation results in fragmentation, habitat alteration and loss of habitat and nesting sites, these factors resulting in the negative effects of urbanisation on raptors (Berry et al. 1998). However, varying land use will influence the effects on avian species (Fairbanks 2004). Land use and landscape changes have dramatic effects on raptors due to their low densities within an area and large home ranges (Berry et al. 1998). Subsistence cultivation and vegetation degradation have positive or negative effects on generalist species richness (Fairbanks 2004). Urbanisation effects on raptors have been documented in terms of nesting failures; lowered nesting success, displacement and changes in wintering distribution and behaviour (Anderson et al. 1990). These all being short term effects, however many of these short term effects may lead to long term effects such as density and species composition changes (Anderson et al. 1990). Landscape ecology is an effective way of quantifying land use in percentages of land cover and use (Berry et al. 1998). Urban environments often seem ideal for bird species, especially raptors, due to the abundance of unexploited resources such as increased nest sites and prey availability (Rutz 2008). However, these urban habitats may
result in either delayed or long term negative effects on populations due to new diseases, persecution and removal of alien trees (Allan et al. 2005; Rutz 2008).

Climate change is simultaneously affecting wildlife and biodiversity, resulting in changes in migratory behaviour, phenology and distributions of plants and animals (Crick 2004; Hockey and Midgley 2009). Animals have shown a trend in poleward and more specifically northward movements in the northern hemisphere and reductions in home range due to climate change. (Crick 2004; Hockey and Midgley 2009). Although these trends are speculated to be caused by climate change this is difficult to support scientifically due to other confounding factors which may be overlooked (Crick 2004). Southern African bird species have been predicted to show climate induced range changes (Hockey and Midgley 2009; van der Wal et al. 2012). Climate change can affect avian species with regard to their metabolic rates, foraging conditions, breeding success, population sizes and distributions as well as changes in breeding time, laying dates and migration times (Crick 2004; Thomas et al. 2004). Over the past 60 years the effects of climate change on Australian bird species have been studied and it has been concluded that the fingerprint of climate change on the poleward distribution shifts have been underestimated by 26% in the temperate regions and on average 95% in the tropical regions (van der Wal et al. 2012). Range expansion and colonisation has occurred in the Cape Peninsula, South Africa, due to changes in the physiological and ecological niches due to changed thermal environments and habitat changes (Hockey and Midgley 2009).

In addition, both human altered and natural landscapes are at risk of biodiversity losses due to the increase in destructive alien species worldwide (Richardson and van Wilgen 2004). Following habitat destruction, biological invasions are the one of the largest threats to biodiversity (Richardson and van Wilgen 2004). Alien invasive species are affecting all land uses including agriculture and forestry thus affecting human health and biodiversity (Richardson and van Wilgen 2004). In South Africa, 10 million ha are invaded by approximately 180 alien species; the Working for Water initiative was started in 1995 to control alien plant management (Hosking and du Preez 2004; Richardson and van Wilgen 2004). The purpose of the Working for Water programme is to remove alien species and rehabilitate the area with indigenous vegetation (Hosking and du Preez 2004). Many non-invasive alien species are at risk of becoming invasive following the effects of climate change (Richardson and van Wilgen 2004).
**Black Sparrowhawk**

The Black Sparrowhawk (*Accipiter melanoleucus*) is a medium-sized raptor species, found occupying a large proportion of sub-Saharan Africa (Curtis *et al.* 2005). It is typically a territorial species which breeds in forested habitats (Curtis *et al.* 2007). The Black Sparrowhawk is one of several raptor species that appears to have successfully colonised urbanised habitats in South Africa. In South Africa, urban and agricultural environments are found to have many large copses of tall alien invasive tree species (Allan 1997; Allan *et al.* 2005). Black Sparrowhawks nest and hunt within such tree stands (Allan 1997). The diet of these birds is composed largely of pigeons, doves, francolins and domestic fowl (Allan 1997).

The Black Sparrowhawk is a secretive bird often going unnoticed (Brown and Brown 1979; Malan and Robinson 2001). It spends a large proportion of its time in forest canopy and is very seldom seen flying and soaring above the forest, although they do sometimes hunt in open savannas (Brown and Brown 1979). Following 20 years of observation in Kenya, less than 15 individuals were observed a distance greater than 200 m from the nest (Brown and Brown 1979). Although secretive this species is not shy and will be attracted to free range poultry in human settlements (Brown and Brown 1979; Allan *et al.* 2005). This species is generally a quiet species unless at the nest (Brown and Brown 1979), when they can be quite vocal (Allan *et al.* 2005). They inhabit the vicinity of the nest throughout the year (Brown and Brown 1979). The Black Sparrowhawk in South Africa, a generalist species, has shown a range expansion of 28% (Fairbanks 2004; SABAP 2). This expansion appears to be moving west with a reduction in the range on the east (SABAP2). As a generalist species range changes and in this case expansion may be inevitable due to landscape changes, however, sensitive indigenous species may become regionally or locally extinct as they cannot adapt to landscape change (Fairbanks 2004).

**Range Change and Land Use**

Raptor distribution is heavily influenced by landscape use as the availability of both prey and nesting sites is largely dependent on land use (Berry *et al.* 1998). Within an urban environment, habitats are composed of a mosaic of land use types within a successional gradient (Grimm *et al.* 2008; Evans *et al.* 2009; Pautasso *et al.* 2011). Raptors are sensitive to land use alteration or changes in ecological surroundings and the effects of such varies depending on the species (Herremans & Herremans-Tonnoeyr 2000). Range changes could be a result of a number of factors including climate change, invading species, habitat
availability, dispersal and environmental heterogeneity (Hockey and Midgley 2009; Veech et al. 2011). Range expansion and range changes have both been extensively studied and modelled in order to improve understanding of such a phenomenon and to make predictions of future range changes. However in order to understand the effects of habitat changes on a species and more specifically on their range and distribution a thorough understanding must be had of the species in question (Okes et al. 2008). Thus range changes, expansions, and shifts are highly complex processes that require thorough research and understanding (Okes et al. 2008; Veech et al. 2011).

**Home Range**

Home range is determined in terms of size, shape and structure (Kenward et al. 2001). The shape of a home range can indicate the land use of the species as well as the degrees of territoriality (Kenward et al. 2001). Every home range has a core area wherein the bird spends most of its time (Kenward et al. 2001; Olsen et al. 2011).

Although avian urban communities are generally dominated by a few species, some raptor species appear to have the ability to thrive in such environments (Chase and Walsh 2006). This may be due to larger home ranges, enabling them to not rely solely on the urbanised area to meet all ecological needs where resources are limited, as individuals can venture beyond the urban boundaries when required to (Chase and Walsh 2006). In Hamburg, Germany, Northern Goshawks (*Accipiter gentilis* L.) were historically never found in the city but rather in the forests, they were a shy species, wherever possible avoiding any humans. They now live in the city and hunt within the parks and suburbs (Rutz 2008). This raptor species is now dealing every day with the challenges faced by living in a highly urbanised city (Rutz 2008). An estimation of home range and use is a good indicator of the suitability of particular habitat (Peery 2000). A small home range may indicate low flight activity patterns and thus the bird must be achieving relatively high hunting success (Rutz 2006). A large home range may indicate low hunting success within the vicinity of the nest and thus greater flight activity beyond the immediate range of the nest (Peery 2000; Rutz 2006). Home range size, overlap and use needs to be interpreted in terms of several factors including food availability, territoriality, and nest and roost sites. Home range analysis can also be used to indicate the landscape use by a particular species, as well as territoriality, both of which can be used in conservation management and rehabilitation and release programs (Kenward et al. 2001).
Home range of male raptors has been found to be larger than that of the females (Bloom et al. 1993; Peery 2000). Within every home range is what is considered as the ‘core area’, this is the area wherein the individual spends around 50% of their time (Bloom et al. 1993). For many raptor species this area is centred on the nest (Bloom et al. 1993). Male Red-shouldered Hawks have a measured home range of 1.21 km² of which the core area is only 7.5 % of this area (Bloom et al. 1993). Females have a total home range of 1.01 km² of which the core area is only 4 % (Bloom et al. 1993). It is not clear how the Black Sparrowhawk demarcates and defends their territory. They are quiet birds seldom seen calling and defending their territory unlike other raptor species who call whilst soaring over the territory (Brown and Brown 1979). In Great Horned Owls (Bubo virginianus), high human activity resulted in birds increasing their home range and using areas not usually included in the home range (Anderson et al. 1990). The range changes of a number of raptor species were investigated and it was found that changes in range were species specific which will over time result in changes in species composition, as some species are more tolerant than others (Anderson et al. 1990).

The home range of the Black Sparrowhawks at Karen in Kenya was not determined, but was known to include land made up of forest, savannas and cultivated land (Brown and Brown 1979). Using prey evidence and the location of the prey species, it was predicted that the home range was between 3 – 5 km, however the birds were believed to have extended this range to between 10 – 15 km at some times for hunting (Brown and Brown 1979).

**Nest Site Selection**

The success of urban avian species is largely limited by nest site availability and avian abundance within an area, both of which will affect habitat suitability (Tella et al. 1996; Bisson et al. 2002). The selection of a nest site by avian predators can have major consequences on the fitness of those individuals, with fitness being dependant on food availability and negatively related to competition (Cardador et al. 2012). Thus with regard to density dependence, for every new individual within an area, the fitness for other individuals with the same area will decline (Cardador et al. 2012). The selection of nest sites by avian predators may be based on numerous factors including nest tree species, nest tree height and diameter, overhead cover and nest tree stability as well as orientation with respect to protection from weather conditions, sun exposure, predation risk and nest accessibility, surrounding habitat type and land use (Abe et al. 2007; Sullivan et al. 2011). Nest site
selection can greatly affect reproductive success and alter reproductive behaviour and trends depending on resource availability, competition, and disturbance (Cardador et al. 2012).

**Reproduction**

Reproductive behaviours vary from species to species and even between populations depending on resource availability and nest site characteristics. For example, rural populations of Cooper’s Hawks (*Accipiter cooperii*) breed in habitats ranging from large forests to small stands of trees, with nesting sites being selected based on the characteristics of tree stands (Boal and Mannan 1998). This species has suffered habitat loss due to urbanisation and now inhabit urban landscapes, where understanding their choice of nest sites allows management of the species (Boal and Mannan 1998). Cooper’s Hawks occur at greater densities in urban areas than rural/natural areas (Boal and Mannan 1998). This could be due to the attractiveness of some urban areas. Cooper’s Hawks select small pockets of tall exotic trees as nests sites and the level of human disturbance is not important in nest choice (Boal and Mannan 1998). Prey density and abundances within the area of the nest may also have favoured the increase of this species in urban areas (Boal and Mannan 1998). It is assumed that increased density in urban areas reflect a higher quality habitat, however this may not be the case. There may be a greater density of breeding pairs in urban areas, but comparisons of nesting success in urban and rural areas will give a more accurate indication of habitat quality (Boal and Mannan 1998).

Black Sparrowhawks line their nests with fresh green leaf material this thought to be to repel parasites and mites on the nest (Malan et al. 2002). However, other theories include the lining showing nest occupancy, used to soften the nest or creating nest camouflage (Wimberger 1984; Heinrich 2013)

There have been few published descriptive studies on detailed Black Sparrowhawks breeding behaviour. Brown and Brown (1979) studied a breeding pair of Black Sparrowhawks in Kenya. Between 1972 and 1978 it was found that birds laid eggs at the ‘height of the long rains’ (Brown and Brown 1979). Incubation was for a period of 37-38 days with 37-40 days pre-fledgling period, the post-fledgling period was 50-55 days. The female incubated for 80,7 % of the time, while she spent 9,2 % of the time standing off the nest and 10,0 % of the time neither of the adult birds were on the nest (Brown and Brown 1979). The male did no incubating. Throughout the days of incubation the male was scarce, seen only for very short periods when bringing the female food (Brown and Brown 1979). The young remained inactive for 12-13 days then were seen standing in nest, at day 14 first
feathers begin showing and the birds are able to defecate off the edge of the nest (Brown and Brown 1979). Juvenile males can be distinguished as they are smaller, more active and have very thin legs compared with females (Brown and Brown 1979). Of nine chicks raised, sex ratio was five females to four males (Brown and Brown 1979). Differences were observed in brooding patterns of the adult and sub-adult female (Brown and Brown 1979).

Black Sparrowhawk studies in South Africa have investigated multiple brooding, nest site selection, diet, competition and green nest lining material (Malan and Robinson 1999; Malan and Robinson 2001; Malan et al. 2002; Curtis et al. 2005, Curtis et al. 2007). The first nests found in the Cape Peninsula were between 1994 and the late 1990’s, most of these in large forest clusters (Curtis et al. 2007). Extensive studies have been done of this founding population focussing largely on competition, range changes and multiple brooding (Amar et al. In Prep; Curtis et al. 2005; Curtis et al. 2007; Hockey and Midgley 2009). In the Cape Peninsula, all Black Sparrowhawk nests were in exotic Pine trees (Pinus sp.) except for two that were in exotic Poplars (Populus sp.). These two were abandoned and the birds moved to alternative nest sites (Curtis et al. 2007). Average breeding success of this population over a five year study period was 1.20 ± 0.97 fledglings per breeding attempt, 70 attempts in total from 26 breeding pairs (Curtis et al. 2007). Attempts where Egyptian Geese (Alopochen aegyptiaca) were present produced an average of 0.76 chicks; those without geese produced an average of 1.58 chicks. 80 % of those usurped by geese (12 out of 15) already had or made alternative nests (Curtis et al. 2007).

A considerable difference has been noted in the heights of exotic and indigenous trees, exotic trees are generally 9 – 15 m taller than the indigenous trees which average a height of 18 m (Malan and Robinson 2001). Malan and Robinson (2001) noted that most Black Sparrowhawk nests were in trees taller than 23 m, with a diameter of at least 30 – 40 cm. The size of the tree stand in which Black Sparrowhawks nest is thought to be important, nest position is thought to be a trade-off between a well protected nest in the middle of the stand and easy hunting access near an open flypath (Malan and Robinson 2001). The minimum and maximum stands widths respectively were determined to be approximately 25 and 70 m (Malan and Robinson 2001).

**Diet**

Nest site selection and reproductive success can be largely determined by prey species richness and abundances (Brown and Brown 1979). Prey items of Black Sparrowhawks are not plucked anywhere near the nest, with plucking posts usually outside a 500 m radius of the
nest (Brown and Brown 1979). When prey is delivered onto the nest it is plucked and headless making it difficult to identify (Brown and Brown 1979). Few were identified by Brown and Brown (1979) as Scaly (Pternistis squamatus) and Yellow-necked Francolins (Francolinus leucoscepus), dove species (Streptopelia sp.) and a Fischers Greenbul (Phyllastrephus fischeri). Prey items have been identified from bone remains found under perches within a 60 m radius of the nest (Brown and Brown 1979). Most of the bones are completely devoured except for the ‘handle’ of bone, a part of the sternum, juveniles will leave more bone than adults (Brown and Brown 1979). The prey species mostly include pigeons and doves however in savanna habitats prey species include larger species such as francolins (Brown and Brown 1979). The most common recorded prey species is Red-eyed Dove (Streptopelia semitorquata), Green Pigeon (Treron calvus) and Laughing Dove (Streptopelia senegalensis) (Brown and Brown 1979; Malan and Robinson 1999). Documented prey items in Kenya also included an African Goshawk (Accipiter tachiro) (Brown and Brown 1979). During periods when the male Black Sparrowhawk is bringing food for the female and chicks, smaller food items are brought to the nest than when the female is hunting for prey items (Brown and Brown 1979). The breeding season of Black Sparrowhawks in Kenya is largely correlated with the peak abundances of prey individuals. Red-eyed and Laughing Doves have their peak breeding after the April-June rains and therefore reach a maximum abundance during May-July (Brown and Brown 1979).

**Urban Problems Faced**

Egyptian Geese (Alopochen aegyptiaca) in South Africa have not shown a significant range expansion however they have increased in abundance across their South African distribution, and markedly within the Western Cape (Little and Sutton 2013). In the Western Cape Black Sparrowhawks whose nests were usurped by Egyptian geese raised fewer chicks than those pairs where the geese were absent (Curtis et al. 2007). Consequently the presence of Egyptian geese within a Black Sparrowhawk nesting site had a significant negative effect on overall productivity (Curtis et al. 2007). In their study 60 % of the Black Sparrowhawks nests were usurped by geese (Curtis et al. 2007). Displacement of the Black Sparrowhawks by Egyptian Geese either occurs before the Black Sparrowhawks have laid eggs or during incubation or brooding if the nest is left unattended by the mother for any period of time (Curtis et al. 2007). This invasion by the geese will delay the Black Sparrowhawk breeding cycle by at least 28-30 days, as this is the duration of the goose nesting period (Curtis et al. 2007). Black Sparrowhawk pairs often have more than one nest site and this allows them to change nest
sites and continue breeding, however those with only one nest have to compete with the geese or wait for them to finish their breeding (Curtis et al. 2007). Curtis et al. (2007) found that out of 15 nest sites usurped by geese, 12 (80%) had alternative nests or built alternative nests when needed, the other three were nesting in very small forest patches and failed to reproduce successfully. Egyptian Geese have similarly been reported in the Cape trying to take over the nests of the breeding visitor, the Booted Eagle (*Hieraaetus pennatus*) as far back as 1979 (Steyn and Grobler 1981).

**Conservation Planning and Management**

Conservation biologists’ major challenge is to construct management recommendations to minimise the effects of urbanisation and land development on wildlife (Blair 1996; Bloom et al. 1993). One commonly used management approach is to identify and conserve the habitat and resources of a single species whose home range includes those of many other species (Bloom et al. 1993). Raptor species are often considered as one of these ‘umbrella species’ as they are at the top of their food chain and generally have large home ranges (Bloom et al. 1993). In order to determine effective and relevant conservation planning decisions ecologists need to fully understand how human activities are changing the landscape and the effects of this change on species presence and abundance (Fairbanks et al. 2002). The relationship between distribution and abundance of species has important implications for measures of species diversity and community structure (Fairbanks et al. 2002). The urban gradient analysis can be used to estimate bird densities considering all factors resulting in fragmentation through a range of habitats from natural, unaltered landscapes to heavily urbanised (Blair 1996).

**Aim**

The aim of this thesis was to investigate and describe the reproductive behavioural trends as well as trends with regard to nest sites, range changes and home range of Black Sparrowhawks.

**Objectives**

The first objective in this thesis was to determine the distributional range change of Black Sparrowhawks in South Africa by comparing historical and current distribution data (Chapter 2). The second objective was to determine the correlation between the probability of encountering a Black Sparrowhawk and different land cover types or use, as well as the
number of hectares that would need to be added to each land cover type/use to double the
probability of a Black Sparrowhawk encounter (Chapter 2). The third objective was to
investigate Black Sparrowhawk nest success and failures as well as the number of active
ests in the 2011 and 2012 breeding season along an Estcourt, Pietermaritzburg and Durban
gradient (Chapter 3). The fourth objective was to determine the amount of time spent by both
the male and female Black Sparrowhawk on both incubation and brooding and to determine
the frequency and duration of feeding of the chicks and the frequency of bringing fresh leaf
material onto the nests (Chapter 3), using a combination of video and motion-activated
camera to collect data on the nest. The fifth objective was to determine what factors influence
Black Sparrowhawk nesting sites, focusing mainly on tree height, nest height, nest tree
diameter at breast height, ‘greenspace’ surrounding the nest and associations with water
sources, roads and buildings (Chapter 3). Additionally nesting tree species, the size of tree
clumps in which the nest was found and the position of the nest tree within such clump were
investigated (Chapter 3). The sixth objective was to determine the home range size of a
breeding female and a young juvenile male, using GSM GPS transmitters (Chapter 5).

**Arrangement of thesis**

As each chapter is presented as a manuscript for publication, a degree of overlap and
repetition between chapters was unavoidable. This thesis is composed of chapters which have
been produced as manuscripts to be submitted for publication in international peer-reviewed
journals as follows:

Chapter 2: Range change and habitat use of Black Sparrowhawks (*Accipiter melanoleucus*) in
South Africa.

Chapter 3: Nest site dynamics of Black Sparrowhawks (*Accipiter melanoleucus*) in KwaZulu-
Natal, South Africa.

Chapter 4: Reproductive success and breeding characteristics of Black Sparrowhawks
(*Accipiter melanoleucus*) in peri-urban and urban areas in KwaZulu-Natal, South Africa

Chapter 5: Home range size of two Black Sparrowhawks (*Accipiter melanoleucus*) in
KwaZulu-Natal, South Africa: case study
Chapter 6: Concluding chapter

Supporting material: In addition, another paper in preparation on Black Sparrowhawks clinal variation is included as an Appendix to this thesis: Clinal variation in the morph ratio of a range expanded polymorphic raptor: influence of climate conditions on polymorphism.

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Chapter 2

Range change and habitat use of Black Sparrowhawks (*Accipiter melanoleucus*) in South Africa

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Urbanisation is one of the fastest changing and growing land uses worldwide, generally impacting negatively on fauna and flora community composition, species density and species ranges. Despite this the Black Sparrowhawk (*Accipiter melanoleucus*) is one raptor species that appears to be thriving in urban habitats and has seemingly undergone recent range expansion, largely into urban areas. The first aim of this study was to determine whether Black Sparrowhawks have changed their range over recent years in South Africa. This was determined using data from the South African Bird Atlas Projects (SABAP 1 and 2) and showed a definite shift and increase in the Black Sparrowhawk distribution. The second aim was to compare Black Sparrowhawk habitat use in terms of indigenous forest, commercial plantations and urban areas in South Africa. Data from the SABAP 2 project were analysed together with land cover types using generalized linear models with binomial errors and a logit link function. The results showed that the probability of encountering a Black Sparrowhawk varied in areas of different land use. A positive relationship was found between the encounter probability and both plantations and urban land use while no significant relationship was found with indigenous forests. Black Sparrowhawks appear to be a common urban species, however it seems they are limited to certain land use areas and this could affect their persistence in the future, particularly in urban areas.
Keywords: urbanisation, distribution, SABAP, general linear models, supplementary feeding, range expansion.

INTRODUCTION

Many species recent range changes are attributed to climate change, however often other biological impacts are not properly investigated and thus conservationists ‘ignore’ issues resulting in such range changes (Simmons et al. 2004; Hockey and Midgley 2009). Species range expansion has been extensively studied and modelled in order to understand and predict such changes. Range expansion is however dependant on a variety of factors including invading species, interactions with invading species, environmental heterogeneity, habitat preference and availability and density-dependant reproductive success and therefore range expansion is not as simple as the mathematical models used to understand and predict it (Veech et al. 2011).

In order to monitor and predict the effects of habitat change on avian species a basic understanding on the species biology is required (Okes et al. 2008). Range expansion occurs only when a species colonises a new habitat and is able to successfully reproduce there, starting a new population (Veech et al. 2011). Thus ranges changes will be associated with particular habitats (Veech et al. 2011). Birds have an advantage in regard to adaptation due to climate change as they can more easily move and colonise new areas while sessile plants and terrestrial animals and limited in movements and dispersal abilities (Simmons et al. 2004). However they are largely limited by land transformation limiting suitable areas for occupancy (Simmons et al. 2004). For example, the Cape Peninsula in South Africa has undergone many structural changes due to urbanisation, afforestation, and the increase, spread and introduction of alien plants (Hockey and Midgley 2009). Many of these anthropogenic changes in this area occurred before the dramatic effects of climate change accelerated in the 1970’s (Hockey and Midgley 2009). Many South African bird species undergoing range changes have colonised the Cape Peninsula since the 1940’s (Hockey and Midgley 2009). Reasons proposed for these colonisations include changes in rainfall and temperature, altered thermal environments and habitats due to climate change and an increase in water and forest associated species due to plantations and an increase in artificial water sources (Hockey and Midgley 2009). Even though the range changes of many avian species follow the model predicted by climate change, it is not necessarily the ‘ultimate force’ driving such changes.
(Hockey and Midgley 2009). Many changes can be explained by other anthropogenic changes (Hockey and Midgley 2009; Veech et al. 2011).

Human altered landscapes are dynamic systems, composed of habitats within a successional gradient (Grimm et al. 2008; Evans et al. 2009b; Pautasso et al. 2011). This is different in every situation where in some cases the centre (core) of an urban area is highly developed then irregular rings are then formed around this core with habitats diminishing in urbanisation as they get further from the core (Melles et al. 2003). Other urban landscapes are a mosaic of different habitats and levels of urbanisation (Melles et al. 2003; Evans et al. 2009b). Urbanisation can thus provide a wide range of available habitats from early stages of urban development to habitats within the latter stages of urban development/highly urbanised habitats (Melles et al. 2003; Evans et al. 2009b).

Many urban areas and particularly residential areas have parks and areas of natural or minimally altered land (Chamberlain et al. 2008; Goddard et al. 2009). In terms of birds these areas may be used as resource areas when birds cannot obtain all the resources they need in urban areas (Melles et al. 2003; Chase and Walsh 2006; Rutz 2006). This may include parks, nature reserves and natural habitat fragments (Chamberlain et al. 2008; Melles et al. 2003). Associations are also generally found between urban birds and streams, tall trees, fruit producing trees and shrubs (Melles et al. 2003). These species showing strong associations can be considered as sensitive species (Melles et al. 2003). Thus higher bird species richness are generally found in neighbourhoods around large parks or in areas of low density housing with well establish gardens and large trees (Melles et al. 2003). Land transformation can be a contributing factor to range changes where species either move to suitable habitats or exploit the transformed habitats (Ratcliffe and Crowe 2001). Many bird species in southern Africa have expanded their ranges as they exploit the abundant resources in transformed land use areas, both in agricultural and urban areas (Ratcliffe and Crowe 2001).

Predation risk can be largely influenced by habitat structure, where thick vegetation may make the nest less visible, it also reduces the visibility of the parents to detect predators (Chamberlain et al. 2008; Evans et al. 2009b). Urban areas provide additional-supplementary feeding in the form of bird feeders in gardens, this together with additional nesting sites and nest boxes alter the density and occurrence of many urban bird species (Chamberlain et al. 2008; Evans et al. 2009b; Fuller et al. 2007; Robb et al. 2008).

Human activity and urbanisation is resulting in accelerated losses in biodiversity (Fairbanks et al. 2002). Increased urban activity and urbanisation has resulted in behavioural changes of wildlife, often due to habitat fragmentation, loss or alteration of habitat, as well as
physical, noise, and visual disturbance (Anderson et al. 1990; Berry et al. 1998; Melles et al. 2003; Bautista et al. 2004; Evans et al. 2009a). For example, behavioural changes have been documented in a number of mammal and bird species in areas of increased human activity (Anderson et al. 1990). These changes are species dependant and can be either positive or negative (Rutz 2008).

Bird populations are threatened worldwide by the combined effects of urbanisation, human development and land transformation, all of which result in the loss of avian habitats (Barnes 2000; McKinney 2006). The effects of urbanisation on bird species has been relatively well researched (Evans et al. 2009b), while little research has been done on the effects on bird communities as a whole (Blair 1996). Bird communities in urban areas generally show a trend of decreasing species richness as urbanisation increases with communities being dominated by a few largely abundant species (Melles et al. 2003). Bird species in general, and more especially ground nesting birds and birds of prey, are largely influenced by urbanisation, these influences may be either positive or negative depending on the species (Berry et al. 1998; Evans 2009b).

Raptors are influenced largely by landscape use, as this determines the availability of both prey and nesting sites (Berry et al. 1998). Raptors are generally known as being sensitive to changes in their ecological surroundings with varying effects depending on the species (Herremans & Herremans-Tonnoeyr 2000). For studies examining these effects in birds of prey, generally short-term impacts are monitored, looking mainly at reproductive success, wintering distribution, behaviour and resource availability (Anderson et al. 1990; Blair 1996). However, a large number of short-term effects will result in more dramatic long-term changes in species composition, diversity and community structure (Anderson et al. 1990; Fairbanks et al. 2002). In urban areas the presence of pigeon and dove species provide a food source which could be considered a source of supplementary feeding (Malan and Robinson 1999). However, negative effects of such supplementary feeding include increases in disease and attraction of predators (Evans, et al. 2009b; Robb et al. 2008). Supplementary feeding has been shown to positively affect clutch size as well as the size of eggs where larger eggs are beneficial as they have higher hatching success (Mackintosh and Briskie 2005; Robb et al. 2008). The availability of an additional food source in urban habitats may also minimise time spent foraging and allows parents to spend more time at the nest (Robb et al. 2008).

Urbanisation can affect species differently where some species will decline as urbanisation increases while a few species will increase in heavily urbanised areas (Blair
Species that thrive by exploiting highly urbanised habitats are referred to by Blair (1996) as ‘urban exploiters’ and these species will reach their highest densities in such conditions. On the other extreme, species that are very sensitive to urbanisation changes, have been termed ‘urban avoiders’ (Blair 1996), these species reaching their maximum densities in undisturbed/natural sites. The intermediate species are termed ‘suburban adaptable’ and these species exploit supplementary resources in habitats of intermediate urbanisation (Blair 1996; Kark et al. 2007). Species living as urban exploiters are usually successful because of their ability to utilise additional (human-related) resources and their tendency to live, nest and forage within the vicinity of humans without fear, as well as being able to survive in non-natural surroundings (Blair 1996; Kark et al. 2007). However this depends largely on whether they are behaviourally flexible and able to shift normal foraging and survival tactics to utilise such human-related resources (Blair 1996; Kark et al. 2007). Although some species appear to be doing well in urban habitats, it is thought that human disturbance may reduce their breeding success and thus the position of paths in parks should be carefully managed and perhaps an increase in provision of habitat cover is necessary to assist such species (Evans et al. 2009b). The monitoring of urbanisation effects on biodiversity can be used to determine conservation management planning (Fairbanks et al. 2002). However in order for these monitoring projects to be successful, researchers and planners must have a thorough understanding of the species presence and abundance in a specific landscape and the degree of human-inflicted modification (Fairbanks et al. 2002).

The Black Sparrowhawk (*Accipiter melanoleucus*) is a medium-sized raptor species, found occupying a large proportion of sub-Saharan Africa (Curtis et al. 2005). It is typically a territorial species which breeds in forested habitats and is thus associated with trees (Curtis et al. 2007). The Black Sparrowhawk is one raptor species that appears to have successfully colonised urbanised habitats in South Africa and its distribution in South Africa has increased over the past 20 years (Allan 1997; Allan et al. 2005). It appears that their distribution has expanded largely into areas which previously did not have tall tree stands and also widely into urbanised areas (Allan 1997). It is one of several species that has recently colonised the Cape Peninsula; it was absent in the Cape Peninsula from the 1940’s to the 1980’s but has been common there from the 1990’s to present (Curtis et al. 2007; Hockey and Midgley 2009; SABAP 2). Forest dependent species such as the Black Sparrowhawk require ‘stepping stones’ to expand their range. Black Sparrowhawks had the advantage of many commercial plantations to the east of the Cape Peninsula with the last largest stepping stone being of 40 km (Hockey and Midgley 2009).
Our aim was to determine the range change of Black Sparrowhawks in South Africa by comparing historical and current distribution data. We also aimed to determine the correlation between the probability of encountering a Black Sparrowhawk and different land cover types or use, as well as the number of hectares that would need to be added to each land cover type/use to double the probability of a Black Sparrowhawk encounter. The objectives of the study were, (i) to determine Black Sparrowhawk range expansion, and (ii) to determine the correlation between the probability of encountering a Black Sparrowhawk and different land cover types. We hypothesised that Black Sparrowhawk occurrence and density is larger within plantations and urban land cover types/uses when compared to that in indigenous forest. Thus we predict that Black Sparrowhawks have undergone a range change and are prominent within urban and altered land use areas.

**METHODS**

**Range Expansion**

The most recent range distribution map of Black Sparrowhawks was downloaded from the Animal Demography Unit (ADU) SABAP 2 (http://sabap2.adu.org.za/sp_summary.php?Sp=159&section=2) website on 28 September 2012. The SABAP 1 distribution data which were collected between 1987 and 1992 is compared with the more recent SABAP 2 data which were collected since 2007 (Fig. 1). This distribution map provides us with a descriptive look at historical distribution (1987-1992) compared with the more recent distribution (2007) as well as where the two distributions overlap. The data were summarised in quarter degree squares across South Africa.

Occupancy and persistence modeling was performed using the SABAP 1 and SABAP 2 data. The two SABAP projects provide two data sets with can be used in the analysis. The SABAP data were collected in the resolution of QDGC (Quarter Degree Grid Cells) across South Africa, providing either presence or absence data for each species. The occupancy model predicted baseline occupancy for Black Sparrowhawks on a Bernoulli Distribution where each QDGC across South Africa was assigned either a 1 or 0 based on presence and absence respectively. From this baseline the occupancy probabilities for each QDGC was calculated. The model used a two-level autologistic model fitted with a Bayesian framework using WinBUGS (Bayesian inference Using Gibbs Sampling) (Latimer et al. 2006). The Bayesian inference derived a posterior probability, using Bayes Rule (Kery 2010). The occupancy probabilities, persistence, colonization and extinctions were then determined for
each QDGC based on both the initial occupancy of the specific QDGC as well as the occupancy on neighboring QDGCs.

**Land Use**

We examined the relationship between the proportion of SABAP2 checklists (sightings) reporting Black Sparrowhawks (reporting rates) and land cover types (National Land Cover Dataset of 2000, CSIR) using generalized linear models (GLM) with binomial errors and a logit link function. We fitted the models using function GLM in R 2.15.0 (R Development Core Team 2012). We included all SABAP2 data submitted to the project by 25 April 2012. A total of 67,000 checklists were available for 10,120 pentads across South Africa, Lesotho and Swaziland. The number of checklists per pentad ranged from 1 to 542. The three land type covariates used included indigenous forests, commercial plantations and urban. Due to the large number of land use categories listed within the National Land Cover Dataset, land cover types used were grouped into only these three covariates (see chapter 2, appendix 1).

As Black Sparrowhawks are associated with trees and appear to benefit from urban development, we examined a number of explanatory variables related to habitat type and land use (Appendix 1). As a more readily interpretable measure of the effect size, we calculated how many hectares of associated land cover types would need to be added to double the rate at which Black Sparrowhawks are encountered (D) as

\[ D = \frac{\ln 2}{\text{coefficient}} \]

**RESULTS**

**Range Expansion**

When Black Sparrowhawk historical (1987-1992, SABAP 1) distribution was compared with the 2007 SABAP 2, most current distribution (Fig. 1), a change in distribution was found with a range expansion as well as the overlap between 1997 and 2012. This showed a shift in Black Sparrowhawk distribution (Fig. 1) (SABAP, 2012). They were no longer present in 144 quarter degree squares where they previously occurred, but have new distribution presence in 153 quarter degree squares where they were previously absent (Fig. 1). The frequency of squares on the SABAP map show Black Sparrowhawk presence, which appears to have increased over the major urban centres of South Africa (Fig. 1). Their reporting rates increased in 110 squares and decreased in 65 of the squares that remained occupied,
remaining constant in only 1 square. A more in-depth analysis of these results showed SABAP1 and SABAP2 occupancy comparison where a large increase in Black Sparrowhawk occupancy is visible between the SABAP 1 and SABAP 2 data sets (Fig. 2). The persistence and colonisation by Black Sparrowhawks are shown in Fig. 3. Persistence probability of Black Sparrowhawks in South Africa was between 76% and 99% across a large proportion of the country. The colonisation probabilities were relatively high within the Cape and along the east coast of South Africa where the probabilities decreased further inland.

Land Use
Three covariates were used to determine the land use of Black Sparrowhawks. These covariates were indigenous forests, commercial plantations and urban land use areas. These covariates were not strongly correlated with each other. The highest correlation was between indigenous forest and plantations ($r = 0.21$). The other correlations were -0.01 between plantations and urban, and -0.002 between indigenous forest and urban.

Black Sparrowhawk reporting rates were positively related to commercial plantations and urban areas (Table 1, Figs 2-4), while no significant relationship with indigenous forests was found. The Akaike’s Information Criterion AIC values for plantations, urban land use and indigenous forests are 11324.2, 10501.7 and 11442.4 respectively. The coefficients given in Table 1 are on the logit scale and represent the log odds of the probability of encountering Black Sparrowhawks per hectare of land cover (Hosmer and Lemeshow 2000).

The various models used include the number of estimated parameters (K), the maximised log likelihood (L), Akaike’s Information Criterion (AIC), the slope with standard error of the relationship between reporting rates and covariates on the logit scale (Coefficient, SE) and the number of hectares of each land cover type that would need to be added to double the encounter probability (D) (Table 1). The Δ AIC values for forest and plantations were 904.7 and 822.5 respectively. This indicated that the urban land use areas had the strongest slope (0.000290), the lowest standard error (0.000009) and in order to double the encounter probability only 2388 ha of urban land must be added, which was lower than those predicted for both indigenous forest (9156 ha) and plantations (2943 ha).

DISCUSSION
The Black Sparrowhawk’s distribution appears to have expanded largely into urban areas and areas which did not previously have tall tree stands (Allan 1997). This was supported in the
current study which has shown that the distribution of Black Sparrowhawks in South Africa has shifted and increased, in terms of numbers of pentads reporting the species in SABAP 2 compared to SABAP 1. The probability of a Black Sparrowhawk encounter and their documented reporting rates showed no significant relationship with indigenous forest stands in South Africa while it showed positive relationships with both commercial forest stands and urban land use.

**Range Expansion**

Habitat changes can result in species becoming either expansionists, expanding their current distribution or contractionists, reducing their distribution (Okes et al. 2008), range shifters or stable species. Our analyses of bird atlas data indicated that Black Sparrowhawks have increased and shifted their range westwards, showing expansionist tendencies on the west of its range, and contractionist tendencies on the east of its range, resulting in an overall range shift westwards over the last 20 years.

The colonisation of an expansionist species into multiple urban areas can be explained by either a leapfrog model of urban colonisation or by multiple independent colonisation events. Any colonisation event results in a loss of genetic diversity due to a single founder population. However when leapfrog colonisation occurs, the individuals from the newly formed population then rapidly disperse and colonise a new area and this continues through generations, resulting in a more dramatic loss of genetic diversity than multiple colonisation events. It can be suspected then that the Black Sparrowhawks have undergone a leapfrog colonisation westwards to the Cape Peninsula where the normally rare melanistic colour form is now the most common form seen (Amar et al. in prep). This apparent loss of genetic diversity leads us to believe a leapfrog colonisation event has occurred within this species.

A similar dramatic range expansion has been seen in several southern African bird species including Hadeda Ibis (*Bostrychia hagedash*), Acacia Pied Barbet (*Tricholaema leucomelas*), Southern Masked-Weaver (*Ploceus velatus*) and many tree-nesting raptors, this largely due to invasive alien plant species, both cultivated stands and invasive stands (Richardson and van Wilgen 2004). The change in Black Sparrowhawk distribution as well as the overlap between the 1987-1992 Black Sparrowhawk SABAP distribution with the more recent 2007 SABAP 2 distribution was investigated. The overall population has seemingly increased as the reporting rates have increased. Koeslag (2012) has commented on the range change map stating that a possible explanation for this shift into urban areas is due to the decline of rural chickens. As rural human population move into urban areas the prey items
(largely including rural chickens) have declined (SABAP, Koeslag 2012). Thus these birds have adapted to feed on urban and suburban pigeons and doves and have thus shifted into appropriate areas (SABAP, Koeslag 2012). However this speculation has little evidence to support it as there are a number of other factors which need to be considered when analysing range changes.

**Land Use**

High intensity human activity and land use results in high intensity structural changes including the planting of trees, and an increase in infrastructure and artificial water sources, which seems to have a positive influence on avian species richness (Fairbanks 2004). The Black Sparrowhawk was found to be one out of 46 species to have a range expansion in South Africa greater than 20% between two census periods, the first census was conducted between 1975 and 1980 and the second between 1988 and 1992 (Fairbanks 2004). The current study further supports the continued range expansion of Black Sparrowhawks. The Black Sparrowhawk’s range expansion determined by Fairbanks (2004) was 28% with a preference for forest and plantations respectively. The Feral Pigeon (*Columba livia*), a common prey item of the Black Sparrowhawk has had a range expansion of 63% with a preference for urban habitats (Fairbanks 2004).

The Black Sparrowhawk was previously known as a shy, forest raptor species. This species however, has recently become common in urban areas and altered landscapes, showing a higher encounter probability in plantations and urban areas than in indigenous forests in South Africa (Figures 4, 5 and 6) (Curtis *et al.* 2007). Similarly, the Northern Goshawk (*Accipiter gentilis* L.) in Hamburg, Germany was recorded as a shy, secretive forest species; however, it is now a well-adapted urban species (Rutz 2008). They now live in the city and hunt within the parks and residential areas (Rutz 2008). Recently urbanised species have adapted to face a variety of different conditions that can have both positive and negative effects on a population (Rutz 2008; Veech *et al*., 2011). Avian species adapting and thriving in urban habitats are thought to favour the structurally open environment which presents them with an all year round food source (Rutz 2008; Veech *et al*., 2011). The Black Sparrowhawk is typically known to be a shy forest raptor species but has similarly colonised urban areas and increased in abundance within these areas.

Many bird species range expansions are positively related to both agricultural and exotic tree stands as well as to water sources and urbanisation and traditional homeland management areas (Fairbanks 2004). An increase in human activity results in increased
fragmentation, habitat loss and alterations, and also an increase in habitat diversity (mosaics) within an urban area (Melles et al. 2003; Fairbanks 2004; Evans et al. 2009a). This alteration of land uses has resulted in behavioural changes of wildlife and changes in both species richness and abundance (Melles et al. 2003; Fairbanks 2004; Evans et al. 2009a). Mosaic habitats form fragments of undisturbed habitats which act as islands sustaining the original bird populations (Fairbanks 2004; Chamberlain et al. 2008; Goddard et al. 2009).

Urbanisation

Avian diversity is affected by urbanisation in two major ways depending on the level of urbanisation (Blair 1996). Severe urbanisation results in low overall diversity of both native and exotic species (Blair 1996). Moderate urbanisation results in an increase in overall avian diversity whilst native avian diversity decreases (Blair 1996). Residential and recreational areas result in additional supplementary resources added by altering vegetation structure, supplementary feeding, and nest site availability and due to the addition of ornamental plant species (Evans et al. 2009b; Blair 1996). Severely urbanised areas, in comparison, result in a reduction of resources and no additional or supplementary resources and therefore lower species richness is found in these areas (Blair 1996). Black Sparrowhawks have shown recent colonisations of urban habitats within South Africa increasing their range, the colonisation of the Cape Peninsula being the most well known example (Allan 1997, Allan et al. 2005; Curtis et al. 2007). Our results support this in that the probability of encountering a Black Sparrowhawk in urban areas is higher than that in commercial plantations or indigenous forests. Black Sparrowhawks may be colonising such urban habitats as they can exploit the abundant availability of resources (Ratcliffe and Crowe 2001). Supplementary feeding is very popular in urban habitats with people supplying supplementary food in the form of bird feeders (Fuller et al. 2007; Robb et al. 2008). This has varying effects on many bird populations where food is the major limiting factor (Fuller et al. 2007; Robb et al. 2008). This practice can influence bird communities in many ways including changes in species abundances, reproductive success rates and the health condition of the birds (Fuller et al. 2007). Additional food resources results in a higher chance of survival over winter months and higher breeding success and survival rates (Robb et al. 2008). Although the research on supplementary feeding largely reflects the effects of additional food resources on small granivorous and nectarivorous bird species, these additional resources are indirectly supplementing urban raptor species which prey on these smaller species. Many raptor species, including the Black Sparrowhawks, primarily hunt other bird species. The
supplementary feeding of these other bird species results in dense populations of these prey species for raptors, providing in its own way a supplementary food source for raptors. This may allow them to minimise foraging time and increase egg size, hatching and survival rate (Robb et al. 2008).

**Management Implications**

With respect to conservation management and biodiversity maintenance in urban areas, it is vital that the difference in the overall number of species and the quality of these species is considered, i.e., quality versus quantity (Blair 1996). Management of urban avian assemblages can take one of two paths, the first being to increase the density of a few bird species populations that appear to be doing well in human altered landscapes, alternatively the aim may be to increase the total species richness (Evans et al. 2009b). Urban avian communities are often determined more strongly by local factors than factors functioning at larger spatial scales (Evans et al. 2009b). Species richness is largely dependent on fragmentation, the larger the patch size the higher the species richness due to a reduction in isolation (Evans et al. 2009b; Grimm et al. 2008; Pautasso et al. 2011). In Canada a number of forest raptor species are present in urban areas but given the size of the habitat patches they are currently found in, it is unlikely that they will be able to maintain such populations on a long-term time scale (Evans et al. 2009b). Due to the dynamic structure of urban habitats, the vegetation is structurally diverse, similarly allowing greater species richness (Evans et al. 2009b). In urban habitats, habitat diversity is constantly increasing, however for a new habitat type to be formed, a habitat must be lost, and this increase in habitat diversity must be dependent on the conservation value of existing habitats (Evans et al. 2009b). In conclusion, Black Sparrowhawks appear to have undergone a range shift and expansion in South Africa where the reporting rates and probability of encountering a Black Sparrowhawk showed no significant relationships within indigenous forests. There was however a positive relationship with their reporting rates and both plantations and urban land use types.

**ACKNOWLEDGEMENTS**

We would like to acknowledge all who contribute to bird atlassing in South Africa as without their support and dedication of South African birds, projects such as this one would not be possible. We would also like to thank the Animal Demography Unit (ADU) who assisted with analyses and made these data available.
REFERENCES


APPENDIX 1

1) Indigenous forest: the number of hectares covered by the land-cover type “Forest (indigenous)”.

2) Plantations: the number of hectares covered by the sum of the land-cover types consisting of plantations ("Forest Plantations (Acacia sp)", “Forest Plantations (clearfelled)”, “Forest Plantations (Eucalyptus sp)”, “Forest Plantations (Other / mixed sp)”, “Forest Plantations (Pine sp)").

Table 1: Model Selection analysis for generalised linear model relating Black Sparrowhawk reporting rates to land cover types including indigenous forest, plantations and urban.

<table>
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Figure 1: The 1987-1992 SABAP 1 distribution, the 2007 SABAP 2, more recent distribution and the overlap between the two distributions of the Black Sparrowhawk in South Africa. (http://sabap2.adu.org.za/sp_summary.php?Sp=159&section=2, data accessed 28 September 2012). This map shows a visual descriptive analysis of the changes of the range of the Black Sparrowhawk, where a dramatic increase in new distribution (red squares) can be seen. Each square represents a Quarter Degree Grid Cell (QDGC).
Figure 2: Occupancy models comparing Black Sparrowhawk distribution from SABAP 1 and SABAP 2. Each grid cell provided a probability of Black Sparrowhawk occupancy for that specific quarter degree grid cell. The covariates considered within these occupancy models include the biomes and spatial effects of South Africa.
Figure 3: An autologistic model of the persistence and colonisation of Black Sparrowhawks across South Africa. Colonisation probability is the probability of a previously unoccupied site now being occupied, while the persistence probability is the probability that a site that was previously occupied has remained occupied.
Figure 4: The expected possibility of encountering a Black Sparrowhawk within the indigenous forest land-use areas of South Africa, determined using a generalised liner model with binomial errors and a logit link function. Data used were obtained from the SABAP reporting rates, using all data submitted to the project by 25 April 2012. Each dot on the figure represents one pentad; the diameter of these dots represents the number of checklists for that pentad. Therefore the larger the diameter of the dot the more checklists there are within that pentad. The y-axis represents the probability of encountering a Black Sparrowhawk (BSP Hawk) while the x-axis is the hectares of indigenous forest. The probability of encounter in this case remained relatively low even as the number of hectares of indigenous forest reached 6000 ha.
Figure 5: The expected possibility of encountering a Black Sparrowhawk within the plantation land use areas of South Africa, determined using a generalised linear model with binomial errors and a logit link function. Data used were obtained from the SABAP reporting rates, using all data submitted to the project by 25 April 2012. Each dot on the figure represents one pentad; the diameter of these dots represents the number of checklists for that pentad. Therefore the larger the diameter of the dot the more checklists there are within that pentad. The y-axis represents the probability of encountering a Black Sparrowhawk (BSP Hawk) while the x-axis is the hectares of Plantations. The probability of encounter in this case increased gradually (> 0.2) as the number of hectares of plantations reached 6000 ha.
Figure 6: The expected possibility of encountering a Black Sparrowhawk within the urban land use areas of South Africa, determined using general liner models with binomial errors and a logit link function. Data used were obtained from the SABAP reporting rates, using all data submitted to the project by 25 April 2012. Each dot on the figure represents one pentad; the diameter of these dots represents the number of checklists for that pentad. Therefore the larger the diameter of the dot the more checklists there are within that pentad. The y-axis represents the probability of encountering a Black Sparrowhawk (BSP Hawk) while the x-axis is the hectares of urban land use. The probability of encounter in this case increased as the number of hectares of urban land use reached 6000 ha. Due to the large variation this was described as a general trend.
Chapter 3

Nest site characteristics of Black Sparrowhawks (*Accipiter melanoleucus*) in KwaZulu-Natal, South Africa.

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Black Sparrowhawks (*Accipiter melanoleucus*) are typically known as a shy forest species, but they are now frequently seen and heard in urban areas in South Africa during the breeding season. The spatial and environmental factors that influence Black Sparrowhawk nesting sites in urban and peri-urban areas were investigated along a gradient between Estcourt, Pietermaritzburg and Durban, in KwaZulu-Natal. The trends in our data suggest that Black Sparrowhawks appear to have specific nest site characteristics, particularly with respect to nest tree species, tree and nest height and area of ‘greenspace’ surrounding the nest, as well as nest associations with water sources, roads and buildings. Black Sparrowhawks showed a trend in selection for a particular tree height class (20 – 29 m) as well as trends for a specific nest height class (10 – 19 m). Similarly the selection of distance classes to the nearest water sources, buildings and roads all showed a significant trend by Black Sparrowhawks. Nests sites were most commonly found in *Eucalyptus Sp.* nest trees. Due to ever changing urban habitats and human altered landscapes, as well as the removal of alien tree stands within urban areas, the availability of nest sites and foraging habitats may decline. Consequently understanding the nest site needs of a species like Black Sparrowhawks in urban and peri-urban areas is important for their success and management programmes for their persistence.

**Keywords:** Nest site selection, nest ‘greenspace’, nest characteristics, *Accipiter melanoleucus*, and urbanisation.
INTRODUCTION

Urban habitats are comprised of a mosaic of various land use types as natural and existing land uses are transformed via urbanisation (Reale and Blair 2005). Many avian population declines worldwide have been caused by habitat loss and urbanisation, thus it is important to understand the specific habitat requirements for species’ (Bisson et al. 2002). In particular, nest site availability may be crucial in determining habitat suitability and avian abundance as this may be one of the vital limiting factors for urban avian species (Tella et al. 1996; Bisson et al. 2002). Avian predators may base nest site selection on a number of factors (Abe et al. 2007; Sullivan et al. 2011). Urban and rural habitats inflict varying costs and benefits on avian species and these can vary widely between the two habitat types (Tella et al. 1996).

Urban habitats can be limiting with regard to resource availability in terms of nest sites as well as prey species richness and abundances (Cardador et al. 2012). These factors reduce the suitability of urban habitats for many species and can largely result in a reduction of biodiversity, most specifically of the indigenous and specialist species, sometimes leading to a regional or local extinction of a species (Fairbanks 2004). Positively however, many urban areas and suburban areas have parks and areas of natural or slightly altered land. Bird species in particular can use these as additional resource areas when they cannot obtain all the resources they need in urban areas (Melles et al. 2003). This may include gardens, parks, nature reserves and natural habitat fragments (Melles et al. 2003). Many species have been shown to be associated with natural forest areas and parks within the urban gradient thus these ‘urban birds’ are maintained in the urban landscape by such areas, which provide habitat, food and nest sites (Melles et al. 2003).

Nest site selection of bird species is dependent on particular structural features (Saliva and Burger 1989; Malan and Shultz 2002). This can include both the factors within the immediate vicinity of the nest as well as the factors within the habitat patch in which the nest is found (Saliva and Burger 1989; Malan and Shultz 2002). Associations as mentioned above may form one aspect of nest site selection in avian species. However many other factors may too be included in nest site selection, including orientation, protection from weather conditions, sun exposure, predation risk, accessibility, nest tree species, height, width, overhead cover, stability and surrounding land-cover types (Abe et al. 2007; Malan and Shultz 2002; Saliva and Burger 1989; Sullivan et al. 2011). Nest cover is largely determined by vegetation density which can be instrumental in nest site selection as the density of vegetation will provide varying degrees of cover and thus protection from predators making
the nest less visible, and reducing the attraction of predators by inhibiting chemical and auditory signals of nest presence and occupancy (Saliva and Burger 1989). Suburban bird species will base their nest site selection on features different to those in natural landscapes due to a difference in available habitats, resources and predation risks (Saliva and Burger 1989; Dykstra et al. 2000). Urban avian communities are largely dependent on vegetation, where dominant species are able to use fragmented mosaics of vegetation (Reale and Blair 2005).

Raptors are long-lived birds with relatively large home ranges and thus need to select suitable habitats that will sustain lifelong survival and successful breeding (Abe et al. 2007). Raptors require suitable habitats and nesting sites in order to breed successfully and thus increase their fitness (Abe et al. 2007). The Crowned Eagle (Stephanoaetus coronatus) is an example of a raptor species which nests in tall tree forest where they can easily access the nest (Malan and Shultz 2002). In South Africa a conflict has developed between human activities and these forest nesting birds as the number of indigenous forest tree stands have declined (Malan and Shultz 2002). However, exotic commercially grown forest patches have increased in number and size (Malan and Shultz 2002). These include *Eucalyptus*, *Pinus*, *Acacia* and *Populus* (Malan and Shultz 2002).

The Black Sparrowhawk (*Accipiter melanoleucus*) appears to have benefitted from afforestation and is successfully using exotic tree stands for nesting (Malan and Robinson 2001; Chapter 2). Black Sparrowhawks noticeably show a preference for nesting in large trees (Malan and Robinson 2001). Exotic trees are on average 9 – 15 m taller than the average 18 m high indigenous trees (Malan and Robinson 2001). Being large enough to defend their nests from predators, they nest within or just below the leaf canopy. Black Sparrowhawk nests are generally found 2-7 m below the tops of the surrounding trees (Malan and Robinson 2001). Furthermore although typically known as a shy forest species (Curtis et al. 2007), the Black Sparrowhawk is now frequently seen and heard in urban areas in the breeding season and appears to be thriving in such urban habitats (Chapter 2).

The aim of this study was to determine the characteristics of Black Sparrowhawk nest sites, identify possible trends in specific spatial and environmental factors to allow further studies to investigate selection preferences. We determined the land cover and vegetation type used by Black Sparrowhawks as well as nest site parameters including tree height, nest height, nest tree diameter at breast height, ‘greenspace’ surrounding the nest, and possible associations with water sources, roads and buildings. In addition, we looked at the size of tree clumps in which the nest tree was found and the position of the nest tree within such clumps.
Our objective was to describe what nesting habitats Black Sparrowhawks use in urban and peri-urban areas in order to assist with municipal management and to conserve particular areas within human altered landscapes. We expected that Black Sparrowhawk nest site localities were highly selective based on numerous nest characteristics as well as nearby associated features and were not simply randomly selected nest sites.

METHODS

Sample Sites
Black Sparrowhawk nests were located along a rural/peri-urban and urban gradient from Estcourt (2929 BB), through Pietermaritzburg (2930 CB), to Durban (2930 DD), KwaZulu-Natal (KZN). Data were collected for both the 2011 and 2012 Black Sparrowhawk breeding seasons which ranged from March to October.

Data Collection
Nesting sites were located with the help of numerous bird clubs, the Natal Falconry Club and the general public. Following the discovery of each nest, the nests were monitored every two weeks during the breeding season. During a pilot investigation of nest selection analysis it was found that the traditional quadrat method where randomly selected trees are selected to determine selection over availability (Malan and Robinson 2001; Malan and Shultz 2002) was found unsuitable within a highly urbanised habitat due to the variability of the habitat. Thus the land cover and vegetation type surrounding each nest were analysed using spatial analyses in ArcMap (Version 9.3, ESRI). Active nests were then identified and these further monitored and analysed (Chapter 4). Tree species in which the nests were found were identified. On conclusion of the 2012 breeding season, specific characteristics of the active nesting areas were recorded. Due to the inaccessibility of many of the Black Sparrowhawk nests the sample size of those measured was dependant on the nest trees whose base could be reached for data to be collected. The nest height and total tree height was measured using a forestry Vertex height measurer (Vertex III, Version 1.5). The circumference of the nest tree at breast height (1.3 m) was measured and converted to the diameter at breast height (DBH) measurement. The number of mature trees per clump was recorded. A mature tree was defined as any tree that could structurally accommodate a Black Sparrowhawk nest. The clump size was determined as mature trees with canopies touching. The position of the nest tree in the clump was also recorded; the nest tree was classified as either an edge tree, being in the outermost ring of trees or as a tree in the middle of a clump, not the outermost tree. The
distance of each nest to the nearest water source, paved road and human-occupied buildings were then measured for each nest using satellite imagery in ArcGIS (Version 9, ESRI, 2008). ArcMap was similarly used to measure the ‘greenspace’ area surrounding each nest, this was defined as the habitat suitable for breeding and hunting and thus included the tree clump in which the nest was found as well as open and undeveloped (green) land space immediately surrounding the nest tree base.

Statistical analyses
The home ranges of each breeding pair were unknown so in order to analyse possible selective features a buffer of 1000 m was formed around each nest using ArcMap. An intersect analysis was then performed between all active nests from both 2011 and 2012 and the Land Cover shapefile (2000) for KwaZulu-Natal. This analysis was performed in ArcMap and determined all the land cover types within the 1000 m buffer of each nest. Similarly the intersect analysis was performed between the active nests and the Mucina and Rutherford Vegetation shapefile (2006). The results from both of these analyses were summarized in Microsoft Excel and displayed graphically to show the trends.

The specific nest site and nest tree trends were similarly displayed graphically in histograms to visually see selection trends in size classes. Descriptive statistical analyses were performed on the data to determine the trends within particular parameters. Due to data being categorised into size classes a chi square analysis was used. Statistics were performed in SPSS (Version 21).

RESULTS
A total of 40 Black Sparrowhawk nests were located within the study area. Of these 35 % were rural or peri-urban while the remainder were urban, found within a human altered landscape/city (n = 40; Fig.1). Twelve of the nests were inaccessible to identify and measure, due to their location in inaccessible forests, private land or overgrown alien invasive vegetation. Thus only 28 individual nest trees used by Black Sparrowhawks were identified to species level, of this sample of 28 trees, 79 % were Eucalyptus sp. while 7 % were Ficus sp. Other tree species used as nest sites included Agathis sp., Crysaphilm sp., Laguncularia racemosa (white mangrove) and Syringa reticulata (syringa) (Fig. 2a).

The spatial intersect analysis showed that the 30 nest buffers, that were confirmed active during the breeding seasons out of the 40 nests located in total, encompassed 13 different vegetation categories as described by Mucina and Rutherford (2006). The most
frequently intersecting vegetation type was the KwaZulu-Natal Coastal Belt (32%) followed by KwaZulu-Natal Hinterland Thornveld (14%) and Ngongoni Veld (14%) (Fig. 3a). The nest buffers encompassed 15 different land cover types, of which the most frequent was the urban/built up land: residential (18%), followed by unimproved grassland (14%) and thicket and bushland (12%) (Fig. 3b).

The distance between nests and the closest water sources, roads and buildings were measured. These distances for all features varied from 1 m to up to 2525 m (n = 26). 58 % of the nests were within 200 m of the nearest water source. Similarly 67 % and 81 % were within 200 m of the nearest road and buildings respectively (Fig. 4). Statistically it was found that the distance between Black Sparrowhawk nests and these three features appear to show a trend in which the birds are selecting nests at specific distances and nests are not found equally at all distances away from these specific features. Chi-square analyses for all three features was significant (p < 0.001). Therefore a significant preference in Black Sparrowhawk nest site selection with regard to nearest water sources, buildings and roads was found.

The specific nest tree characteristics could only be determined where the surrounding vegetation allowed space for the vertex to be visible from the required distance. The sample size was therefore reduced to 19 nests. Nest trees of Black Sparrowhawks were in tree clumps varying in size from 0-10 trees to > 50 trees (n = 19). 31 % of nest trees were in clumps of between 10 – 19 trees while 21 % were found in both classes 0 – 9 trees and > 50 trees (Fig. 2b). Within the tree clumps, Black Sparrowhawk nest trees were classified by their position in the clump as either middle or edge. Most nest trees were not on the edge of a tree clump (68%) whilst only 32% were on the edge of a tree clump (n = 19; Fig. 2c).

Tree and nest height of active nesting trees of Black Sparrowhawks measured were categorised into height classes. Nest trees ranged in height from 14.7 m to 54.0 m. Birds selection of nests trees was not equal. A chi-square analysis showed a significant selection trend for a specific height range (p = 0.001, df = 4). 58 % of the nests were in trees within the height class of 20 – 29 m. In addition 58 % of the nests were at a height of approximately 10 – 19 m (Fig. 5a). Similarly a chi-square analysis showed a significant nest height selection by Black Sparrowhawks (p = 0.001, df = 4).

Nests of Black Sparrowhawks were only in trees of a diameter (DBH) greater than 0.34 m, the frequency increased with diameter to four nests in the diameter class between 0.6 – 0.8 m and 5 nests within the diameter class of 1.4 – 1.6 m (n = 19). We found a positive relationship trend between frequency of nests and diameter of nest tree at breast height (r² =
0.5034; Fig. 5b). However this selection trend was not statistically significant ($p = 0.551, df = 6$).

**DISCUSSION**

A species can be constrained by the habitat type within their environment (Slaght *et al.* 2013). A spatial analysis is an objective method that can be used to determine the resource selection of a species (Slaght *et al.* 2013). Black Sparrowhawks appear to be thriving in human altered landscapes however within both peri-urban and urban habitats appear to be selecting nests based on similar spatial and environmental factors. A spatial intersect analysis was performed to determine possible selection trends in both vegetation type and land cover. The vegetation features analysed within the nest buffers may not show a true representation of nest site selection as this is biased based on the sample area with KwaZulu-Natal. The most favoured vegetation was the KwaZulu-Natal Coastal Belt with 32% of the intersected vegetation polygons being the Coastal Belt. The land cover intersect analysis however displays a remarkable trend towards urban/built up residential land (18%) of a total of 15 land cover types found within the nest buffers. Similarly using spatial analysis it was found that Blakistons fish owls *Bubo blakistoni* showed a selection within their home ranges for areas with valleys close to waterways (Slaght *et al.* 2013).

Within the nest buffers the above mentioned trends were found in land cover types which may influence the nest site selection of Black Sparrowhawks. The specific nest parameters were also determined as a pilot study to investigate what features may or may not be used in nest site selection. Nest trees may be selected based on stability or on overhead nest cover (Abe *et al.* 2007). Northern Goshawks (*Accipiter gentilis*) for example use the same nests year after year and may build onto the nest every year increasing its diameter to about 1 m, thus nest tree stability is important (Abe *et al.* 2007). Eurasian Sparrowhawks (*Accipiter nisus*) in the Ishikari plain of Hokkaido, Japan, however showed a distinct preference for evergreen conifers. At the beginning of the deciduous broad leafed nest trees had no leaves whereas evergreen conifers do and thus provide nest cover (Abe *et al.* 2007). With respect to cover, broad leaf trees provide less cover then evergreen conifers, thus where aerial predators are prominent, nest selection may be dependent more on cover then stability (Abe *et al.* 2007). These conifer forests also had larger basal cover and higher tree density than randomly selected forests (Abe *et al.* 2007).

A large percentage, 79 %, of the Black Sparrowhawk nests examined in our study were in *Eucalyptus* *sp*. These are exotic trees in South Africa, originally from Australia and
brought to South Africa particularly as a commercial plantation species (Forsyth et al. 2004). About 149 Eucalyptus sp. had established in South Africa by 1940 (Forsyth et al. 2004). They are used commercially for timber, firewood, poles and ornamental, and have become common in cities across South Africa (Forsyth et al. 2004). Generally Eucalyptus sp. are large trees reaching heights of up to 50 m. They are evergreen trees and thus provide cover year round. Black Sparrowhawks breed during the winter months and most indigenous trees are then leaf-less and provide no nest cover during the vital breeding months. Black Sparrowhawks may then select Eucalyptus sp. to breed in to obtain added cover in the form of both protection from predators and shade, or because of the above average height provided by them when compared to indigenous tree height (Malan and Robinson 2001). The Working for Water Programme, established in South Africa in 1995 aims to remove alien vegetation and re-establish indigenous vegetation (Richardson and van Wilgen 2004). Considering that almost 80 % of the Black Sparrowhawk within the study area were nesting in alien tree species, this removal by the Working for Water Programme may have deleterious effects on the Black Sparrowhawk persistence particularly in periurban and urban areas.

Where raptors nest in large mature tree stands, a human-wildlife conflict often arises. For example the Bald Eagles (Haliaeetus leucocephalus) in Oregon nest in mature coniferous forests and thus create a conflict between forestry industry and raptor management programs (Anthony and Isaacs 1989). Malan & Robinson (2001) similarly highlighted the potential conflict between forestry and Black Sparrowhawks in South Africa.

It appears that clump size had little influence of the nest site selection of Black Sparrowhawks in KZN. The largest percentage of Black Sparrowhawk nests in this study, 31 %, were in the trees clump class of between 10 and 19 trees while 21 % were in both the smallest and largest clump sizes namely between 0 and 9 trees and more than 50 trees. The majority of nest trees examined were positioned in the middle of the tree clump (68 %), while only 32 % of nest trees were found on the clump edges. Being in the middle of the clump may provide more protection as the nest is less visible to predators and less affected by adverse weather conditions such as excessive rain, wind or sunshine.

Nest height of bird species has been found to be negatively related to urbanisation, thus as urbanisation intensity increases nest height decreases, this is proposed to be due to a lack of nesting sites and birds having to choose less suitable sites to nest (Reale and Blair 2005). The majority of Black Sparrowhawk nests (58 %) were in trees between 20 and 29 m high and 58 % of the nests were between 10 and 19 m high. The lowest nesting tree was only 14.8 m high, this nest tree was a white mangrove (Avicennia marina) found within the middle
of a large mangrove, the tree density was high and thus the nest was well protected within a mangrove forest where twice a day the tides would come in and cover the base of the tree. Very few ground predators would be a threat to this pair and it thus may be an outlier. All other nest trees were all higher than 20 m. The white mangrove nest was at a height of 7.5 m however this too would be considered an outlier (pers. obs.). All other nests were higher than 13 m. Black Sparrowhawks are thus assumed to be selecting nest trees only over a particular height, limiting appropriate nest sites in urban habitats. Similarly over 53% of Red-tailed Hawks \((Buteo jamaicensis)\) nests were higher than 10 m whereas > 50 % of both the Ferruginous \((B. regalis)\) and Swainson’s Hawks \((B. swainsoni)\) were below 10 m (Bechard \textit{et al.}, 1990).

Raptor species have generally shown to select nesting sites using two main features, water sources and mature forests (Dykstra \textit{et al.} 2000). Nests were found in mature forest stands near to a water source (Dykstra \textit{et al.} 2000). The nearby water sources were most often small streams found at the bottom of valleys (Dykstra \textit{et al.} 2000). Similarly, many eagle and hawk species have shown nesting associations with water sources (Anthony and Isaacs 1989; Bechard \textit{et al.} 1990). Owl species have also shown a significantly higher number of urban nests that were in conifers compared to rural (Smith \textit{et al.} 1999). No significant difference in distance to water source between urban and rural Great Horned Owl \((Bubo virginianus)\) nests but significantly different from random sites therefore showing a selection for this feature (Smith \textit{et al.} 1999). Rural nests were not as close as urban but closer then random sites to human habitation, possibly due to associations with fragmentation and edge etc. or for food availability, mice, farm animals etc. (Smith \textit{et al.} 1999). We determined that 58 % of Black Sparrowhawk nests were within 200 m of the nearest water source, this being a dam, river or stream. Roads as a feature in this study were classified as paved roads not including small or gravel roads, 67 % of the Black Sparrowhawk nests were within 200 m of such described roads. Similarly 81 % of nests were found within 200 m of buildings; here buildings were classified as farm compounds, residential, commercial or industrial buildings. Thus a large proportion of nests were found within a 200 m radius of these features showing a possible association between Black Sparrowhawk nesting sites and water, and human habitation. Nest sites of African Crowned Eagles in KZN appeared to be non-selective and tolerant of human disturbances including water sources, roads and buildings (Malan and Shultz 2002).

Further recommendations for similar studies performed in the future would be to determine an estimate of the age of the nest trees as well as surroundings trees, to compare height of the nest tree with height of surrounding trees and the mean tree height per tree.
stand/clump, to determine a measure of openness and accessibility to nest sites and to measure height of the first side branch of each nest tree as well as number of forks in each nest tree to determine the number of suitable nesting sites and more specifically how a nest tree is selected within a tree clump. In terms of long term studies, the nest age should be determined along with respective nest success, as recommendations made in this short term project may show selective characteristics on new nests which may in fact prove to be unsuccessful and detrimental to this species. We therefore suggest that a long term nest site selection study be correlated with nesting success in order to make informative management recommendations. As urbanisation and human development increases the natural undeveloped land fragments are disappearing with many old tree stands being removed, especially those of *Eucalyptus sp.* as this is an alien species. The Working for Water program in South Africa aims at removing alien species and restoring indigenous vegetation (Hosking and du Preez 2004). Thus from a management point of view suitable nesting sites and particularly large mature forest tree stands need to be conserved and monitoring of this species and other raptor species in urban and rural environments has to be continued over a long time period looking at both reproductive success and survival rates (Poirazidis *et al.* 2007). In conclusion Black Sparrowhawks nest site localities appear highly selective based on various nest characteristics as well as nearby associated landscape features. The results from this study form a descriptive foundation and further studies should build on this foundation to determine nest site selective preference of Black Sparrowhawks.

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REFERENCES


Figure 1: Active Black Sparrowhawk nests in KwaZulu-Natal over the 2011 and 2012 breeding season, showing nests that were active in both seasons, or only one of the seasons (n = 28).
Figure 2: Black Sparrowhawk nest sites along a rural/peri-urban and urban gradient in KwaZulu-Natal, where (a) is the nest tree species used in the 2011 and 2012 breeding seasons (n = 28) and (b) is the frequency of nest trees found within tree clumps of varying number of trees (n = 19) and (c) is the frequency of nest trees position on the edge (outer ring of trees) of the tree clump or within the tree clump.
Figure 3: Percentage results from polygons found within the nest buffers of Black Sparrowhawks where (a) is the percentage of the top four vegetation types and (b) the percentage of occurrence of each land cover type within the nest buffers (n = 30).
Figure 4: Distance from Black Sparrowhawk nesting trees to the closest water sources (including rivers, streams and dams), roads and buildings (n = 26).
Figure 5: Active Black Sparrowhawk nests along a rural/peri-urban and urban gradient in KwaZulu-Natal over the 2011 and 2012 breeding seasons where (a) is the frequency of nest and nest tree height (n = 19), and (b) is the diameter at breast height (DBH) of the nest trees (n = 19).
Chapter 4

Reproductive success and breeding behaviour trends of Black Sparrowhawks (Accipiter melanoleucus) in peri-urban and urban areas in KwaZulu-Natal, South Africa

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Black Sparrowhawks (Accipiter melanoleucus) appear to be increasing in human altered landscapes, however little is known about their breeding success and characteristics. Consequently their reproductive behaviour and trends were investigated in a descriptive study in KwaZulu-Natal, South Africa. Over the 2011 and 2012 Black Sparrowhawk breeding seasons the majority of successful nests raised two chicks. The Black Sparrowhawk nests monitored in 2011 and 2012 had success rates of 74% and 41% respectively. Nest preparation was done predominantly by the male with incubation then predominantly by the female. An increase in fresh leaf material being brought to the nest as chicks aged suggested that this was more likely due to parasite control rather than showing nest occupancy as has been previously speculated.

Keywords: Nest building, incubation, brooding, parental care, reproductive success
INTRODUCTION

Urbanised areas are a mosaic of industrial, commercial and residential habitats, all of which have a generally high human population density (Reale and Blair 2005; Grimm et al. 2008; Pautasso et al. 2011). The human population density is constantly growing due to expanding economic and social developments and rapid human population growth rate in South Africa (Grimm et al. 2008). In South Africa, urban environments, including agricultural lands, have many large copses of tall alien trees (Allan 1997; Allan et al. 2005). Black Sparrowhawks (Accipiter melanoleucus) nest and hunt within such tree stands (Allan 1997). Black Sparrowhawks have been predicted to have undergone a range shift where the probability of encountering a Black Sparrowhawk is higher in urban areas than in plantations and indigenous forests (Chapter 2). Diet of Black Sparrowhawks is composed largely of pigeons, doves, francolins and domestic fowl (Allan 1997), all abundant in urban areas. Urban environments often seem ideal for bird species, especially raptors, due to the abundance of unexploited resources such as increased nest sites and prey availability (Rutz 2008). However urban habitats and human altered landscapes can result in additional threats to avian species due to removal of alien trees, disease and persecution (Allan et al. 2005; Rutz 2008).

Biparental care is expected in raptor species where multiple mating opportunities do not occur and is largely dependent on the extent of sexual dimorphism where size may influence the roles played by each adult (Margalida et al. 2007). A number of factors can influence avian incubation behaviour including adult body weight, food availability, hunting success, nest predation and ambient temperature (Conway and Martin 2000). Avian species whose nests face a high predation risk will maintain longer periods on the nest and longer periods off the nest, reducing the total number of nest visits which may attract the attention of predators to the nest (Conway and Martin 2000). In North America between temperatures of 9º and 26º C, incubation bouts are positively correlated with temperature, however outside of this temperature range both on an upper and lower scale; no correlations are found (Conway and Martin 2000). During incubation shifts the bird is seen to stand, change position and resettle within a short time period, this can be termed ‘re-settling’ (Drent et al. 1970).

Multiple brooding in birds appears to be positively related to urbanisation, thus showing a shift in the breeding strategy for birds across an urban gradient (Reale and Blair 2005). Species that energetically rely on a single brood per season may be unable to maintain a sustainable urban population whereas those that can have two broods a year due to low
nesting success may be better adapted to maintain an urban population (Reale and Blair 2005). Multiple brooding has been recorded in Black Sparrowhawks (*Accipiter melanoleucus*) in two study areas in South Africa, where the breeding season began in autumn or early winter and ended around the mid-summer months (Curtis *et al.* 2005). This typically winter breeding species has thus extended its breeding season within the Cape Peninsula to include some of autumn as well as spring and early summer, thus giving them a total of 9 months breeding season (Curtis *et al.* 2005). Within natural environments specialist species like Black Sparrowhawks are not expected to double brood within one breeding season, due to the fact that they are specialist bird prey feeders, who are believed to have lower hunting success than raptor species hunting non-flying prey items (Curtis *et al.* 2005). However, their ability to succeed in human altered landscapes where nest sites and prey items are readily available is thus thought to enable this species to double brood in some areas (Curtis *et al.* 2005).

Certain raptor species line their nests with green leaf material; it forms no part of the structural design of the nest but lines the interior or rim of the nest (Wimberger 1984; Heinrich 2013). This green material is refreshed or added to on a daily basis during both incubation and nestling (Wimberger 1984; Heinrich 2013). It is thought that the compounds in such material may function as olfactory repellents or toxins which deter insects and ecoparasites; to control nest moisture; show occupancy or serve as camouflage for the nest (Wimberger 1984, Malan *et al.* 2002). Heinrich (2013) concluded that the green leaf lining of raptor nests serves to improve nest hygiene. Malan *et al.* (2002) investigated the lining of Black Sparrowhawk nests with green material concluding that this behaviour most likely serves as a mite repellent role on the nest.

The aim of this study was to determine the reproductive behaviour and trends of Black Sparrowhawks in peri-urban and urban areas in KwaZulu-Natal, South Africa. The objectives were to determine reproductive success of known nests and to describe the behaviour of a male and female in nest preparation, incubation and parental care as well as the frequency and duration of feeding and the frequency of both delivery of fresh leaf material to the nest and nest aeration of a pair of Black Sparrowhawks.

**METHODS**

**Study sites**

Data were collected during the Black Sparrowhawk breeding seasons of 2011 and 2012 in peri-urban and urban areas of KwaZulu-Natal. The nests were found along a rural/peri-urban
and urban gradient between Estcourt (2929 BB), Pietermaritzburg (2930 CB) and Durban (2930 DD) (Chapter 3). Nest locations were found with the help of the KwaZulu-Natal Falconry Association, BirdLife South Africa members, as well as the general public. Using a global positioning system (GPS- Garmin eTrex) the coordinates of all the nests were recorded and mapped according to whether they were active in 2011 or 2012 or both years (Chapter 3). Nests were monitored during the breeding season by observation at least once every two weeks, where it was then recorded whether the nests were active or not based on whether or not the bird was seen, heard, and the amount of defecation on or around the nest as well as visual confirmation of birds, green leaf material or chicks on the nests.

**Fecundity**

Reproductive success was determined by monitoring the number of eggs, chicks and fledglings from camera footage, and from direct observations at other nests. From this, the number of successful fledglings was determined as a measure of fecundity (reproductive output). Basic data such as nest preparation, incubation shifts, brooding shifts, frequency and duration of feeding and frequency of delivery of fresh leaf material to the nest were also determined using the nest cameras. The cameras were then removed from the nest once the chicks had fledged or for failed nests once the nest had been abandoned.

**Green Nesting Material**

The footage obtained from the nest cameras was used to determine the frequency at which fresh nesting material was brought to the nest as nest lining material. This data were then correlated with both egg age and chick age to determine if any correlation was present.

**Data Summary Analyses**

Cameras were used at three Black Sparrowhawk nests in 2011 and six nests in 2012. Nests were monitored using either video or still cameras placed approximately 1 m away from the nest. Video recording cameras (CCTV, Vivotek IP7330) recorded all activity on the nest during the breeding season; these were used on three nests in 2011. The still cameras, camera traps (Bushnell Trophy Cam; Ltl Acorn 5210 and Ltl Acorn 6210), were motion censored, taking photographs whenever there was movement on the nest, an interval of 10 s was set. These trail cams were used in 2012.

Only one video camera recorded a successful breeding attempt for the majority of the nesting period at a Black Sparrowhawk nest and therefore this data were summarised
graphically to show trends, although no statistical conclusions could be drawn. Trends and findings from other cameras and observations are also discussed. However no analyses could be performed on these data as the data collected were inconsistent and insufficient to make any conclusions. The amount of time spent on the nest during both incubation and brooding was determined as a sum for each 12 h day, from 06h00 to 18h00. The frequency of feeding for each day was also determined as a total for each day while the duration of feeding events was determined as both a total and average duration for each day. The number of times fresh leaf material was delivered was determined as a total for each day. The proportion of time spent incubating by both the male and female were plotted with the incubation time period to determine if these incubation shifts changed as the eggs got closer to hatching.

The remainder of the variables looked at, including brooding shifts, feeding frequency and duration and frequency of delivery of fresh leaf material and nest aeration were all plotted with age of the chicks to determine the changes in these factors as the chicks grew and became more independent prior to fledging.

RESULT AND DISCUSSION
The annual breeding periods of Black Sparrowhawks varied from nest to nest but were all within the months of May to October. Nesting success was determined for 40 nests over the 2011 and 2012 Black Sparrowhawk breeding seasons. Fourteen nests were not found within a city/human altered landscape while the remains were classified as urban nests (Chapter 3). Over the 2011 breeding season 19 of these nests were confirmed active while only 22 of these were confirmed active in 2012. Very few active Black Sparrowhawk nests were found in 2012 and a number of the nests from 2011 were abandoned in 2012. This could be due to the death of one or both of the adults, the use of the nest by other species or extensive nest damage, the use of alternative, undiscovered nest sites, or perhaps that some pairs do not breed every year. Active Black Sparrowhawk nests were classified as successful or unsuccessful and further classified under successful according to the number of chicks successfully raised to fledging. Unsuccessful nests were further classified into failure due to Egyptian geese (*Alopochen aegyptiacus*) disturbance or failure due to other unknown factors (Fig. 1). 2011 Black Sparrowhawk nests investigated had a relatively high success rate of 74 %, while the success in 2012 was comparably low with a success rate of only 41 % which therefore yielded a higher unsuccessful number of breeding attempts. All of the known ‘rural’ Black Sparrowhawk nests were found in *Eucalyptus sp.* while some of the urban nests were found in indigenous tree species (see chapter 3 for more detail of nest site dynamics).
Detailed nest data were from only one nest with a camera and therefore are
descriptive and cannot be used to draw conclusions until further research has been performed.
A total of 80% of nest preparation at this nest was conducted by the male Black Sparrowhawk with the remaining 20% by the female (Fig. 2a). These percentages were
determined from the total number of visits to the nest where video footage recorded the nest
preparation period.

Generally raptors are biparental, sharing the role of incubation. Similarly Black Sparrowhawks in the current study showed shared incubation. The total hours incubated by
both adults each day was measured over a period of 24 h, these variables varied greatly (Fig.
2). The female incubated between 20 and 22 h 30 min of 24 h while the male only incubated
between 30 min and 2 h a day (Fig. 2). This visual representation of the incubating patterns
showed that on days when the female incubated less the male incubated more and vice versa
thus providing the eggs with an almost constant period of incubation each day. Similarly
Spanish Imperial Eagles (*Aquila adalberti*) share the role of daytime incubating although the
female does most of this with the male only taking part while the female fed (Margalida *et al.*
2007).

During incubation the Black Sparrowhawk adults appeared to ‘turn’ the eggs on a
regular basis (Fig. 3). The frequency of this behaviour appeared to increase as the hatching
date approached between incubation days 30 and 40, with hatching occurring on day 40 ($R^2 =
0.3743$) (Fig. 3). The female did most of the incubation. During this time we noted her
turning the eggs and position changed on average every 20 min during day light hours,
however she only repeated this behaviour at night every 2 h.

Although no quantitative data were obtained on diet and prey items, observations
showed urban Black Sparrowhawks preyed primarily on racing pigeons, laughing doves etc.
At one particular rural nest site a plucking post was found. Feathers found there belonged to
Helmeted Guineafowl (*Numida meleagris*), Cattle Egret (*Bubulcus ibis*) and Hadeda Ibis
(*Bostrychia hagedash*). There were also bones and the skull and beak of a Hadeda Ibis. No
food was brought onto the Black Sparrowhawk nest during the incubation period until the
male brought food to the nest for the first time at 06h57 on the morning before both chicks
hatched. At 08h58 the female left the nest for over 11 min, the male did not go onto the nest
at this time but sat close to the nest on a side branch. It seemed that both the adult birds knew
the chicks would hatch this day. This was probably due to the chicks pipping from within the
egg, in the same way as the chicks ‘call’ for food or warmth the chicks become vocal in the
days prior to hatching (Poisbleau *et al.* 2013). A brood of two Black Sparrowhawk chicks
hatched, the chicks were fed by the parents from the day they hatched, day 0, the number of feeds per day varied from 1 to 8 times per day (Fig. 4a). Chick age showed a general trend of increased frequency of feeding with chick age.

Feeding rates of the Lesser Kestrels (*Falco naumanni*) in Spain were similar in urban areas and rural areas (Tella *et al.* 1996). We did not obtain enough data to determine this in Black Sparrowhawks however this is something that should be considered in future research.

The total duration of feeding each day in Black Sparrowhawks similarly appeared to increase with chick age ($R^2 = 0.7682$, Fig. 4b). However as this is the total of time spent feeding this will be dependent on the frequency of feeding (Fig. 4). Therefore the average duration of each feed was calculated showing the feeds in fact increase in duration with chick age ($R^2 = 0.7285$).

Two of the Black Sparrowhawk nests failed because of presumed nest predation, where chicks were known to be on the nest and subsequently disappeared (Fig. 1). We were unable to confirm how many of the other nest failures may have been due to predation. On 25 August 2012 during a nest observation, the female whilst brooding young chicks began calling, as the male flew in and landed on the nest with food. A Vervet Monkey (*Chlorocebus pygerythrus*) that had not been seen jumped down towards the nest, this may have been in an effort to steal the prey items or attack the nest during the food delivery. Both adults flew at the monkey chasing it away. The adults remained agitated for some time after this. We suspect that the Vervet Monkey may have learned this food call and reacts thereafter to steal newly delivered food.

Following the hatching of the eggs the female Black Sparrowhawk started brooding and left the nest only occasionally. Similarly Spanish Imperial Eagle chicks were brooded by the female with the male contributing very little (Margalida *et al.* 2007). When she was not brooding the female Black Sparrowhawk spent a large proportion of her time preening on the edge of the nest or seemingly ‘shading’ the chicks, this possibly a thermoregulatory behaviour (Brown and Downs 2003). Her presence on the nest is most likely a form of nest defence, ensuring the chicks are not predated or threatened in any way. The time each day that the nest was unattended by both adult birds is shown in Fig. 4c. This showed a positive relationship with chick age ($R^2 = 0.6035$).

Wimberger (1984) found that the use of green material was not related to diet with respect to species found within the Order Falconiformes. The use of greenery varies geographically within a species, possibly due to availability of plant species and time of leafing and the regional abundance of ectoparasites (Wimberger 1984). Fresh green leaf
material was brought to the Black Sparrowhawk nests frequently by both adult birds during nest preparation, incubation and increasingly during chick rearing \((R^2 = 0.5743; \text{ Fig. } 4d)\). The frequency of green leaves being brought to the nest increased with chick age, an analysis of nesting material of Broad-winged Hawks \((Buteo platypterus)\) produced a result with an average of two sprigs brought each day for the first 18 days and an average of 0.8 sprigs per day over the last 17 days (Heinrich 2013). A number of different plant species were noted in the nest lining of the Black Sparrowhawks nests although these species were not all identified. Similarly Heinrich (2013) reported up to 55 plant species used in raptor nest lining.

A strange behaviour noted in the video footage is the chicks sleeping with one leg completely out stretched for periods up to 20 - 30 min. This may be a simple stretching behaviour, a thermoregulatory response, or for vitamin D absorption, however further studies would need to be conducted to confirm this.

Camera footage allowed us to capture the following milestones in the development of the Black Sparrowhawk chicks. At 14 days old the chicks were able to move to the edge of the nest to defecate off the edge. A day later at 15 days old the chicks started to explore their surroundings, moving around the nest with increasing confidence. At 17 days old the chicks were too big to be brooded and so the female no longer brooded at night but slept closely next to the chicks. On several occasions the female appeared threatened whilst incubating and brooding where she suddenly spreads her wings over the eggs and chicks. Mice were seen on the nest after dark on a few occasions and bats and smaller bird species were frequently seen flying within the cameras field of view.

Urban birds are more accustomed to human presence, often seemingly unaffected by human presence (pers. obs.), whereas rural birds or birds in a more protected area started calling when observers approached until they left. Furthermore they did not continue with normal behaviour and either sat watching or flew around calling. This made it extremely difficult to trap such birds as they would show no interest in the traps whilst the observers were anywhere within the vicinity.

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We are grateful to all property owners, who allowed us onto their property to set up cameras, monitor and service them. Many people are protective of the birds nesting in their garden and this study would not have been possible without them trusting us and allowing us to observe, ring and study the birds. We would also like to thank S. Gunter for testing the cameras prior
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Figure 1: Black Sparrowhawk nesting success for the 2011 (n = 19) and 2012 (n = 22) breeding season, displaying success in terms of the number of chicks successfully raised to fledging and well as breeding attempt failures in terms of Egyptian Geese and other unknown factors.
Figure 2: Reproductive roles shared by the adult male and female Black Sparrowhawk where (a) shows the percentage of nest preparation visits by both the male and female prior to the laying of eggs at the beginning of the breeding season \((n = 1)\), and (b) the total time in hours spent incubating the eggs by both the male and female in the last ten days before hatching \((n = 1)\).
Figure 3: The number of times the Black Sparrowhawk eggs were ‘turned’ per day for the data obtained during the incubation period, this behaviour was performed by both males and females (n = 1).
(a) Frequency of feeding vs Age of chicks (days) with $R^2 = 0.2558$

(b) Time in Hours:Minutes:Seconds vs Age of chicks (days) with $R^2 = 0.7682$

- Total feed duration
- Ave feed duration

$R^2 = 0.7285$
Figure 4: Developmental and behavioural trends shown with Black Sparrowhawk chick age where (a) is the frequency of feeding of chicks shown with the age of the chicks in days, hatching day = day 0, (b) the total duration of all feeding per day (12 h) versus chicks’ age as well as the average duration of a feeding item, (c) the time the chicks were left unattended on the nest versus age of the chicks (days), and (d) the frequency of fresh leaf material brought to the nest versus the age of the chicks in days.
Chapter 5

Home range size of Black Sparrowhawks (Accipiter melanoleucus) in KwaZulu-Natal, South Africa: a case study

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There is little known about the movements and home range of Black Sparrowhawks (Accipiter melanoleucus), particularly in an urban environment. Consequently the home ranges of both an adult breeding female and a juvenile male Black Sparrowhawk were determined during the 2012 breeding season in Durban, KwaZulu-Natal. Transmitters were attached to the individuals recording their locations at regular intervals between 6h00 and 18h00. An adult female was trapped and had the transmitter placed approximately a week prior to the chicks fledging the nest. Her breeding season home range remained within close proximity to the nest. A juvenile male from the same nest was trapped approximately 2 weeks after fledging at the point of starting to learn to hunt independently. The data produced a minimum convex polygon (MCP) for the adult female of 0.0025 km² while the young male remained within an MCP of 0.4554 km². This pilot study allowed us to determine a successful method to obtain Black Sparrowhawk home range information and this can now be applied to numerous pairs within a population to determine home range overlap, territoriality as well as post natal dispersal.

Keywords: Raptors, Hunting Success, Juvenile, Post Natal Dispersal, MCP, Kernel Density.
INTRODUCTION

The analysis of home range provides fundamental information on the land use and resource requirements of a species, simultaneously indicating the suitability of the habitat (Peery 2000). Home range can be defined as the area used by an animal or bird in which all normal day to day activities occur, while the core area is found within a home range and is the area where the individuals spends the majority of its time (Kenward et al. 2001; Olsen et al. 2011). During the breeding season, individuals use the core area of the home range intensely as they spend most time within the vicinity of the nest (Bloom et al. 1993; Olsen et al. 2011). Home range is determined in terms of size, shape and structure (Kenward et al. 2001). The shape of a home range can indicate the land use of the species as well as the degrees of territoriality (Kenward et al. 2001). Behaviour can also be influenced by additional food supplies as there is less competition for resources and therefore birds may be less territorial and or maintain smaller foraging home ranges (Robb et al. 2008).

Raptors have the ability to maintain large home ranges thus being able to search a greater area for essential resources. This provides them with an advantage within human altered landscapes as they can venture beyond the urban boundary when resources may be limited (Chase and Walsh 2006). Therefore an estimation of home range and land use can be a good indicator of the suitability of a particular habitat for a species. A small home range may indicate low flight activity patterns and thus the bird must be achieving relatively high hunting success (Rutz 2006). A large home range may indicate low hunting success within the vicinity of the nest and thus greater flight activity beyond the immediate range of the nest (Rutz 2006). Home range size, overlap and use needs to be interpreted in terms of several factors including food availability, territoriality, and nest and roost sites. Home range analysis can also be used to indicate the landscape use by a particular species, as well as territoriality, both of which can be used in conservation management and rehabilitation and release programs (Kenward et al. 2001).

In raptors there has been an increase in the number of home range studies as the technology allowing such research to be conducted has improved. However, in South Africa the home range and movement studies on raptors are few and are largely dependent on older technology. As shown in chapter 2, the range expansion of Black Sparrowhawks is rapidly changing with urbanisation and thus this pilot study determined the home range size of two Black Sparrowhawk individuals in Durban.
METHODS

Data Collection
On 30 July 2012 an adult female Black Sparrowhawk was trapped near her nest in Durban (2930 DD), she was fitted with a GSM GPS transmitter (KCS Micro 9). The transmitter was fitted using a Marshall type Teflon harness (Yamac and Bilgin 2012). The female weighed 995 g, and the transmitter 40 g (4% body mass). The GPS location of the bird was then recorded every 2 h between 06h00 and 18h00 on a daily basis. This gave us a total of 7 GPS location points each day. The transmitter recorded these points from fitting until the 8 August 2012 at 08h00 when the transmitter failed to record any further points (n = 9 days). This gave a total of 65 data points which were used in the home range analyses. The transmitter is believed to have malfunctioned due to a heavy downpour during which moisture presumably entered the transmitter.

Similarly, a juvenile male Black Sparrowhawk was trapped at the same nest site on the 16 August 2012, he was sexed using average body mass for males and females. He was fitted with a slightly different transmitter (Wireless Wildlife WW1500-Avian Device) which was more suitable to a male due to decreased mass of the transmitter (32 g) allowing them to be close to the 5 % body weight (590 g) threshold recommended for transmitters. This transmitter recorded the males’ location every half an hour between daylight hours of 06h00 and 18h00. This produced a total of 25 points per day. Data were collected until 20 November 2012 and thus a total of 1935 points were used in the home range analysis. This transmitter was attached in the same way as the previous one, using a common falconry Marshall Teflon harness (www.marshallradio.com).

Numerous other attempts to trap birds and fit transmitters were made, however all proved to be unsuccessful and thus we could not increase our sample size for comparisons. All trapping and attaching of transmitters onto the Black Sparrowhawks was approved by the Animal Ethics Sub-committee of the University of KwaZulu-Natal.

Data Analyses
Home range analyses were performed in Hawths Tools (Version 3.27) in the Geographic Information Systems (GIS) program ArcGIS (Version 9.3, ESRI, 2008). Hawth’s Tools then estimated a home range area for both the individuals using a minimum convex polygon (MCP). There are mixed views on the reliability of this as a method to analyses home range however it is the most widely used method for comparing home range data.
RESULTS AND DISCUSSION

Due to the limited amount of data that were obtained it was difficult to make accurate conclusions regarding the home range of Black Sparrowhawks in an urban habitat in KZN. The adult female Black Sparrowhawk whose home range data we have analysed was trapped and data collection started prior to the chicks fledging the nest. This female thus had a relatively small home range, what may be termed here as the breeding home range. On the first eight nights of data collection, the female is assumed to have spent the nights in the nest tree, we are unable to say whether she was on the nest or not however both the first and last GPS recordings were in the nest tree. The last two nights that the transmitter was operational she appeared to have slept in a tree across the road, leaving the vulnerable chicks on the nest. Adult female MCP estimated a breeding home range area of 0.0025 km$^2$ (Fig. 1a). A fixed kernel density estimated determined the 90, 75 and 50% contour lines (Fig. 2a). It can be predicted that as the chicks grew and became more independent the female may have moved further from the nest, however further studies must be performed in order to accurately conclude this.

Similarly with the Black Sparrowhawk juvenile’s home range, during the first three weeks of data collection almost all points were in the vicinity of the nest tree as the bird was just learning to fly confidently and was not hunting for survival but rather exploring its capabilities. As the juvenile gained more independence, the GPS points increased in distance from the nest tree and the individual was no longer confined to a specific area but was found in a large home range area. The Hawth’s Tools analysis estimated a home range area of 0.4554 km$^2$ for the juvenile male post-natal home range (Fig. 1b). Similarly the 90, 75 and 50% contour lines were determined (Fig. 2b).

Thus for both the adults and juveniles further research on their home ranges are required with data collection stretching over a longer time period to obtain an accurate measure of breeding home range as well as when in the breeding season the independence of the chicks affects both their home ranges and the adults’ home ranges.

The Black Sparrowhawk juvenile’s home range towards the end of the data collection was larger and included four other known Black Sparrowhawk nest sites, with the adult female’s breeding home range included within his MCP (Fig. 3). The birds position varied on a daily basis and it did not settle into a territory or specific home range area. Thus in order to determine post-natal dispersal a long term analysis of fledgling home range must be performed, we predict that a territory or home range will only be established when the bird
reaches breeding maturity, with the juvenile crossing various other territories in the meantime.

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FIGURES:

(a)

Figure 1: Minimum Convex Polygons predicted using ArcGIS 9.3 Hawth’s Tool, where (a) is the estimated home range area of 0.000025 ha for a breeding adult female Black Sparrowhawk, and (b) is the estimated home range area of 0.004554 ha for a juvenile male Black Sparrowhawk.
Figure 2: Fixed kernel density estimator showing the 90, 75 and 50% contour lines of (a) the adult female’s home range movements and (b) the juvenile male’s home range movements.
Figure 3: Visual comparison of the MCP of an adult female Black Sparrowhawk (a) and a male juvenile (b) and as estimated by Hawth’s Tools in ArcGIS (Version 9.3), when overlaid on a satellite image baselayer.
Chapter 6

Conclusions

Biodiversity worldwide are undergoing behavioural changes, range changes and thus invasions and colonisations due to habitat loss, fragmentation and alteration caused by land transformation (Anderson et al. 1990; Fairbanks et al. 2002; Bautista et al. 2004; Keough and Conover 2012). The effects of urbanisation may therefore result in range changes as some species can no longer inhabit certain areas and thus colonise new areas whilst other species may thrive in urban areas and expand their range within such areas. Colonisation occurs when a species moves into a new area and is able to successfully reproduce there. The effects of urbanisation may therefore result in range changes as species can no longer inhabit certain areas and therefore colonise a new and more suitable area (Anderson et al. 1990; Fairbanks et al. 2002; Bautista et al. 2004; Keough and Conover 2012). Climate change is simultaneously affecting wildlife and can result in similar effects, changes in behaviour, migration and distribution (Crick 2004; Hockey and Midgley 2009). The Black Sparrowhawk (Accipiter melanoleucus) is a medium sized raptor species recently seen shifting its range westward across South Africa. It appears to be widely moving into urban areas and are seemly thriving in these areas. The aim of this dissertation was to investigate and describe the reproductive behavioural trends as well as trends with regard to nest sites, range changes and home range.

The fitness and success of a species is largely dependent on the availability of resources, prey and nesting sites, as well as the suitability of the nest site which will affect competition, cover and protection, nest tree height, diameter and stability, sun exposure and predation risk (Tella et al. 1996; Bisson et al. 2002). We determined what factors influence Black Sparrowhawk nesting sites, focusing mainly on tree height, nest height, nest tree diameter at breast height, ‘greenspace’ surrounding the nest and associations with water sources, roads and buildings (Chapter 3). As well looking at nesting tree species, the size of tree clumps in which the nest was found and the position of the nest tree within such clump (Chapter 3). It is apparent from the results of this study that Black Sparrowhawks do not select random nest sites. They appear to have specific spatial and environmental nest site characteristics they require when selecting a nest site. Black Sparrowhawks seem to select Eucalyptus sp. as nest trees. Tree clump size does not seem to be an important factor with nests being found in tree clumps of between 4 and >50 trees. However, the nests were associated with being in the middle of the clump as opposed to being on the edge. Birds generally select trees over 20 m high and nests are located higher than 10 m above the
ground. Tree diameter must be greater than about 0.5 m. Nest trees seemed to have a strong association with water sources, roads and buildings with the majority of the nests being found within 200 m of these features. Thus even though this species appears to be thriving in urban habitats, their nesting sites appear to be strongly limited by the above mentioned factors.

We determined nesting success and failures of active Black Sparrowhawk nests (Chapter 4). The amount of time both the male and female performed incubation and brooding, the frequency and duration of feeding of the chicks as well as the frequency of bringing fresh leaf material onto the nests was determined (Chapter 4). Although Black Sparrowhawks appear to be doing well in urban habitats, their failure rate was relatively high in 2012. Biparental care is evident in the Black Sparrowhawks and various roles are shared by the adults. This care behaviour occurs in species where there are no opportunities for multiple breeding and thus they invest large amounts of energy into ensuring their breeding success (Margalida et al. 2007). The increase in the frequency of fresh leaf material with chick age is important in understanding the purpose behind this practice, which is believed to be for nest hygiene (Heinrich 2013). The current study has provided descriptive trends in the breeding behaviour on which further research can be built. I recommend that a longer term studies is conducted based on the findings in this dissertation.

Finally we determined the home range size of a breeding female and a young juvenile male, using GSM GPS transmitters (Chapter 5). This was a pilot study on which further research can be based. Avian urbanisation generally results in a few species in large numbers within urban areas, these being the species that have the ability to exploit the resource an urban habitat can provide (Fairbanks 2004). Determining the home range of raptors within urban cores can be fundamental in understanding their resource requirements and habitat suitability (Peery 2000).

We predicted that Black Sparrowhawks have largely increased their range and density in urban and altered landscapes, and that they are reproductively successful in urban habitats with nest site selection determined by specific spatial and environmental nest site traits. The current study has shown that the Black Sparrowhawks range has increased in South Africa, largely in urban and altered landscape areas where various aspects of their natural ecology may be altered. Conservation of this species may be vital to maintain urban populations of Black Sparrowhawks. Considering the increase in land transformation across South Africa as well as the removal of alien plant species by the Working for Water Programme, Black Sparrowhawks may in the near future be faced with limited available breeding sites (Barnes 2000; Hosking and du Preez 2004; McKinney 2006). This together with their already high
failure rate and the increase of failures due to Egyptian Geese (*Alopochen aegyptiaca*), the Black Sparrowhawks may readily be approaching population declines (Curtis *et al.* 2007; Little and Sutton 2013).

Despite Black Sparrowhawks appearing to be increasing in human altered landscapes and expanding their range, further studies on their home range and reproduction are required in order to identify the degree of threat this species faces. A longer term study can provide long term management strategies to facilitate the Black Sparrowhawk presence within changing land use areas in South Africa.

**REFERENCES**


Appendix 1

Publication currently in preparation in which I collaborated by providing information on the KwaZulu-Natal Black Sparrowhawk populations.

Clinal variation in the morph ratio of a range expanded polymorphic raptor: influence of climate conditions on polymorphism.

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Keywords: Polymorphism, Gloger’s ecogeographic rule, black sparrowhawk, \textit{Accipiter melanoleucus}, rainfall, range expansion, clinal variation, climate change,
Abstract
Morph distribution of polymorphic species often varies clinally, with a gradual change in morph ratios across the distributional range of the species. In polymorphic bird populations clinal variation is often suspected but rarely quantified in a rigorous manner. Even fewer studies have demonstrated links between such clines and potential drivers, such as environmental variables. We describe a cline in the morph ratios of black sparrowhawks across South Africa, which is principally driven through a higher ratio of dark morph birds in the newly colonised south west of the country. Across the 1400 km of our cline, the probability of being a dark morph declined from over 80% (close to the Cape Peninsula) to under 20% (in the North East). Both rainfall and temperature were associated with these spatial patterns, with high frequencies of dark morphs being associated with higher rainfall and lower temperatures. These relationships were strongest with climate conditions during the breeding months suggesting that if morph colour is an adaptive trait, selection pressure may be greatest over this period rather than year round. These results provide some support for the hypothesis that the higher frequency of dark morphs in the south west is an adaptive response, rather than the result of a founder effect or genetic drift. These findings also suggest that, in theory, polymorphic species may be better able to expand their ranges into novel climatic areas, since selection pressure can act on an existing trait which may be beneficial in those new regions. Similarly, given the relationships between morph ratios and climate variables for many species we suggest that polymorphic species may be better able to cope with climate change through a change in their morph frequencies.
**Introduction**

Genetic colour polymorphism is the occurrence of two or more distinct and genetically determined colour morphs within a single population, the rarest of which is present at a frequency that is too great to be maintained purely by recurrent mutation (Ford 1945; Huxley 1955). One interesting phenomenon frequently found in polymorphic species, from variety of different taxa, is that morph ratios vary clinally, with a gradual change in morph frequencies across the distributional range of a species. The scale of these clines can vary, for example the morph ratio in barn owls (*Tyto alba*) varies at the continental scale, with light birds predominating in southern Europe and reddish-brown birds in the north (Roulin 2003). Similarly, frequency of pale-morph arctic skuas (*Stercorarius parasiticus*) increases from south to north throughout their breeding range (Berry & Davis, 1970). In contrast, the bananaquit (*Coereba flaveola*) displays clinal variation on the island of Grenada over a very small spatial scale, from exclusively dark to exclusively yellow birds over only 3 km (Wunderle 1983; MacColl & Stevenson 2003). Melanic morphs of the Hamster (*Cricetus cricetus*) increase with changes from steppe to sub-steppe habitat (Huxley 1942). Clinal variation in polymorphism has also been detected for a number of insect species (de Jong & Brakefield 1998) and reptile species (Gould & Johnston 1972; Alsteadt et al. 2006).

These patterns have been viewed as implying that there is important selective advantage for genes associated with the different morphs in the different areas (O’Donald 1983). For bird species the adaptive significance of different morphs is poorly understood, although a few studies have demonstrated links between these clines and potential drivers such as environmental variables (Wunderle 1981a), whilst others have failed to find any such relationships (Galeotti & Cesaris 1996; Atkinson & Briskie 2007). Identifying the environment covariates that are associated with these ratio-clines may therefore be useful for indicating the selective forces operating on the balancing mechanisms of the different morphs (Galeotti et al. 2003).

Genetic colour polymorphism occurs in around 3.5% of bird species (Roulin 2004), but more frequently in raptorial species (Galeotti et al. 2003, Fowlie & Krüger 2003), and especially in the *Accipiter* genus, where 11 of the 46 species (24%) are polymorphic (Ferguson-Lees & Christie 2001). Plumage colour in polymorphic raptors can vary continuously (Briggs 2010, Kruger et al. 2001) or may show two or more discrete morphs (e.g. Schmutz & Schmutz...
1981, Gangosa 2011, Amar et al. in press). Many studies have now shown that polymorphic phenotypes are genetically determined and follow a Mendelian mode of segregation (Wunderle 1981a, Schmutz & Schmutz 1981, Briggs 2010, see Roulin et al. 2004 for a review). Although some studies have suggested clinal variation for raptors species (Brown & Amadon 1968, Wheeler 2003, Ulfstrand 1977), few have actually documented its occurrence empirically, nor have any tested the environmental correlates for such patterns.

The Black Sparrowhawk (*Accipiter melanoleucus*), is a widely distributed polymorphic *Accipiter* species occurring throughout much of sub-Saharan Africa (Ferguson-Lees & Christie 2001); within South Africa it has recently expanded its range and colonised the south-west, including the Cape Peninsula, with the first nest recorded here in 1993 (Oettlé 1994), although the precise reason for this range expansion is not known (Hockey & Midgley 2009). Adults of the species occur in two morphs, being either dark or light, and these morphs follow a typical Mendelian inheritance, with an apparent one-locus two-allele system where the allele coding for the light morph is dominant (Amar et al. in press). The dark morph of this species is usually described as rare (Steyn 1982, Kemp & Kemp 1998, Ferguson-Lees & Christie 2001, Hockey, Dean & Ryan 2005). Amar et al. (in press), reporting previously unpublished data from Tarboton and Allen (1984), found that in the north east of the South African range only around 20% were dark morphs, whereas on the Cape Peninsula, 76% of birds were dark. How these morph ratios vary across the species range, and whether this varies clinally, is however, not known.

Two contrasting hypotheses have been proposed for the high frequency of dark morph birds in the Cape Peninsula population (Amar et al. in press). Firstly, that this variation is non-adaptive, and is simply due to a founder effect and genetic drift, with the first colonising birds being dark morphs simply by chance. An alternative hypothesis proposes an adaptive response, with dark morphs having a selective advantage in the south west, where breeding occurs during the wet winters, as opposed to the dry winters experienced in the species’ historical South African range. Such a pattern would fit Gloger’s climatic rule (Gloger 1833), which predicts that darker birds occur more frequently in areas of higher humidity (higher precipitation) and paler birds more often in drier areas. These patterns have been found for a variety of species (Mayr 1963, Kamiler & Bradley 2011). For birds, this has more typically been examined with respect to the geographic variation in plumage (e.g. Zink & Remsen 1986, Hogstad et al. 2009), but can equally apply to the ratio of dark and light morphs of
species showing discrete polymorphism. For example, Wunderle (1981a, b) found that the prevalence of dark morph banaquits in Grenada was correlated with rainfall levels. The functional significance of these patterns however remains unclear.

In this paper, we collate a variety of unpublished data on the morph ratios of black sparrowhawks throughout their South African range to explore whether the species exhibits clinal variation in the ratio of its two morphs. We then use the spatial distribution of these morphs to explore the evidence in support of the two contrasting hypotheses proposed for the high frequency of dark morphs in the Cape Peninsula (Amar et al. in press). If the frequency of morphs is an adaptive trait linked to different climatic conditions experienced across the range, rather than simply being driven by genetic drift, we predict morph ratios will be correlated with climate. Being correlative, however, we acknowledge that any such relationships would not necessarily refute a selectively neutral, founder effect hypothesis. The nature of these relationships may also provide suggestions on the mechanisms that might be involved (Galeotti et al. 2003). Finally, we test whether climate conditions during the breeding season, or throughout the year, best fit the data to indicate the life history stage that is likely to be under strongest selective pressure.

Methods
Data collation
We collated previously unpublished data on the morph ratios of breeding black sparrowhawks from four different sources to explore variation across the South African range (Table 1). Three of these data sets monitored populations centred on a specific locality, and the fourth across its South African range. The first is an intensive study ongoing since 2000 on the Cape Peninsula in the Western Cape (see Curtis et al. 2007; Amar et al. in press for further details). Only data from 2010 were used in this study, to eliminate pseudo-replication of the same individuals monitored between years, and provided data on the morph of both male and female from 40 pairs. In the second, Tarboton and Allan (1984) monitored colour ringed black sparrowhawks in north-eastern South Africa within a 30 km radius of the town of Nylsvley. This study monitored around 90 nesting attempts between 1977 and 1987, recording the morphs of a total of 36 different individuals. The third is an ongoing study of black sparrowhawks spread across a large area of KwaZulu Natal, but centred on the towns of Pietermaritzburg and Durban. This study monitored 29 nests in 2011 and recorded the
morphs from 16 pairs. In the final study, Malan and Robinson (1997) monitored 77 nests across South Africa and obtained the morphs from 88 birds. The species is easy to sex with males being around 60% the size of the females, therefore, for each study we had the proportion of dark males and dark females as well as the proportion of both sexes combined.

Data on the morphs of birds were grouped into 16 spatial clusters (Figure 1). Two clusters were from the intensive studies on the Cape Peninsula (Amar et al. in press) and from around the town of Nyilsley (Tarboton and Allan 1984). Seven clusters were in KwaZulu Natal using data from Brown et al. (unpublished) and Malan and Robinson (1997). The remaining seven clusters contained information on the morphs from the work by Malan and Robinson (1997) and were spread throughout South Africa. The average sample size of the 16 clusters was $14.75 \pm 4.8$ birds and ranged from three birds to 80 birds (Appendix A). These samples covered the bulk of the distributional range of the breeding black sparrowhawks in South Africa. To examine the shape of any cline, we also calculated the distance of each cluster of birds to the Cape Peninsula population (centred on the Kirstenbosch Weather Station). For some analyses we grouped data into three regions: Western, South-eastern and Northern (see Appendix A and Figure 1 for these groupings).

**Rainfall, temperature and Altitude data**

For each month, we collated data on the average total rainfall and the average maximum temperature from weather stations nearest to and centred on each of the 16 clusters with morph ratio data (see Appendix A for a list of all weather stations used). Data on rainfall and temperature were obtained from specific weather stations from the Climate Information Portal (CIP: http://cip.csag.uct.ac.za/webclient). The time period over which weather variables were collected varied between the weather stations, but generally covered most of the second half of the 20th century up until 2010, although extremes from 1902 -2010 (Krugersdorp) to 1999-2010 (Kirstenbosch) were also present. In almost all cases weather data overlapped the period from which data on morphs were obtained. We also recorded the elevation of the weather associated with each cluster.

Depending on which life stage selection may be acting on, selection pressure for the different morphs may operate throughout the year, or may be strongest during the breeding period. To explore this issue, we calculated the average weather conditions throughout the year, and during the breeding period only. For the breeding period we used weather data only from April to October that covers the months when the vast majority (99%) of breeding is initiated.
Thus, in our analysis we used altitude plus four weather parameters: 1) average total monthly rainfall across all months (hereafter termed average rainfall/AvR), 2) monthly mean daily maximum temperatures across all months (hereafter termed average temperature/AvT), 3) average total monthly rainfall across breeding months (hereafter termed breeding rainfall/BrR), and 4) monthly mean daily maximum temperatures breeding months (hereafter termed breeding temperature/BrT). In our analysis, we only combined terms derived over the same times of year (i.e. either year-round or just during the breeding season). We also calculated a seasonality index, which described how Mediterranean the climate was. This index was the proportion of the total rainfall in the year that fell during the breeding months (i.e. April to October).

Statistical analyses
To examine whether the proportion of dark birds differed spatially and in relation to our weather variables and altitude, we used a Generalised Linear Model with a binomial error distribution and logit link function. Our response variable was a binomial response, with the numbers of dark birds present in a cluster as the numerator, and the total number of birds in that cluster as the denominator. Using this approach, we therefore incorporated the different sample size of each cluster, with the sample being weighted according to the total number of birds in each cluster. To examine the evidence of a cline, we examined whether the proportion of dark birds in a cluster was correlated with the distance from the most south-western population (Cape Peninsula) and also explored if this related to our seasonality index. We then tested whether the proportion of dark birds in each cluster was correlated with rainfall or temperature variables separately, and in combination, plus altitude and included only measures from the same period (i.e. year-round or breeding) in any single model. For the models including both rainfall and temperature variables, we also explored whether there was any interaction between the temperature and rainfall.

Models were ranked based on their Akaike Information Criterion scores (AICc), which is the AIC corrected for a small sample size (n) relative to the number of parameters being estimated (K) (i.e. where n/K < 40). The Kullback-Leibler set of “best” models was identified using AICc differences (Δi) and Akaike weights (wi); and we calculated the
evidence ratio of the best fitting model relative to the other candidate models. All models were implemented in R version 2.15.1 (R Development Core Team 2009)

Results

Clinal variation in morph ratios

Clinal variation in morph ratios of breeding adults was apparent across their south African distribution; ranging from c. 70-80% dark birds in our Western region, to 25% in our South Central region, to between c. 5-20% in our Northern region (Table 1, Figure 1). Examining this pattern empirically, we found a strong negative relationship between the proportion of dark birds and the distance from the Cape Peninsula ($\chi^2_{1,14}=87.96; P<0.0001$). The same pattern was found for all breeding adults, as well as for males and females analysed separately (males: $\chi^2_{1,13}=54.24; P<0.0001$; females: $\chi^2_{1,14}=35.83; P<0.0001$).

Across all sites we found that the proportion of birds that were dark morphs was slightly higher for males than for females (males: 55/159, 35%; females 55/187, 29%), although this was marginally non-significant ($\chi^2_{1,29}=2.94; P=0.08$). However, there was a significant interaction between region and sex ($\chi^2_{1,25}=7.96; P=0.02$). Pairwise comparisons revealed that the proportion of dark morphs in the North and South Central regions did not differ between the sexes, but that there were significantly more dark males than females in the Western region ($P=0.01$). In this region 91% of males were dark, whereas only 70% of females were dark morphs.

Relationship between climate conditions and the proportion of dark birds.

The cline we detected appeared to closely follow the seasonality of the region, with more dark birds in regions with winter rainfall and more light birds in regions with summer rainfall, with a strong relationship between the proportion of dark birds and our seasonality index ($\chi^2_{1,14}=83.49; P<0.0001$). Testing the relationships with the climate variables themselves we found a relationship between the proportion of dark morph birds and both rainfall and temperature during the breeding period, and our best fitting model included both terms together in the model (Table 2). The proportion of dark birds showed a positive relationship with breeding rainfall (Fig 3a) and a negative relationship with breeding temperatures (Fig 3b). Both terms were highly significant (breeding rainfall: $\chi^2=71.61$, df=1,14, $P<0.0001$; breeding temperature: $\chi^2=69.51$, df=1,14, $P<0.0001$). From the Akaike
weights, our top model had 43% of the support relative to the other models for being the best model in our set.

The next best fitting model included both these two terms and their interaction, the shape of this interaction suggested that in cool conditions, there was a positive influence of rainfall on the proportion of dark birds, whereas in warmer conditions this relationship was no longer evident. The ΔAICc score between these two models was 1.01 (i.e. less than 2), suggesting that there was some support for this model, although the evidence ratio suggested 1.86 times more support for our top model (i.e. without the interaction term). There was considerably less support for any of the other models including those with climate conditions throughout the year, rather than just during the breeding season, or for altitude and all these models had ΔAICc of more than 4 (Table 2).

**Discussion**

Our results show that polymorphism of the black sparrowhawk is spatially structured across its South African range, with a higher frequency of dark birds in the south west and a low frequency in the east and north. Amar et al. (in press) described the high frequency of dark morphs in the breeding population in the Cape Peninsula, however, it was not previously known whether this population was a unique isolate or whether it represented the extremities of a clinal trend for an increasing frequency of dark birds. Our data show that morph ratios in the species demonstrate a cline, with the proportion of dark birds decreasing at distances further from the Cape Peninsula. This cline spans a large distance of nearly 1 500 km, with the frequency of dark morphs falling from 80% to around 20%. Although not linear, the slope of the line approximates to around 5% fewer dark morphs for every 100 km away from Cape Town. To our knowledge, this is the first time clinal variation in the morph ratio of a raptor species has been empirically documented.

Changes in the species distribution between the first and the second South African Birds Atlas Project (http://sabap2.adu.org.za), and data from Hockey & Midgley (2009), show that the species has expanded its range westwards over the past 30 years, particularly into our Western region (Western Cape). If we exclude birds sampled in our Western region, on average only 23% of birds were dark morphs, supporting previously published accounts describing the dark morph of this species as rare (Steyn 1982, Kemp & Kemp 1998, Ferguson-Lees & Christie 2001, Hockey, Dean & Ryan 2005). The cline we
document is therefore driven principally from the newly colonised areas comprising of more dark morph birds. Thus, this cline has apparently developed over approximately the last 30 years, and represents a rapid establishment of a cline created through a species expansion. Although the species is believed to be a new colonist to the Western Cape, there is a possibility that the species did historically occur there, but was wiped out with the arrival of the first European settlers (Boshoff et al. 1984), if true this might also explain the presence of the dark morph genes within the northern and eastern populations.

We found that the cline correlated closely with our seasonality index. South Africa has two principle rainfall zones. In our Northern and South Central regions, the majority of rainfall occurs during the summer (on average 68% from our samples) which is outside of the breeding period for this species. However, in our Western region the majority of rainfall occurs within the winter breeding period (76%). Thus, birds living in this newly colonised region are exposed to different climatic conditions than in the rest of their historical range, and in these areas, a greater proportion of birds were dark. Interestingly, in this region we found a difference between the sexes in the proportion of dark morph birds, with 20% more dark morph males than females. Amar et al. (in press) found a similar result when examining only the Cape Peninsula population, they noted that male black sparrowhawks provide most of the food during the breeding season, and that this might explain the different morph ratios between sexes in this region if greater selection pressure exists for males to be dark than females, although the exact mechanism involved to drive this situation is far from clear.

Both rainfall (positively) and temperature (negatively) were correlated with the proportion of dark birds. The model with the greatest support included these two variables during the breeding period rather than throughout the whole year, potentially indicating that it is during this key period when selection favouring the dark morphs may be most acute. Thus, our results provide support for the hypothesis that the higher frequency of dark morphs in this region is an adaptive trait. However, as initially stated our findings, being correlational, do not eliminate the possibility that this clinal pattern is non-adaptive and is simply the result of genetic drift and a founder effect and that these relationships have arisen purely by chance.

Our findings appear consistent with Gloger’s ecogeographic rule (Gloger 1883), whereby darker birds are predicted to be found in areas with greater humidity (precipitation) and lighter birds in more arid areas. This rule has been found to be surprisingly robust, at least
when applied to geographic variation in birds’ plumage (Zink & Ramsen 1986) or primates’ pelage colour (Kamilar & Bradley, 2011). Numerous proposals exist to explain this pattern, including resistance to bacterial degradation (Burtt & Ichida 2004), background matching (Zink & Ramsen 1986), enhanced drying (Burtt 1981) and thermoregulation (Walsberg 1983), none of which are, however, mutually exclusive. The negative relationship between temperature and the ratio of dark morphs provides some support for the idea that thermal regulation might play a role in our study. Under some circumstances (Walsberg 1983) darker birds are better able to absorb the energy of solar radiation, and this may reduce their resting basal metabolic rates (at lower temperatures) (Hamilton and Heppner 1967). Thus, dark morph black sparrowhawks in the cooler south-west may accrue a thermoregulatory selective advantage.

Two recent reviews (Galeotti et al. 2003, Roulin 2004) on the potential adaptive function of polymorphism in birds both highlighted the role that light conditions may play in selecting for different morphs. Galeotti et al.’s (2003) comparative analysis concluded that colour polymorphism probably evolved under selective pressure linked to detectability of birds in differing light conditions and that it is most likely maintained through disruptive selection, whereby different morphs have different selective advantages in different environments. They proposed therefore that the selective agents may be prey, predators or competitors. Our findings potentially support this hypothesis, whereby darker birds may have a selective advantage in the rainier conditions in the west through background matching with the cloudier skies and/or the lusher vegetation which may occur at this time of year in the winter rainfall region. To explore this possibility it would be interesting to test whether hunting success differed between dark and light morph birds within the Western Cape population depending on the day’s weather conditions.

Our findings have implications for range shifts due to habitat or climate change, since it suggests that polymorphic species, in which polymorphism has arisen through disruptive selection, might be better able to shift their ranges into novel climatic zones or to adapt to changes in climate within an area. Selection which favours an already prevalent existing trait (e.g. one morph or another) provides polymorphic species with the potential to adapt more rapidly to changes in climate than monomorphic species which must rely on genetic variability or for beneficial traits to occur through mutations. Thus the evolutionary potential is likely to be weaker in monomorphic than polymorphic species, and the rate of evolution at
the population level may not be rapid enough to cope with the speed of future predicted climate change.

Some of these principals are discussed in relation to another ecogeographic rule (Bergmann’s rule) by Millien et al (2006), which examine changes in morphometrics in relation to climate change. However, many of these issues could equally apply to Gloger’s rule and either geographic variation or ratios of morphs which are distributed in a clinal manner in relation to environmental factors, as found in this study. We do not know of any such research which has attempted to test the theory that polymorphic species may have such an advantage in the face of climate change. However, shifts in morph ratio linked to climate change have already been detected for some species. For example, de Jong & Brakefield (1998) found that the shape of clines in the morph ratio of two-spot ladybird (Adilia bipunctata) have changed over a twenty year period in the Netherlands. Morph ratios were correlated with temperatures, because dark morph individuals warm up quicker, and the cline had become shallower, as the melanic morphs had increased in frequency with warmer springs. Thus tracking morph ratios which show clinal variation may provide an early warning signal for the influence of climate on populations prior to detrimental effects being seen elsewhere within community.

Acknowledgments
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References


Gloger, C.L. (1833) *Das Abändern der Vögel durch Einfluss des Klimas*. August Schulz, Breslau, Germany.


Table 1. Sample sizes and percentage of dark individual black sparrowhawks found in different locations in South Africa. All data are unpublished; reference refers to the study from which the data were extracted.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sample size</th>
<th>Male (% dark)</th>
<th>Females (% dark)</th>
<th>Dark:light (% Dark)</th>
<th>years</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cape Peninsula</td>
<td>40/80</td>
<td>40 (90%)</td>
<td>40 (78%)</td>
<td>67:13 (84%)</td>
<td>2010</td>
<td>Amar 2012</td>
</tr>
<tr>
<td>South Africa</td>
<td>59/88</td>
<td>38 (37%)</td>
<td>50 (30%)</td>
<td>29:59 (33%)</td>
<td>1997</td>
<td>Malan &amp; Robinson 2004</td>
</tr>
<tr>
<td>Mpumalanga</td>
<td>26/36</td>
<td>10 (40%)</td>
<td>26 (15%)</td>
<td>8:28 (22%)</td>
<td>1977-1987</td>
<td>Tarboton &amp; Allan 1984</td>
</tr>
<tr>
<td>KwaZulu-Natal</td>
<td>16/32</td>
<td>16 (13%)</td>
<td>16 (31%)</td>
<td>6:26 (23%)</td>
<td>2011</td>
<td>Brown unpubl.</td>
</tr>
<tr>
<td>Total</td>
<td>141/236</td>
<td>104</td>
<td>132</td>
<td>110:126</td>
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<td></td>
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</tbody>
</table>
Table 2. Results from the GLim Models testing for associations between the proportion of dark birds and climate variables (AvT: average temperature throughout the year, AvR: average rain throughout the year, BrT: temperature during the breeding season (April – Oct), BrR: rainfall during the breeding season) and altitude. * denotes an interaction. Headers for columns are: number of parameters (K), corrected AIC (AICc), residual deviance (dev), change in AICc relative to the optimal model (Δi), AICc weight (w), evidence ratio (ER).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>Log likelihood</th>
<th>dev</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
<th>ER</th>
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<tbody>
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<td>BrR + BrT</td>
<td>3</td>
<td>-122.67</td>
<td>46.57</td>
<td>84.26</td>
<td>0</td>
<td>0.43</td>
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<tr>
<td>BrR + BrT + BrR*Bt</td>
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<td>-121.35</td>
<td>43.94</td>
<td>85.27</td>
<td>1.01</td>
<td>0.26</td>
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<tr>
<td>AvR + AvT</td>
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<td>-122.90</td>
<td>47.04</td>
<td>88.36</td>
<td>4.11</td>
<td>0.07</td>
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Figure 1. Map showing the locations and the ratios of dark and light morph birds (pie diagrams – dark = dark morphs, clear = light morphs) and sample size for each cluster of breeding birds distributed throughout South Africa. Data from these clusters were then matched with rainfall data from a weather station in the centre of each cluster. We also classified the clusters into three regions (South West, South Central and Northern) for the purpose of some analysis.
Figure 2. The Relationship between the proportion of dark morph birds within the sampling clusters and their distance from the Cape Peninsula population. The line is fitted from the parameter estimates produced from the binomial GLM. Size of the circles is proportional to their sample size.
Figure 3. Relationship between the proportion of dark birds in the population and a) the average total rainfall per month (mm) during the breeding period (May – October) and b) the average maximum temperatures (°C) during the breeding period (May – October). Lines are drawn from the parameter estimates generated by a Generalised Linear Model. Size of the points reflects the sample size of each cluster of birds.
b)
Appendix A: Details of the locations (including region), number of dark morphs and sample size for each size and in total, and the name of the nearest weather station for the 16 clusters of birds used in the analyses. Region codes: N = Northern, SC = South Central, SW = Western.

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<th>Region</th>
<th>X</th>
<th>Y</th>
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<th>Total males</th>
<th>Dark females</th>
<th>Total females</th>
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