Factors influencing the timing of breeding in a range expanding raptor at two spatial scales

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Abstract

Range shifts and expansions have been recorded in a number of species and it is expected that as climate change proceeds it will result in more species joining this trend. A major concern with these shifts is the suitability of the receiving novel environments, for example, if these areas experience different climatic conditions or prey phenology. One way to evaluate how expanding populations adapt to the environment is through evaluating their breeding patterns. In southern Africa, the Black sparrowhawk (*Accipiter melanoleucus*) originally existed in Botswana, Mozambique, North Eastern and South Eastern South Africa and Zimbabwe. It has in the past two decades expanded its range into the west of South Africa. This population breeds under different climatic conditions (wet winters) to the ones experienced by the rest of the southern African populations (dry winters). I examined the timing of breeding and the factors influencing this parameter. A total of 517 nesting records from Zimbabwe and South Africa were used at two spatial scales, across South Africa and Zimbabwe, and at a local scale using an intensively studied population on the Cape Peninsula, with a particular focus on differences between the traditional areas and the newly colonised areas. For the large scale study, timing of breeding differed with latitude, with populations at lower latitude initiating breeding earlier. Peaks in laying varied among the different areas. Temperature influences laying date; with most clutches laid in low temperatures. Rainfall positively influenced laying in newly colonized regions and negatively influence it in traditional areas. For the small scale study (within the population around Cape Town), temperature and rainfall had no influence on laying. Breeding success and productivity were influenced by the timing of breeding, both declining as the season progressed. The species has the ability to shift timing of breeding but temperature is the most influential climatic factor in determining when individuals lay. The ability to shift breeding time has probably helped the species to colonise new areas.

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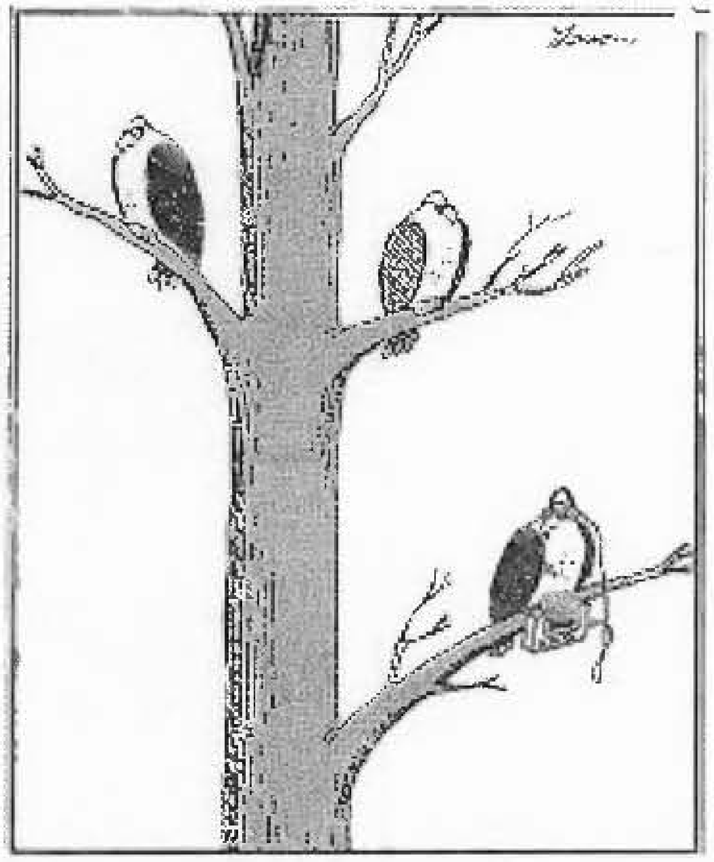

Birds of prey know they're cool

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CHAPTER 1

Literature Review

Range shifts and expansions

There has been evidence of range shifts and expansions in all groups of organisms, both marine and terrestrial over the last few decades (Doak & Morris 2010). Climate change is believed to be a major cause of these range shifts (Brommer 2004; Brommer 2008; Visser 2008) which have occurred in all directions, with organisms moving towards habitable environments with a good food supply (Brommer 2004; Brommer 2008).

Range shifts have been recorded in both hemispheres, with organisms in the northern hemisphere shifting their ranges northwards towards the poles (Walther et al. 2002; Parmesan 2006). Although most range expansions in southern Africa have been westwards, some dry-country species have been noted to be shifting theirs east and southwards leading to the suggestion that the border of the arid zone is also moving (Hockey 2003). Bioclimatic models have also predicted a poleward range shift in southern African birds (Simmons et al. 2004; Hockey & Midgley 2009); although as yet there is less evidence for this directional change.

The ability to expand or shift a range is highly dependent on the species' biology, that is, its ability to disperse, to adapt to the new environment and the availability of migration corridors (Simmons et al. 2004; Brooker et al. 2007; La Sorte & Jetz 2010). This therefore means the combined effects of landuse change and climate change can affect the distribution of species and will lead to extinctions of some species that cannot migrate to suitable habitats and those that fail to adapt to the climatic conditions of their new habitats. (McCarty 2001; La Sorte & Jetz 2010). It is important though to note that although these predictions were made, in reality the data is not showing extinction risk for many species at all. The recent plethora of range change maps using SABAP data suggest that most species are coping well so far (Underhill 2012).

The reason for range shifts among South African birds is still an arguable point as both climate change and habitat alterations are thought to have caused the southward shifts (Simmons et al. 2004; Hockey & Midgley 2009). Some birds have shifted ranges southwards, that is, towards the cooler latitudes consistent with climate change drivers, whilst others have moved westwards, towards the drier and warmer habitat, which has mainly been attributed to land use change (Hockey et al. 2011). These westwards expansions also mean range shifts into regions with different seasonal patterns of rainfall, that is, into regions with winter rainfall for those moving towards the southern parts of the Western Cape.

Predictions of range shifts are usually made based on changes in temperature or changes in rainfall (Walther et al. 2002). However, rarely are the patterns of these climate variables taken into account. Thus, two areas may have the same annual precipitation levels but the timing of when this precipitation occurs may be vastly different. Thus temperature and rainfall changes may mean areas of land become suitable but the timing of these climatic patterns may be different to what the species has previously been exposed to.

Impacts of range shifts on populations

The impact that environmental change exerts on a population is influenced by the ability of individuals to plastically adjust key life-history events (Reed et al. 2006; Reed et al. 2010). Some of the life history changes that organisms undergo as a result of climate change and/or range expansion are changes in lay date or migration times in birds (McCarty 2001; Walther et al. 2002; Coppack & Both 2003; Wormworth & Mallon 2006). Wildlife has also been forced to shift due use urbanization or to adapt to these conditions.

Recent studies on the timing of breeding in birds have tended to focus on the changes in laying dates in an area as the effects of climate change have occurred. Records of the Lapwing's (*Vanellus vanellus*) laydates from 1897-2003 have showed an advance in laydate as a result of warmer spring temperatures (Both et al. 2005).The adjustment of breeding has also been seen in a number of other bird species. A study on 20 species of UK breeding birds done over a period of 25 years revealed that there was a trend towards earlier laying (Crick and Sparks 1999). This adjustment has also been seen in other groups of animals other than birds for example, red squirrels *Tamiasciurus hudsonicus* in Canada have over the past ten years shifted their breeding period to start eighteen days. This trend is set to continue as it is predicted that laying dates will become earlier for 75% of species by the year 2080 (Crick and Sparks 1999).

A shift in migration phenology has been seen in a number of migratory bird species including the Barn Swallow *Hirundo rustica* which has advanced its arrival time in the Northern hemisphere to coincide with earlier springs. To achieve this, the birds have been shown to be spending less time on their wintering grounds in South Africa (Altwegg et al. 2012). Blackcaps (*Sylvia atricapilla*) in central Europe have also had a shift in migration phenology as they are increasingly overwintering in Britain instead of Iberia (Bradshaw & Holzapfel 2006). Although shifts in breeding phenology have been shown within local populations and migrating populations, no study has been intensely done on a resident species suddenly shown to be shifting ranges and breeding time.

Populations cope with environmental change through adaptive responses. An adaptive response can be in the form of either evolutionary or phenotypic plasticity (Visser 2008). Phenotypic plasticity is the ability of a single genotype to produce different phenotypic responses under different environmental conditions, thus allowing a species to adapt quickly to different conditions, for example, a change in breeding time (Visser 2008; Reed et al. 2010). Evolutionary plasticity involves a change in the genetic composition of the population and this change takes time to develop in a population (Visser 2008). Those that are unable to adapt or unable to adapt quickly enough to changing conditions will have to move or will go extinct.

Factors influencing timing of breeding

The timing of reproduction is a fitness related trait and varies with changes in environmental conditions, with animals aiming to breed at a time that will maximise their annual breeding success (Brown 1980; Hau 2001). Each individual within a population alters their breeding time in response to environmental cues leading to within population phenotypic plasticity (Przyblo et al. 2000). A failure by individuals to adjust their lay dates to suit the climatic conditions results in mistimed reproduction relative to peak food availability. This mismatch can lead to reduced reproductive output and population decline (Møller et al. 2008; Wright et al. 2009). The ability of a species to adapt to novel climatic conditions will therefore influence not only a species' ability to persist but also its ability to expand into new areas which may vary in environmental conditions.

Climatic conditions affect not just the phenology of birds but also the length of their breeding period, performance and survival (Møller 2002; Rodríguez & Bustamante 2003; Crick 2004; Møller et al. 2010). This high level of dependence on weather conditions for key-life aspects make birds an ideal model group for examining the impacts of climate change on animals (Brown 1980; Surmacki & Stepniewsk 2007). Rainfall and temperature play an important role in determining the breeding time as organisms have been shown to shift their breeding period in response to these (Moreau 1950; Wilson & Arcese 2003; Crick & Sparks 1999; Reale et al. 2011). This is because rainfall is linked to food availability and abundance (Lark 1950; Voous 1950). Food availability and its quality are factors which determine when breeding occurs as birds want to ensure that the end of the breeding season when energetic demands are greatest as fledglings are becoming independent coincides with maximum food availability (Thomson 1950; Brown 1980) ensuring a high breeding success (Daan et al. 1990; Sydeman et al. 1991).

The woodlark's (*Lullula arborea*) response to climatic conditions has been studied to some length. The species has been shown to have larger clutches when rainfall is low, with the egg laying and pre-laying period occurring when temperatures are high. The number of chicks fledged is highest if temperatures are high during the brood stage. The species has also been noted to breed earlier in years with warm springs, suggesting that high temperatures enhance the start of the breeding season and increase breeding success (Wright et al. 2009).

The photoperiod influences breeding commencement in birds, especially in temperate zones where there is a clear distinction of day length in different seasons. This is due to the fact that day length is linked to changes in food supply and provides the initial predictive information on when food resources will increase (Moreau 1950; Thomson 1950; Newton 1979; Brown 1980; Phillips et al. 1985). This is important because different factors operate in the Northern and southern Hemisphere (Tauber & Tauber 1971; Concannon et al. 1997), influencing breeding in these areas.

Birds may also try to breed at a time when competition for resources is at its lowest (Sinclair 1978) Using the Rufous-capped Warble, *Basileuterus rufifrons*, Jedlicka et al. (2006) were able to show a change in foraging behaviour as a result of competition from migrants. Local birds breed in the absence of migrants whose presence may increases pressure on food resources. Colonial species reduce competition for space by having successive groups occupy the area once earlier breeders have vacated (Brown 1980). Raptor species are faced with different patterns of food availability which are influenced by the activities of their prey species (Newton 1979; Sonerud 1986). Thus to ensure breeding success, the birds adjust their reproductive decisions to environmental seasonality which may differ slightly every year (Hau 2001).

Lay date is also influenced by the nesting conditions required by the species. For example, sand bank nesting plovers such as the Little ringed Plover, *Charadrius dubius* lay only in times when banks are not in danger of flooding (Brown 1980). Birds' laydates are also influenced by predation pressure, as birds may nest at a time when their nests will be most inaccessible to predators (Newton 1979; Brown 1980). Gonadal development must also be initiated in time so that breeding occurs when environmental factors are ideal (Brown 1980; Phillips et al. 1985).

When organisms expand or shift their ranges they may enter different climatic regimes which may affect productivity (West-Eberhard 2003). Most birds within the temperate latitudes in the northern hemisphere experience seasonal decline in productivity as the breeding season progresses. This decline may be an effect of phenotypic or environmental quality and possibly a combination of the two. There is a need to be able to distinguish between the effects of the two in order to be able to tell what impacts different species (Verhulst & Nilsson 2008). This is particularly important as other studies have shown that the decline can occur at a time when prey is most abundant suggesting that the decline is not only linked to prey availability (Simmons 2000), although some Northern hemisphere studies state that food availability is an essential factor in determining breeding success and productivity (Brown, 1980).

Seasonal decline in productivity has also been seen in some African raptors such as the African marsh harrier (Simmons 2000). Birkenhead (1982), Newton (1986) and Sydeman et al. (1991) all found that later laying female birds produce smaller clutches, which they believed was an adaptation to low food availability and hence poor provisioning for the young. This was contrary to Simmons (2000) observations where food was shown not to be the cause of the decline. The seasonal decline in productivity may be a direct effect of the limited breeding time as the season progresses, an effect of individual quality; with individuals with a higher phenotypic quality or experiencing better environmental quality breeding earlier. Skucth (1985) on the other hand says that in the tropics predation is the major factor determining this decline. The decline may also be a result of a combination of the above factors (Verhulst & Nilsson 2008).

Many raptors species breed in the dry season and in areas experiencing a bimodal pattern of annual rainfall, such as East Africa, they prefer to breed in the drier part of the year (Moreau 1950; Brown 1980). Rainfall and temperature in their own rights (rather than as surrogates of prey) have also been shown to determine breeding success in some species (Wilson & Arcese 2003). Persistent strong winds negatively impact on breeding hence breeding occurs in the relatively calm months (Brown 1980). The significance of the impact that weather has on the breeding of a number of bird species has prompted suggestions that weather may be the most important factor influencing their reproduction (McDonald et al. 2004).

Black sparrowhawks' and range change

The Black Sparrowhawk (*Accipiter melanoleucus*) is an African raptor, which together with a number of other bird species (Simmons et al. 2004; Hockey & Midgley 2009) has increased its South African range. It has expanded into parts of the Gauteng, North West, Limpopo and Mpumalanga provinces, previously collectively known as the Transvaal and particularly its range has shifted south westwards into the Western Cape and more recently into the Cape Peninsula (Tarboton & Allan 1984; Underhill 2012 ; Curtis et al.

2007). However, rather than being induced by climate change, the main driver for this range shift is believed to be a result of the creation of a habitat as a result of human altered landscapes (Malan & Robinson 2001; Hockey & Midgley 2009), with exotic plantations providing nest sites, and increases in feral pigeons and other dove species providing an abundance of food (Tarboton & Allan 1984; Curtis et al. 2007).

However the issue of the range shift being a result of habitat creation is debatable as the exotic forests were planted over a hundred years ago (Grut 1977) yet the first sighting of the species was only in 1994 (Oettlé 1994). Although having existed for so long, it is important to note that it has taken a long period of time for clumps of tree which can act as territories to develop. This sudden range expansion by the species could be a result of either climate change or habitat creation. It is suspected though that climate change may be the major cause, as this is also supported by the fact that the Cape Peninsula is within the region to which many bird species are predicted to move to under climate change (Huntley et al. 2006).

Black sparrowhawks are winter-breeding birds throughout their southern African range. Thus, in most of their range, this means that they breed during the dry season. Over the last two decades these birds have extended their range into the Cape Peninsula, which has a Mediterranean climate, characterised by wet winters (Curtis et al. 2007). The Cape Peninsula population is therefore breeding in a different climatic zone from the one experienced by the population in the majority of their southern African range (Curtis et al. 2007).

The different climatic conditions are expected to impact on this population. Rainfall may impact on the hunting time of adult birds by reducing the time available for hunting (Mearns & Newton 1988; Curtis et al. 2007) hence reducing fitness of individuals during the breeding season and food availability for hatchlings. Rainfall might also impact young chicks' ability to thermoregulate and young wet chicks unbrooded may die (Mearns & Newton 1988). Despite the wetness of the Cape winter, the Black sparrowhawk population in the area has continued to breed during the winter months (Oettlé 1994; Curtis et al. 2007) and under these climatic conditions the population has continued to grow from five to ten pairs at the start of the 2000's to over 50 pairs by the end of the same decade. So how has this species successfully adapted to breeding under such different climatic conditions?

Range expansions evidently come at a cost for the shifting individuals as they have to undergo some phenological changes to adapt to the new environment. There is therefore a need to understand how species adapt in this way to understand the strategies that might be employed by species as they are forced to shift their ranges in response to climate change or any other factor.

CHAPTER 2

Introduction: Factors influencing breeding time

The timing of breeding in birds may be influenced by a number of factors, including food availability, day length, rainfall and temperature (Thomson 1950; Newton 1979; Brown 1980, Green 1988, Perrins 1996). Birds aim to breed when conditions favour maximum breeding success (Newton 1979), evidenced by the fact that birds in the northern hemisphere and those in the southern hemisphere breed at different times because ideal breeding conditions occur at different times within each hemisphere (Newton 1979; Altwegg et al. 2012).

Recently a number of species have shifted their ranges or expanded into novel environments as a result of the effects of climate change, habitat loss or an adaptation to urban environments (Thomas et al. 2004; Leemans & Eickhout 2004; Willig et al. 2007). Determining the causal factor for each species' range shift is difficult, since climate change, habitat loss and climatic influences which dominate local, short-term biological changes are occurring concurrently (Parmesan & Yohe 2003). The range expansions have resulted in populations of the same species experiencing different climatic conditions within the same time of year (Curtis et al. 2007). The impacts of this are easier to study in large birds such as raptors which commonly produce one brood in a year, breeding at a particular time in the year (Newton 1979).

To avoid further extinctions of biodiversity as a result of climate change (Thomas et al. 2004; Parmesan 2006), scientists are using bioclimatic envelopes to predict likely distributions of particular species under climate change and to develop appropriate mitigation strategies (Pearson & Dawson 2003; Brooker et al. 2007; Huntley et al. 2010). This will help in efforts to conserve biodiversity by ensuring that the places that animals will migrate to will have suitable habitats for them to settle in (Araujo et al. 2004). This also enables migration corridors to be created in the direction of their likely movement (Tewksbury et al. 2002). Although bioclimatic envelope models provide some hope for conservation, they have been criticized by some as they do not take into account the other factors such as biotic interactions, evolutionary change and dispersal ability which play a role in determining species distributions (Pearson & Dawson 2003). A challenge still exists as the anticipated rates of climate change are predicted to interrupt the interplay of adaptation and migration, threatening the existence of many species (Davis & Shaw 2001).

Other than uncertainties about the direction in which organisms will shift to under climate change, there is also concern about whether species can adapt to their new environments and survive in them. To breed successfully in new environments, organisms may have to shift their timing of breeding (McCarty 2001; Bradshaw & Holzapfel 2006), an inability to do so may lead to a mismatch with their food supplies (Møller et al. 2008; Wright et al. 2009). This is because it is predicted that under climate change food peaks for most species will be different to the ones they are currently experiencing (Thomas et al. 2001). To survive under such shifts species will have to plastically adjust their breeding times to match food abundance (Visser & Both 2005;

Bradshaw & Holzapfel 2006). Breeding times can be adjusted through evolutionary or phenotypic plasticity (Parmesan 2006; Visser 2008). A major concern though is that climate change is rapid and may overwhelm the speed of evolutionary adaptation (Hockey 2003; Jump & Penuelas 2005; Midgley et al. 2006).

One such issue is the timing of breeding. As species move into new environments, they will likely experience different conditions relating to novel climates (for example, rainfall regimes), or different prey phenology. Both factors are known to influence timing of breeding (Brown 1980; Both et al. 2005). How a species adapts its timing of breeding to these novel environments will depend on its phenological plasticity or on its speed of evolutionary adaptation (Visser 2008). One question that still remains is whether shifting species will be able to move their breeding seasons in response to the climate and whether the breeding success of those with altered dates are the same, better or worse than those that fail to modify this parameter?

This study focuses on the Black sparrowhawk *Accipiter melanoleucus* a species that has already shifted its range, although it is not known whether its range shift has been in response to either climate change, habitat creation or a combination of the two (Simmons et al. 2004; Huntley et al. 2006; Hockey & Midgley 2009). In southern Africa, the species originally breeds in north eastern and south eastern South Africa, Zimbabwe, Botswana and Mozambique (Tarboton et al. 1978) and has over the past two decades shifted its range into the south western South Africa (Curtis et al. 2007; Underhill 2012) as seen in Appendix A. However, the traditional and newly colonized ranges (Western Cape) show very different rainfall regimes, with the traditionally occupied areas having a dry winter and wet summer and an opposite regime occurring in the newly colonized areas (Irwin, 1981; Pickford et al. 1989; Curtis et al. 2007) This, therefore, means the Black sparrowhawk breeds in the wet season in the Cape Peninsula whereas it breeds in the dry season in the rest of its range (Curtis et al. 2007).

The aim of the study is to explore whether the timing of breeding has changed for this species as it has colonized this new environment and to establish what climatic factors influence laying dates and whether these differ between the traditional areas and the newly colonized areas (Western Cape). Furthermore, using an intensively studied population within this newly colonized area, I explore which climatic factors influence timing of breeding at a finer scale (that is on a month by month basis) in the different years. The climatic factors whose influence on timing of breeding is being investigated are rainfall and temperature. The consequences of the timing of breeding on the breeding success and productivity of birds in this newly colonised population is then explored to determine whether those that have shifted their lay dates have benefited from the shift, and whether this process has helped the species to colonise and for the population to grow in this new environment. The population was modeled to investigate its growth rate as a result of having both early and late breeding birds and to show how it would have grown without the early breeding birds.

It is expected that the results of the study will show that the birds that has colonized the Cape Peninsula and the Western Cape still breeds at the same time as those in the traditional areas. This will therefore mean that rainfall and temperature have no significant influence on the timing of breeding. These birds are also expected to have the same breeding and fledgling success as those in the traditional areas.

Methods

2.1 Study area

The study was carried out at two scales, that is, at a large scale covering Zimbabwe and South Africa (Fig.1) and at a fine scale, focusing on an intensive study site on the Cape Peninsula (Fig. 2). The Cape Peninsula study area lies along the eastern and western slopes of the Table Mountain range. It covers an area of 300km^2 consisting of a matrix of habitats including urban gardens, pine and eucalyptus plantations, small pockets of indigenous Afromontane forest and fynbos (Curtis et al. 2007). Altitude ranges between 100m and 300m above sea level, with variable winter rainfall (Cowling et al. 1996) with the annual average of approximately 1250mm (South African Weather Services). Average minimum and maximum temperatures are 12^{0}C and 21^{0}C respectively (South African Weather Services).

2.2 Data sources

The data for the large scale study was obtained from the Avian Demography Unit (ADU) (from their collection of nest record cards from 1923-1998), literature (Pringle 1971; Anonymous 1980; Uys 1984; Pepler & Pepler 1990; Oettlé 1993; Breedt 1995; Visser 2004, Tarboton & Allan 1984), the unpublished or ongoing work of Gerard Malan and Mark Brown and the Cape Peninsula intensive study which was initiated by Ann Koeslag and Odette Curtis. This latter data was also used for the fine scale analysis. Climate data was obtained from the Climate System Analysis Group (CSAG, 2012) and the data used was from 1914-2010.

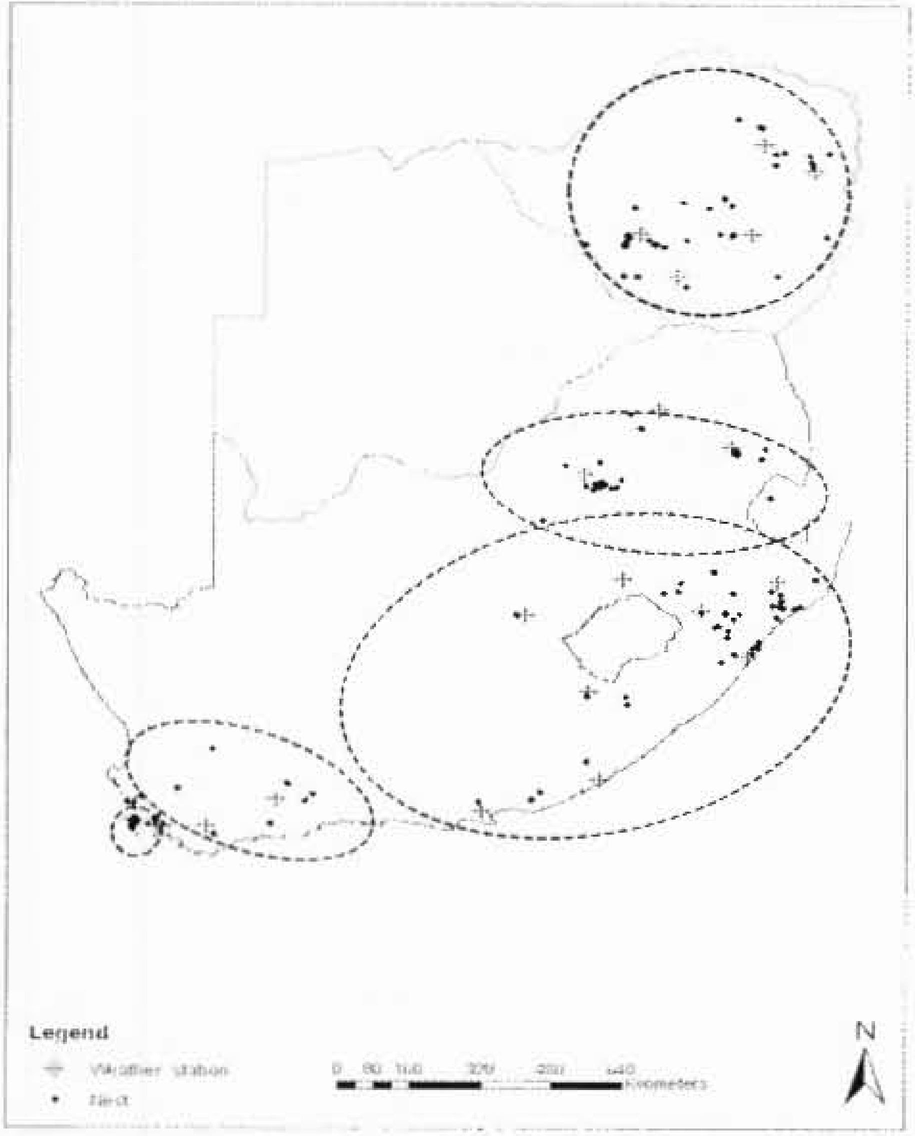


Fig 1. Map showing the study area and the location of all nests (black dots) for which there was laying data and weather stations (cross target circles). These data were used for the large scale analysis exploring patterns of laying in traditional and newly colonized areas. The dashed circles show super-regions used in the subsequent analysis.

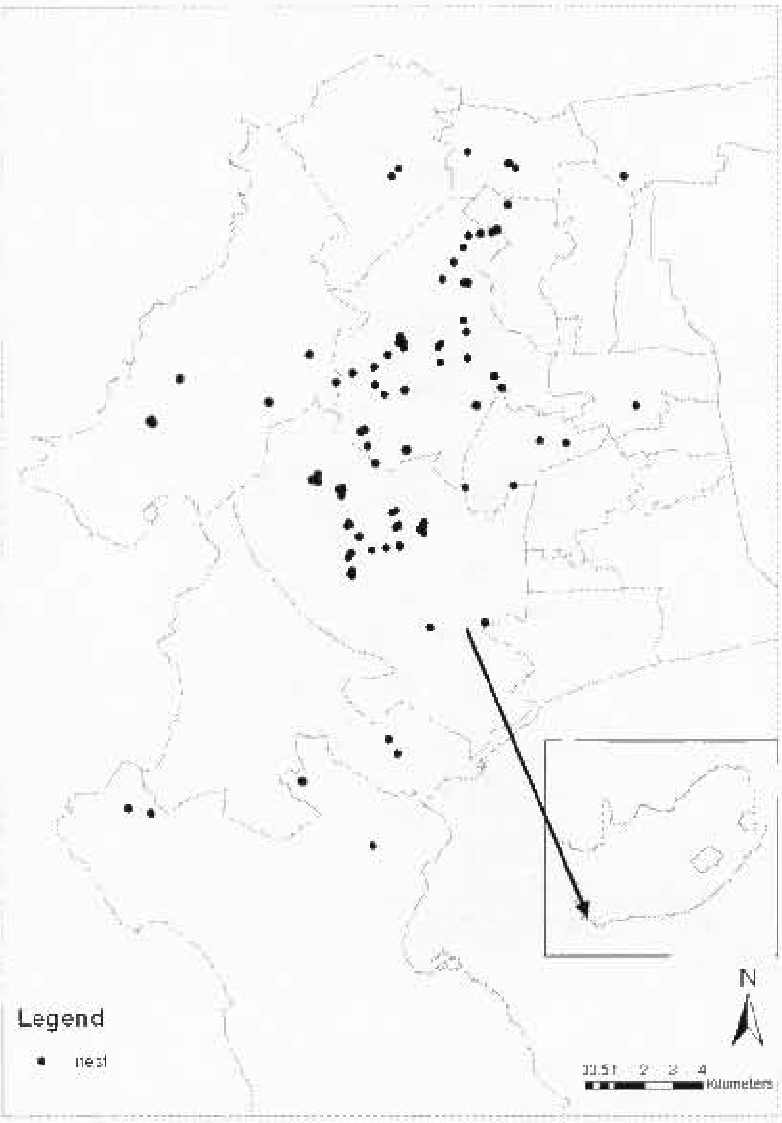


Fig 2. Map showing the location of nests (for which there were laying dates) in the Cape Peninsula for the period 2000-2010. These data were used for the fine scale analysis but also form part of the data used in the larger scale analysis. The map also shows political boundaries within the area.

2.3 Data Collection

2.3.1 Southern Africa

The majority of data outside the Cape Peninsula were collected by members of Birdlife South Africa. These bird watchers voluntarily filled in nest record cards to record the timing and outcome of any nests they found between 1923 and 1998. The observers were only required to record any breeding activity which involved the presence of eggs, young or fledged birds still being fed by their parents. In most cases, the observers continued to visit the nests and the same nest record card was used to record all the events occurring within the nest, giving detail on the life stages of the nest. Some records were obtained from scientific papers by individuals mentioned in Table 1. More Recent data was obtained from the work of Malan and Brown. Table 1 shows the origins of all data that was used in the study.

2.3.2 Cape Peninsula

The Cape Peninsula Black sparrowhawk project is an ongoing project which was initiated in 2000. It is a part of the Western Cape Raptor Research Programme (WCRRP) which aims at understanding the life history constraints and changes of raptor populations in the region (Evans et al. 2004). The Black sparrowhawk project entails locating nests, ringing the birds (adults and nestlings), monitoring of nests and detailed record keeping of events and activities occurring within each territory. The project is carried out during the March to November breeding season.

Table 1. All nests records used in the study and the year of breeding

Source	Years	Area	Number of nests
Nest record cards	1923-1998	South Africa and Zimbabwe	161
WCRRP	2001-2010	Cape Peninsula	232
Tarboton and Allan 1984	1955-1983	Traansvaal	95
Pringle 1971	1947-1949	Cape Town	3
Anonymous 1980	1979	Port Elizabeth	1
Pepler & Pepler 1990	1988	Cape Town	1
Oettlé 1993	1993	Cape Town	1
Breedt 1995	1994	Bloemfontein	1
Visser 2004	2002	Cape Town	1
Gerard Malan	Data from the 90's	South Africa	19
Mark Brown	2011	KZN	1
Uys 1984	1983	Cape Town	1
Total	**1923-2011**		**517**

Nests have been located by surveying suitable stands of trees during the breeding season in search of calling sparrowhawks, prey remains, white wash and nest structures (Curtis et al. 2007). Nests have also been located through the assistance of walkers who spot nests or birds

(Ann Koeslag pers. comm.). This project was initiated by Odette Curtis and is now run by Ann Koeslag who works with a number of volunteers. Bal-chatri traps baited with pigeons are used to catch birds for ringing with SAFRING rings and colour rings, which allow for easy identification of individuals in the field through the use of unique combinations. Three to four weeks old hatchlings are ringed with the help of a tree climber who brings them down for ringing and returns them back to the nest afterwards.

The few incidents of double brooding from the Cape Peninsula were ignored as they constituted 2.3% of the data set with only 0.4% of these being successful. Where the first breeding attempt was unsuccessful, the second attempt was used in analysis for all double breeding birds, the first attempt was taken.

2.4 Lay date determination

Where exact lay dates were not known, they were estimated to the nearest month using the available information on the incubation behavior, observation of eggs, nestlings or fledglings. Characteristics used to determine the lay date include the colour of eggs and the nestling's level of development. Lay dates were back dated using information on the length of the incubation (38 days) and nestling period (45 days) (Steyn 1982). The length of the fledgling period was based on Steyn (1982). Eggs were assumed to have been laid at three day intervals (Steyn 1982). Incubation period was assumed to start on the day the first egg is laid (Steyn 1982). Where a nest was found with an incubating female (if this was the only information) then that month was taken to be the month of laying.

2.5 Super region selection

In order to look at laying in relation to climate at as fine a scale as possible, nests were divided into 5 super-regions based on their spatial location. This was done to ensure sufficient nesting records to produce a realistic pattern and distribution of lay dates. Super region 1 is the Cape Peninsula and is made up of nests from the WCRRP (Fig. 2). Super-region 2 has the rest of the nests in the winter rainfall area (Western Cape). Super-region 3 contains all nest records from Kwa-Zulu Natal (KZN), the Eastern Cape and Free State. Super-region 4 contains all nest records from Gauteng and surrounding areas (including the 95 nest records collected by Tarboton and Allan (1984) in the former Transvaal). Super-region 5 contains all nest records from Zimbabwe (Fig 3). The choice of these datasets was to give an idea of the timing of breeding in the different regions. This objective and the limited number of nest records in each region meant that I made no attempt to split these records up temporally (for example, by year or decade), rather all data were pooled, and used together to describe the laying patterns in each region.

Clusters of nesting points within each super region were identified and a central weather station located for each cluster (Fig 1). The average monthly rainfall and temperature were recorded for each weather station within a cluster of nest sites. The average rainfall and temperature for each super-region was calculated by averaging the data from all weather stations within it. These averages for individual weather stations had been calculated using data from as early as 1914, although the initial date varied among the stations.

2.6 Data Analysis

I had two data sets, that is, I) the large scale data set which consisted of all nest records (from the nest record cards, the intensive Cape Peninsula study and other sources mentioned in section 2.2). These data were used to explore broad scale patterns in laying dates comparing the traditional areas with the newly colonized areas and also exploring whether any climate variables (rainfall and temperature) explained these patterns, in particular, the proportional distribution of laying across the months in the different regions. Although some of the newly colonized areas occur in the Free State which has been classified under the traditional areas in this study, this is expected not to have an effect on the results as there are only a few in this region compared to the Western Cape. II) My second data set consisted of data from the intensively studied Cape Peninsula population (WCRRP) which contained laying dates in each year over a 10 year period (2001-2010); these data were used to explore which climatic factors (rainfall or temperature) influenced the distribution of laying dates from year to year in this population.

2.6.1 Large scale analysis

To investigate what influences timing of breeding between super-regions (large scale), I used a Generalised Linear Model and modeled the (arc-sine square route transformed) proportion of birds laying in each month against rainfall and temperature for each super region. I fitted super-region as a permanent fixed effect in all models, I then tested for the influence of temperatureon laydate and the interaction between temperature and super-region. Next I examined the influence of rainfall again testing for an interaction between rainfall and super-region (after controlling for any significant effect of temperature). I also tested for an interaction between rainfall and temperature.

2.6.2 Fine scale analysis

From observations of laying within the Cape Peninsula population there appeared to be considerable variation in timing of breeding from year to year. For example, see Appendix B for 2006-2009 data. To examine the factors influencing the number of birds breeding in the different months in each year I fitted a Generalised Linear Mixed Model (GLLM) with month and year as random terms in the model. In controlling for month and year, I controlled for the fact that throughout the study period, there are more likely to be nests produced in some months than others, and also for the fact that population size changed each year. This model therefore in effect looks at the variation in laying for the same month between years in relation to the rainfall level in that month between the years. The GLLM had a Poisson error structure and log link function. The number of nests produced in each month in relation to rainfall levels was analysed in order to investigate whether rainfall or temperature had any influence on timing of breeding within the Cape Peninsula population. I also tested for an interaction between temperature and rainfall.

I also explored whether timing of breeding influences breeding performance. The breeding performance measures used to evaluate the population were (i) breeding success, that is, whether a territory produced any fledged young and (ii) overall productivity, that is, the number of young produced per occupied territory per season. Breeding success was a binary measure (success/failure) and was analysed in a GLLM with a binomial error structure and log link function, with territory and year set as random terms to control for non-independence of data collected at these levels, and to account for the unbalanced nature of the data. Productivity was analysed in the same model, but with a Poisson error structure and log link function. The number of fledglings was set as the response variable and the lay date (month of laying) as the explanatory variable. Territory and year were set as random variables. All GLMs and GLLMs were carried out in R version 2.14.1(R Development Core Team 2011) or SAS (SAS Inc. 2004).

Having established the breeding success and productivity of early breeding and late breeding birds, I decided to project population growth for the population. This was to see how the population would grow if all individuals were late laying and how it could be expected to grow when it included both early and late laying birds. To be able to do this, I estimated the annual age-specific survival probabilities accounting for imperfect detection using the Cormack-Jolly-Seber model (Lebreton et al. 1992). I implemented the model in a Bayesian state-space modeling framework (Gimenez et al.2007). The population was modeled in Vortex 9.99 (Lacy 1993).

Results

2.7 Data set

I collated information on the laying dates (to the nearest month) from 517 breeding attempts recorded over a period of 87 years (from the whole study) were used for further study. Of these, 232 were from the Cape Peninsula, 44 from the Western Cape, 46 from Kwa-Zulu Natal, 114 from Gauteng and surrounding areas and 81 from Zimbabwe. All attempts at double brooding were excluded from all analyses. They constituted 2.3% of the data set and their exclusion is expected to have little (insignificant) influence on the results.

A) Large Scale Analysis

2.8 Timing of breeding within the five super-regions.

A comparison of laying dates revealed some interesting differences between the five super-regions (Fig. 3). In particular, there were some striking differences in when breeding occurs in the traditionally occupied (KZN, Gauteng, Eastern Cape, Free State and Zimbabwe) areas relative to the newly colonized regions (Cape Peninsula and Western Cape). For example, in the three traditionally occupied areas laying tended to occur before the rainy season, occurring generally 3-4 months (June-September) before the main rainfall period (Fig. 3). However, in the newly colonized super-regions laying occurred during the rainy season. In the Western Cape (excluding the Cape Peninsula, Fig. 3) laying peaked just after the main rainfall, and on the Cape Peninsula the population showed a bi-modal distribution with laying peaks occurring either side of the peak in rainfall. Within all populations, laying tended to occur over the winter period, that is, when temperatures were at their lowest (Fig. 4; Fig. 5a).

Additionally, the length of the breeding season was also longer in newly colonized areas, lasting 5 months in Zimbabwe and Gauteng, but occurring over an 8-month period in the Cape Peninsula. The length of the breeding season, the first month in which breeding commenced and the mean lay date, appeared to be strongly correlated with latitude (Fig. 3, Appendix C and D), with earlier and longer breeding occurring at lower latitudes.

The effect of temperature on laying dates was also investigated. KZN (super-region 3) had peak laying when temperature was at its lowest. Gauteng (super-region 2) experiences its peak in laying just after the lowest temperature. Zimbabwe's temperature has two peaks, and also experiences cooler average temperature throughout the year compared with other super-regions (Fig. 4(5)). Laying in this super-region commences in the month with the lowest temperature and peaks at medium temperature. The Cape Peninsula has two peaks, both occurring in the winter, when temperatures are low.

I then explored quantitatively whether any climatic factors explained variation in laying between these super-regions. After first controlling for super-region (χ^2_4=11.77, P=0.01), I found, as expected that the proportion of birds laying in each month was related to temperature (χ^2_1=35.65, *P*<0.0001), with a greater proportion of birds laying in the colder months, this relationship seemed to be consistent between super-regions, with the exception of Zimbabwe where no such relationship is apparent and lead to a weakly significant interaction between temperature and super-region (χ^2_4=9.54, *P*=0.048) (Fig. 5a). Interestingly Zimbabwe experiences milder overall temperatures throughout the year with no months being over 25°C on average, unlike the other regions.

After controlling for super-region, rainfall itself had no influence on the proportion of clutches laid (χ^2_1=0.03, *P*=0.85), however, after controlling for temperature, I found both a significant relationship between rainfall (χ^2_1=5.73, *P*=0.01) and a rainfall*super-region interaction (χ^2_4=10.13, *P*=0.03). Figure 5b, shows the nature of this interaction, the traditionally occupied super-regions show a negative relationship with rainfall, whereas the newly colonized areas showed a positive relationship. There was no interaction between temperature and rainfall (χ^2_1=1.21, *P*=0.27).

Thus, it appears that climate appears to have different influences on timing of breeding in the different super-regions.

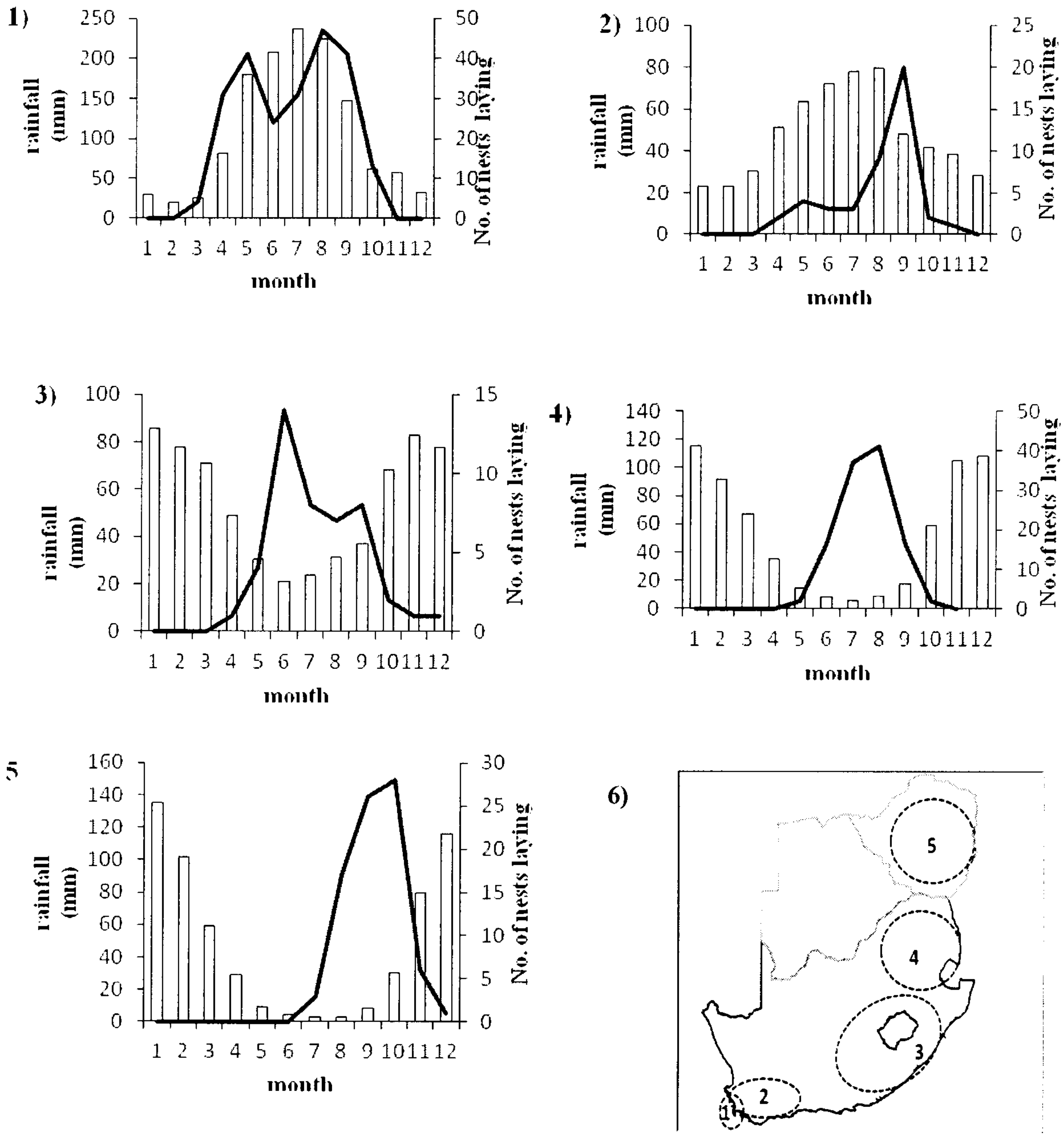


Figure 3. Super-region rainfall (bars) in relation to the number of nests started in that month (line). Figures 1) to 5) represent the different super-regions and Figure 6) shows the position of each super-region in southern Africa.

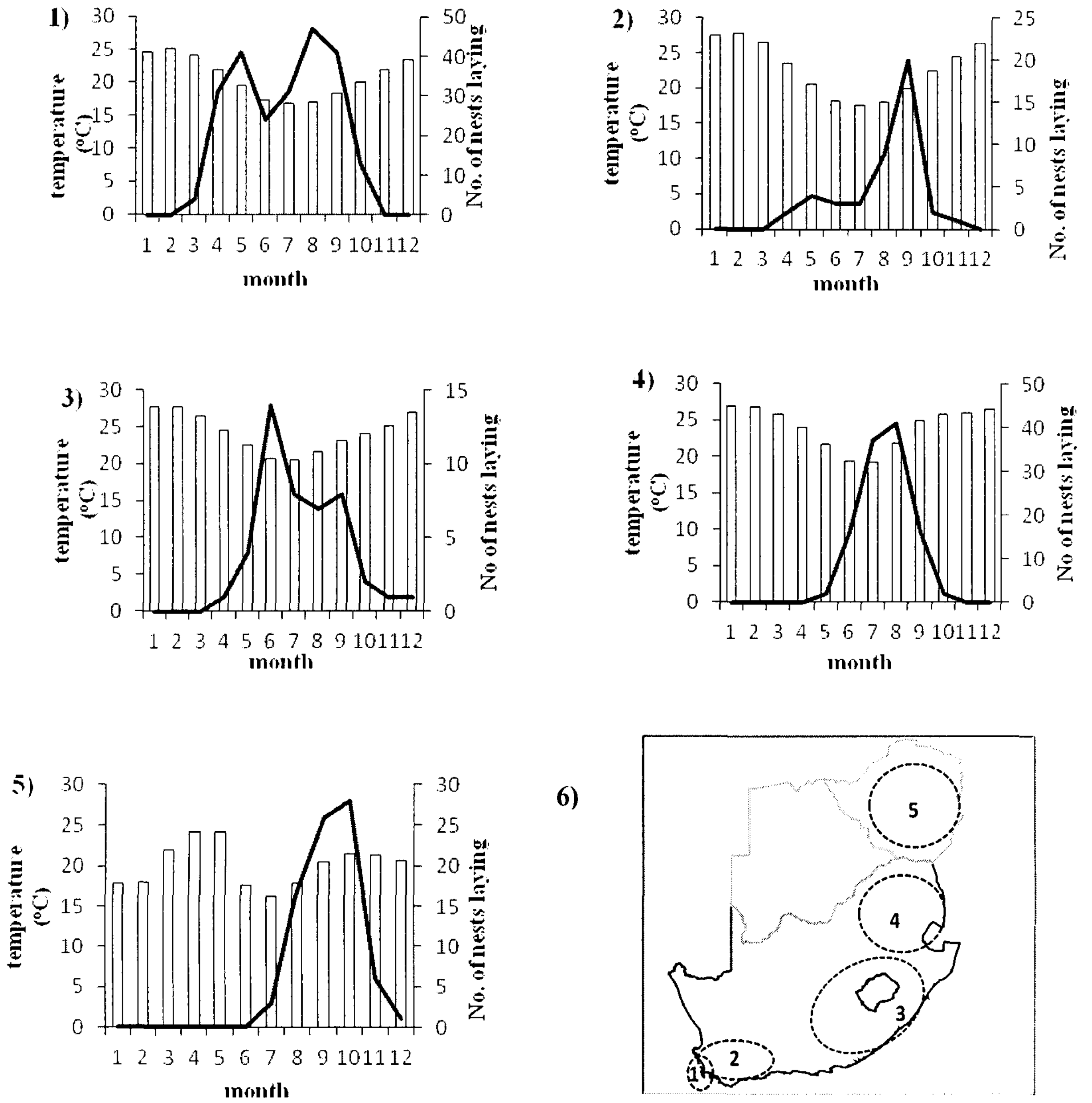
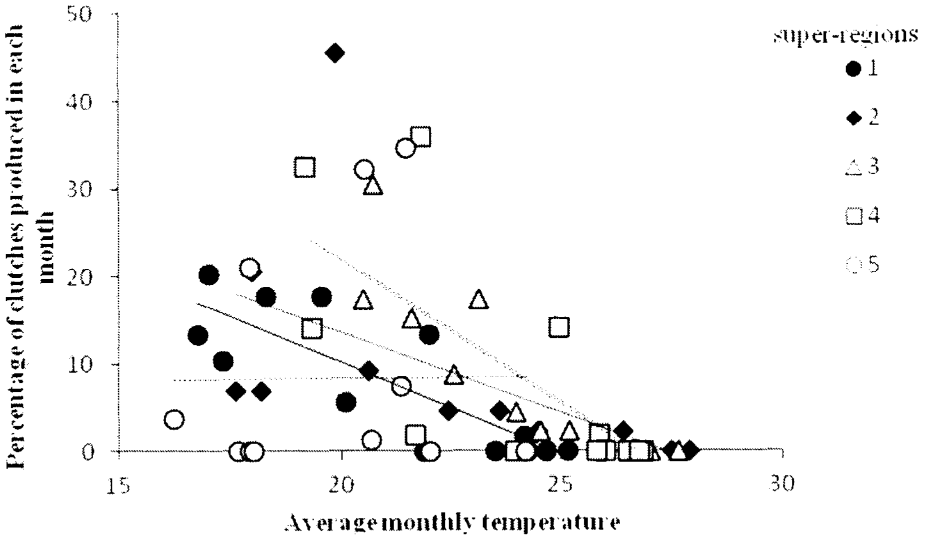


Figure 4. Super-region temperature (bars) in relation to the number of nests started in that month. Figure 1) to 5) represent the different super-regions and Figure 6) shows the position of each super-region in southern Africa.

a)



b)

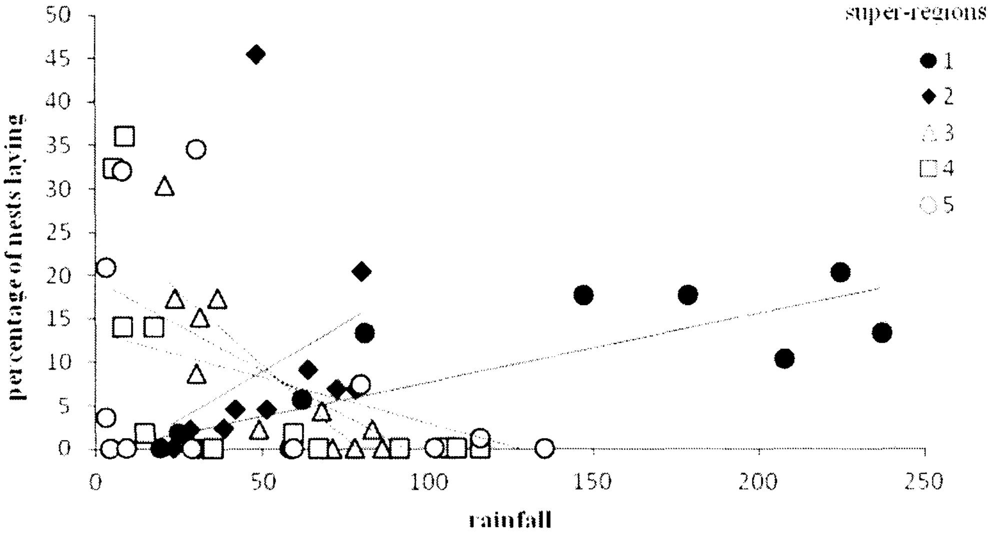


Figure 5. Scatter plot denoting the relationship between a) rainfall b) temperature and the nests started in the super-region in that month. The solid lines show the relationship for super-region 1 and 2 (newly colonized), while the dashed lines show the relationship for super-region 3, 4 and 5 (traditional regions).

B) Fine scale analysis

2.9 The influence of rainfall and temperature on the timing of breeding between years.

There was considerable variation between years in the distribution of laying dates within the Cape Peninsula – although generally there still appeared to be two peaks in laying, one in the early period, around May/June, and another in the later period, around August/September (Appendix B).

Levels of rainfall in a month had no apparent influence on the number of clutches laid in that month ($F_{1,70}=0.42$, $P=0.52$), but temperature did have a near significant negative influence on the number of clutches laid ($F_{1,12}=4.02$, $P=0.06$). Furthermore, I found a significant interaction between temperature and rainfall ($F_{1,68}=4.75$, $P=0.03$), rainfall had a contrasting influence on numbers of nests produced in a month depending on the temperature. Figure 6, shows this modeled relationship, thus, in hot months (for example, fixing average monthly temp at 22°C) there was a negative relationship with rainfall, with less nests produced when the month was rainy; whereas in cold months (for example, fixing average monthly temp at 16°C) there was a positive relationship, with more clutches laid in wet months.

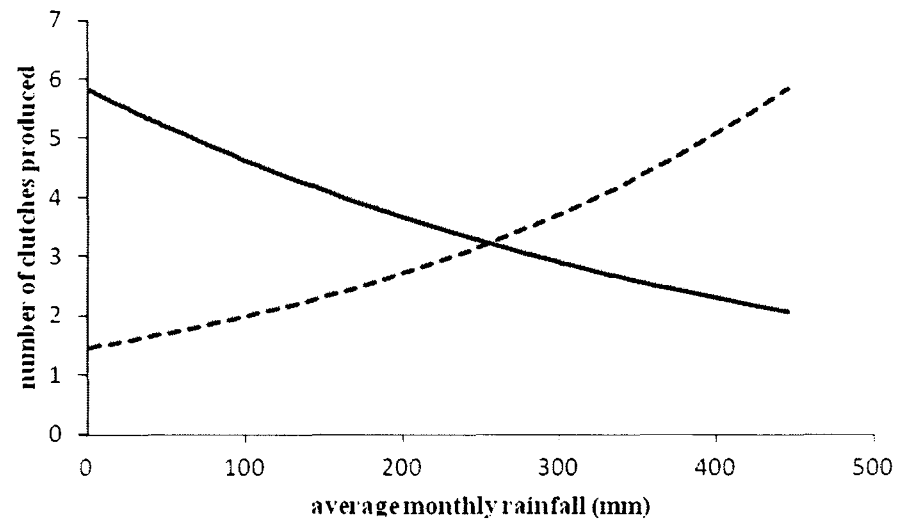


Figure 6. Graph showing the modeled relationship for the interaction between temperature and rainfall (P=0.03). This is the modeled relationship between rainfall and number of clutches produced fixing the temperature for a month either as high (22°C dashed line) or low (16°C solid line) from the Generelised Linear Mixed Model controlling for month and year as random terms in the model.

2.10 The effect of the month of laying on breeding success and productivity

One of the most interesting differences in the timing of breeding between the traditional areas and the newly colonised areas, was that the species had extended the period over which it breeds; principally by shifting their laying forward. Thus I investigated whether there was any difference in breeding success and productivity between early and late breeding birds.

I found that there was a significant decline in both breeding success ($F_{1,3}$=4.58, *P*=0.01) and productivity ($F_{1,3}$=6.86, *P*=0.01) for birds breeding over the course of the breeding season (Fig. 7 and Fig. 8). This was principally driven by very high breeding success and productivity of those breeding at the very start of the breeding period (March) and very poor breeding success and productivity of those breeding very late on (October).

Splitting breeding attempts into early and later period, I found that productivity and breeding success tended to be higher for early rather than late breeders (Productivity: early 1.67±0.14, late: 1.37±0.10; Breeding success: early: 0.87 ±0.04, late: 0.76 ± 0.05). Although these differences were marginally non-significant (Productivity: $F_{1,\ 230}$=4.26, *P*= 0.08; Breeding success: $F_{1,230}$ =3.87, *P*=0.053).

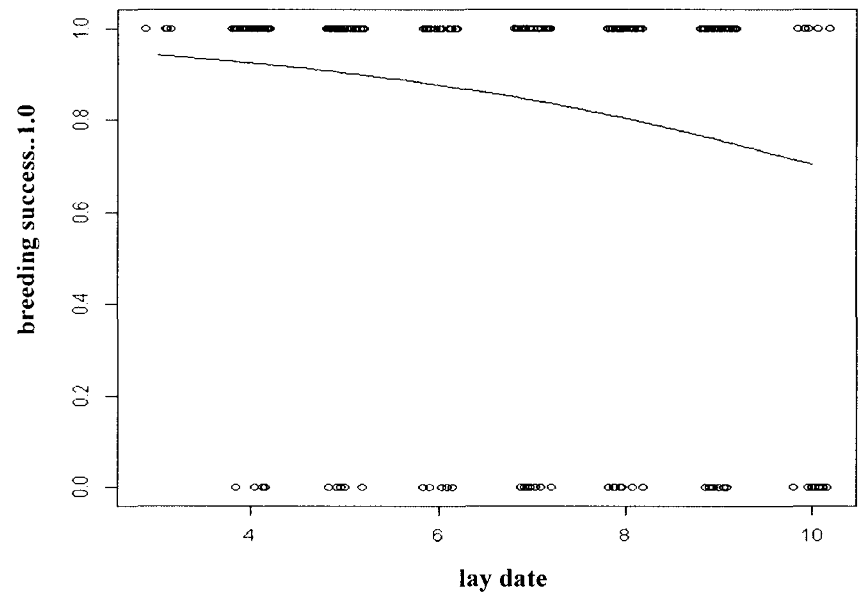


Figure 7. The effect of lay date on the breeding success of Black sparrowhawks. Lay date has a significantly negative effect on breeding success. Breeding success decreases with time, with later breeders having lower breeding success.

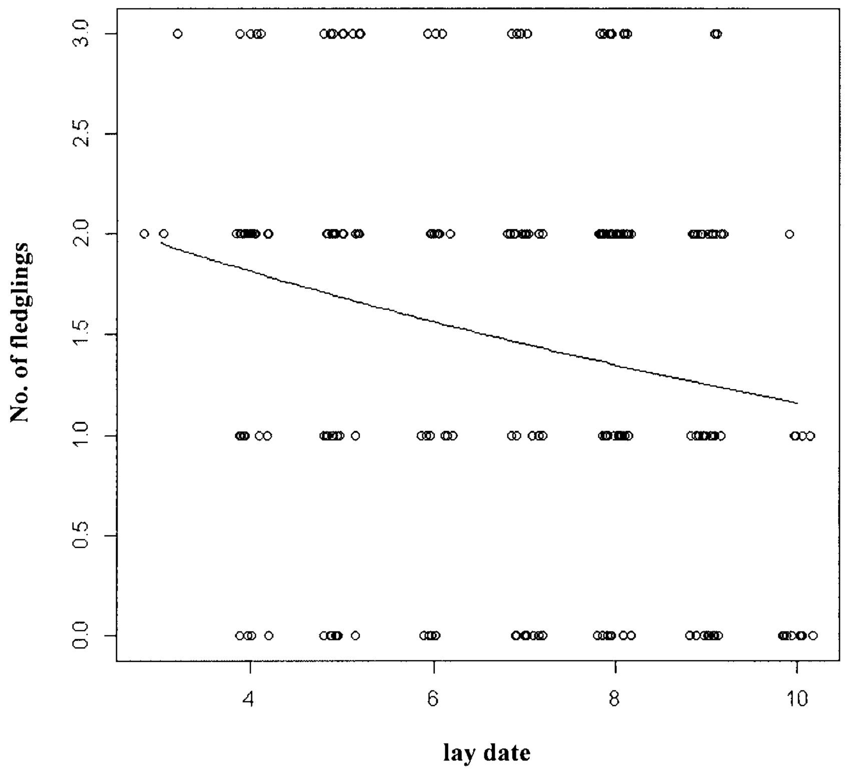


Figure 8. The influence of lay date month on the number of fledglings produced. The number of fledglings that are produced decrease with date.

2.10 Effects of the presence or absence of early laying birds

The early laying birds have helped the population to grow faster than it would have if all birds had been late laying. The parameters used in the model are in Appendix E. The shift by some pairs to lay early has been advantageous for population growth as it has helped the population at a faster rate than it would have otherwise done.

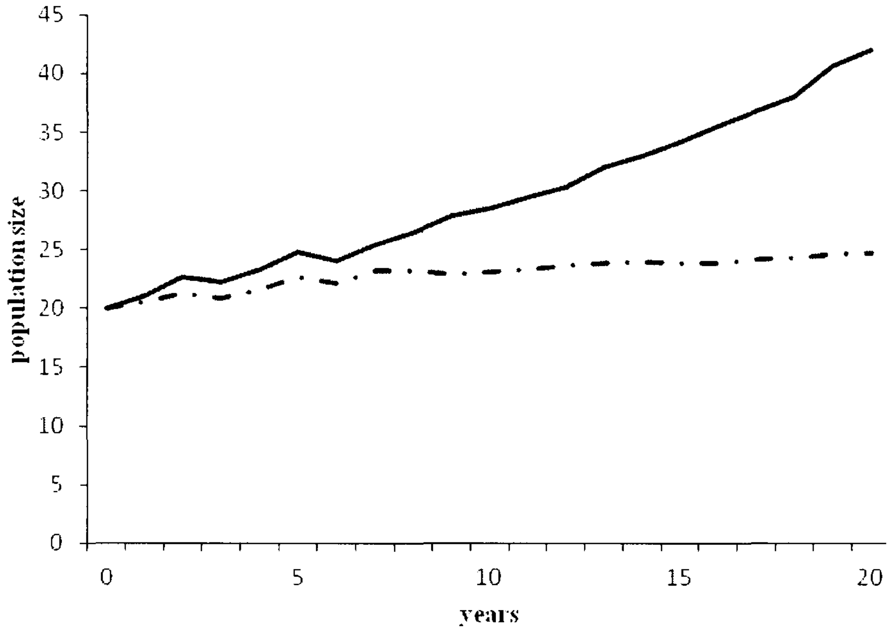


Figure 9. The modeled Cape Peninsula population showing how the population has grown as a result of having individuals that have shifted their breeding (solid line) and how it is expected to have grown in the absence of the shift (broken line).

Discussion

The large scale analysis revealed that Black Sparrowhawks in different super-regions initiate breeding at different times, with breeding peaking in different months, the duration of the breeding season also varied between the super-regions. Both rainfall and temperature appeared to have an effect on when birds laid, but these relationships differed between regions, although temperature had a greater effect.

Birds in newly colonized areas in the Western Cape initiated breeding earlier than birds in the traditional areas. There appeared to be a strong pattern between when breeding was initiated and the latitude of the super-region, with the super-region closest to the equator initiating breeding later (July) than the rest and the one furthest south initiating breeding earliest (March). The other super-regions also followed the same trend in breeding commencement (Appendix C). Breeding peaks were also shown to differ in relation to latitude (Appendix D), with most birds closest to the equator laying late in the season and progressive early laying for birds furthest from the equator. Probably as a result of when breeding commenced, the different super-regions also had different lengths of breeding time, with the populations laying early breeding for a longer period than those that started late. This link between the length of the egg laying season and latitude has also been found in other studies (MacArthur 1964; Ricklefs 1966, Wyndham 1986).

However, although these patterns fit with a latitudinal effect, there is also a chance that it is related to elevation patterns, since it appears that birds at low altitude breed earlier than the other birds. Both populations in the low lying Western Cape started breeding in March while the KZN population started in April and these populations also had longer breeding seasons, Gauteng birds being at the highest elevation in South Africa initiated breeding in May and those in Zimbabwe which were at the highest elevation of all the super-regions starting breeding in July. The population at higher height above sea level also had shorter breeding periods. Birds have been shown to breed later as elevation increases, which has led to the suggestion that elevation might be the primary driver of breeding time (Burgess et al. 2011).

Birds in the newly colonized areas in the Western Cape have shifted their breeding time to start early, a sign that Black sparrowhawks are able to shift their breeding phenology. Although timing of breeding differed amongst the super-regions, all populations seemed to breed in the winter, although the birds in the Cape Peninsula were apparently unique in that they showed a bimodal distribution in their timing of breeding, with peaks either side of the peak in rainfall, which may have been an attempt to avoid this period of high rainfall. The distribution of breeding attempts was negatively related to temperature in all regions with the exception of Zimbabwe. One possible reason for this lack of relationship with temperature is that Zimbabwe had generally lower average temperatures compared with other areas throughout the seasons. For example, Zimbabwe only experiences average temperatures higher than 21°C in three months while the other super-regions have temperatures higher than 21°C for majority of the months. The Cape Peninsula also generally experienced lower average temperatures than the other regions within South Africa. Temperature has also been shown to have a positive effect in the laying of dark-eyed juncos (*Junco hyemalis*) which have also experienced range shift (Yeh &

Price 2004). The population experiencing milder temperatures has been able to double the length of its laying period, an aspect which has enabled it to grow faster than the source population (Yeh & Price 2004; Price et al. 2008).

Interestingly, although both the Cape Peninsula and Zimbabwe had low temperatures throughout the year, they had different breeding seasons. Thus, temperature alone may well not be the only driving force behind the patterns of breeding seasons. This could mean that another factor such as photoperiod determines when most birds will lay. The near absent laying in the early months regardless of temperatures could mean that birds prefer to lay during times when photoperiod is shortest, which occurs in the winter (Bareja 2011). This is also suspected to be the case with the Black Sparrowhawks in the Western Cape since the results have shown that majority of the birds continue to lay in winter regardless of the High rainfall in that region during this time of the year. The fact that temperature also has no effect on timing of breeding also leaves room for this speculation to be made. And certainly in the northern hemisphere species, we know that the length of the photoperiod determines gonadal development in birds (Hau 2001 & Beebe et al. 2005), hence timing of breeding.

Rainfall had an influence on laying date at the super-region level, although the correlation between timing of breeding and the amount of rainfall was different in the traditional and newly colonized areas in the Western Cape, with a negative relationship with rainfall in the traditional areas but an apparently positive relationship in the newly colonized areas. Rainfall has been said to determine prey abundance for African raptors, as most prey species breed in the rainy season

(Brown 1980). Breeding in the traditional areas peaks a few months before the rainfall season. This means that the birds avoid the wet time of year for most of their breeding but also means that their chicks will enter the post fledgling period at a time when there may be an abundance of prey, in particular vulnerable juveniles (Mearns and Newton 1988). The Cape Peninsula population is thus, faced with a tradeoff between laying in the cool but rainy season and laying in the dry but hot season.

Although egg laying in the newly colonised areas in the Western Cape has a positive correlation with rainfall, the graphical representation of the relationship shows that the Western Cape laying peaks after the rainfall peak. Furthermore, the Cape Peninsula population avoids the rainfall peak by having a bimodal distribution of laying dates with a decline in the peak rainfall month. The Cape Peninsula population is not the only population that lays in the rainy season. The East African population also breeds during the rains but also avoids the peak rain by having a bimodal distribution of laying dates, with most breeding falling either side of the peak in rainfall: a sign that the birds are also attempting to avoid the heavy rains (Appendix F) (Brown 1980). The East African population also breeds in the winter (Brown et al. 1982). The bimodal laying and the long breeding season experienced by the Cape Peninsula population act together to allow early and late breeders to avoid the heavy mid-winter rainfall which negatively impacts on breeding success (Curtis & Koeslag 2004).

Looking at the timing of breeding of the species' prey, it appears that prey becomes most abundant in the peak laying season or just after the peak laying season, a sign that food availability may be the ultimate factors influencing timing of breeding (Brown 1980). Black sparrowhawks mainly feed on common pigeons, doves and guinea fowl (Curtis et al. 2004; Curtis et al. 2005). The timing of breeding in these species may therefore influence breeding in the Black sparrowhawks.

The dove species available to the birds in the Cape Peninsula include the laughing dove, speckled pigeon and red eyed doves. These prey species have been known to multiple brood, with some producing a maximum of six broods in a breeding season, thus increasing food availability for the Black sparrowhawks and other raptors (Rowan 1983; Tarboton 2011). Therefore, the Cape Peninsula population has been able to shifts its breeding phenology because of the generally low temperatures experienced and the availability of prey in the area. As Appendix G shows that there are prey species laying earlier in the year in that super-region. The increase in urban gardens in the area has led to increased prey populations (particularly in feral pigeons and starlings), allowing the Cape Peninsula population to grow and extend its laying period.

The results of the study at a fine scale showed that there was year to year variation in laying dates within the Cape Peninsula. Rainfall and temperature had no significant influence on the number of clutches laid in each month, but there was a significant interaction, thus in relatively cool months rainfall had an apparent positive influence, with a greater number of birds laying, but in hotter months rainfall apparently had a positive effect. The mechanism for such a relationship is difficult to explain, but certainly warrants further more detailed research.

The year to year variation in laying dates with the Cape Peninsula shows that there is some year to year variation in factors that influence laying in Black sparrowhawks within the region. This year to year variation has also been seen in dark-eyed juncos and was proven to be linked to environmental conditions (Yeh & Price 2004). The variation could be explained by the unpredictable Cape Peninsula climate, which shows great year to year variation in rainfall and temperature.

Although traditionally a dry season breeder the Cape Peninsula Black Sparrowhawk population breeds in the rain but has continued to grow over time. The effect that rainfall has on laying has been shown to be dependent on the ambient temperatures. When temperature is low, rainfall has a positive effect on laying. This explains why the Cape Peninsula population is still able to breed in the winter. This is also seen in the East African population (Brown, 1980) where breeding occurs in the wet winter (Appendix F).

When I examined how timing of breeding influenced breeding performance, I found that breeding success and productivity of the Cape Peninsula population decreased with time. This pattern has been well established from other studies in the northern hemisphere although it is less well established in Afro-tropical context. Burgess et al. (2011) discovered that Mauritius kestrels (*Falco punctatus*) breeding earlier have a higher reproductive success than those laying late. The reason for this common pattern is still not clear and could be to do with individual or environmental quality or a combination of the two (Verhulst & Nilsson 2008).

It is not clear what factors would be operating to reduce the breeding success of later laying birds in this population. However, it might be the result of geese usurpation as pairs experiencing geese usurpation raise an average of 0,76 chick compared to 1,58 on nest without usurpation (Curtis et al. 2007). Nest record cards show that Egyptian geese (*Alopochen aegyptiacus)* in the Cape Peninsula start breeding in July. This could also be a reason for the reduction in breeding success and productivity with time. There is also a possibility that goose usurpation has been one of the reasons for the shifting of laying dates. But whether other populations suffer from this is not known and warrants further study.

Given that earlier breeding birds tend to breed more successfully, we might have expected the population to have shifted over time to all breed early to maximize output. However this is not actually happening yet in the Cape Peninsula population as just as many individuals continue to breed late two decades after the first recorded sighting. Thus there may be other constraints to laying early which are not apparent from these data. For example the juvenile survival may be lower for the early fledglings. This has been seen in the dark-eyed juncos where late-hatched nestlings have higher survival (Price et al. 2008). Alternatively, there is a possibility that there has not been enough time for evolutionary adaptation to emerge in this population, given that many of the individuals may still be the original colonizing or first generations of the colonizing birds.

However, a good proportion of birds in the Cape Peninsula have been able to shift their laying dates into the warmer months with less rainfall probably in an effort to avoid the rainy season. The ability to shift laying dates in novel environments could also have some other advantages to the shifting individuals as they have been shown to have a higher breeding success and productivity than those that do not shift. This is probably because the shifting individuals take advantage of the reduced competition for resources as only a proportion of the population are breeding during this time.

The ability to shift and increase breeding time in novel environments has also been seen dark-eyed juncos (Yeh and Price 2004; Price et al. 2008). This has allowed the new population to grow at a faster rate as an increase in breeding time reduces the level of competition for resources as it allows for a reduction in the number of individuals laying at any one point in time. The population models I created in this study also suggest that the ability of this species to shift its timing of breeding may well have helped it colonise these new areas with such rapidity. This is because the increased breeding period allows for a spread in the number of individuals breeding at any one point in time, hence resulting in a reduction in competition for resources and thus a higher breeding success. Individuals breeding earlier in the season also have a higher fledgling success than those breeding late and this allows for a higher population growth rate. The models in the absence of this shift in breeding time grow at a far slower rate and will be more prone to negative stochastic events.

Although outside the scope of this thesis, I did note that individual females in this population tended to breed repeatedly at the same time of year. Territories were also found to have an effect on when birds lay (Appendix H). The genetic makeup also influences the adaptability of individuals. A study of great tits (*Parus major*) showed that the variation in individual plasticity in the timing of breeding is heritable (Nussey et al. 2005). If this applies to all bird species, then the initial Cape population of Black Sparrowhawks is likely to comprise immigrants from different super-regions within the country. This is seen in that the current population is made up of both early and late breeders, which would have inherited this trait from their parents, for example, from KZN and Gauteng. Although this may be the case, there are still individuals in this population which breed in March, that is, earlier than either the KZN or Gauteng populations. This indicates that there has been a shift in breeding phenology.

CHAPTER 3

Study Review and Synthesis

Complications with the study

This project was a desk based study and a lot of time was spent transferring data from the nest record cards and notebooks into an electronic data base. Reading what was written on nest record cards was a challenge as some hand writings were quite illegible. Some cards were written in Afrikaans and I had to find an interpreter. This could have lead to inaccurate interpretation of information. Some cards did not have GPS co-ordinates and a lot of time was spent finding these, the challenge was even greater with old cards where colonial names were used as this meant searches into the name changes had to be made so as to allocate the nests to the right places. The bird watchers sometimes recorded the location of the nest by the name of a very small town and did not record the country; as a result another huge amount of time was spent finding out where these areas are located. All these time consuming challenges meant the time to do as much analysis as was possible with the data became limited. The climate data used for the study could have had confounding effects due to the fact that the weather data was pulled temporally to include data from a period when the birds had not actually started shifting. The results of the study do not seem to reveal any confounding effects.

Future research

The populations within South Africa initiate breeding at different times, as a result the Cape Peninsula population could be made up of individuals from both the KZN and Gauteng super-region. If this is the case, this population is bound to be made up of individuals that are early and late simply on the basis of their area of origin, hence their genetic makeup. If this is the case, it is possible that an even smaller proportion of the Cape Peninsula population has shifted breeding time. A proportion of these early laying individuals could be immigrants from an early breeding area such as KZN. There is therefore a need to do this study in years to come with a larger population of individuals known to have hatched on the Peninsula to erase any doubt on whether individuals have had a shift in phenology or not.

This study looked at the influence of average monthly rainfall totals. It is suspected that it may not be average rainfall that influences timing of breeding but the number of days with rain This is because the results of the study have shown that rainfall has no effect yet in most super regions, birds avoid the wet season and even in the Cape Peninsula, they seem to avoid the wettest months suggesting there is some aspect of rainfall that affect their breeding abilities. This was not investigated because of limited time. Further study should therefore establish whether the number of rainy days influence breeding time.

Although not a main part of this study, an influence of individual females on timing of breeding was found. This interesting finding merits further work. A study should be carried out to establish whether it is the amount and quality of food available to the female or genetic traits which influence a female's breeding time. Nussey et al (2005) found individual plasticity in breeding time to be heritable. This should be investigated in the Cape Peninsula in a few decades to establish if females from the same genetic line breed at the same time. In a different study the female's age was shown to determine laying date (Perdeck and Cavé 1992); this could also be investigated in Black sparrowhawks.

A study by Simmons (2000) shows the timing of breeding of other Marsh Harriers whose traditional range spans both the winter and summer rainfall regions. It would be interesting to see whether the same patterns found in his study are also present for other raptor species which presumably has longer time period just like the Marsh Harrier to cope with these different climatic regimes.

Conclusion

The timing of breeding of Black Sparrowhawks has been shown to vary with their location in space, with birds at higher latitude breeding much earlier than those at lower latitudes. This explains the shift in breeding phenology by the Cape Peninsula population. Thus, timing of breeding in a range expanded population is influenced by the conditions of the area they colonise. The Cape Peninsula population also displays a bimodal distribution of lay dates with its second peak corresponding to the distribution of the laydates in the traditionally occupied areas.

This is perhaps a sign that these individuals have failed to shift their breeding time to suit the environment. This potential is further reinforced by the (additional) finding that laying dates of individual females is somewhat consistent between years.

A number of factors (latitude, elevation, photoperiod, food availability, climatic conditions and individual females) seem to influence the timing of breeding. These factors collectively determine how a species performs in an environment. Most studies on range shifts as a result of climate change have focused on the availability of resources as a measure of the suitability of an environment to the survival of the species. This study proves that there are more factors to be considered such as latitude and elevation which influence the length of the breeding season and thus the growth rate of the population which is an essential factor in determining a population's persistence.

Although species ranges have been predicted to be shifting to the poles as a response to climate change (Walther et al. 2002; Parmesan 2006; Hockey & Midgley 2009), it is interesting that this species has moved to a place experiencing different weather patterns to the those occurring in the traditional range and a high percentage of it does not respond to the climatic conditions of the new area and continues to breed late. This means that the ability to shift range is not assurance that a population or species will survive, but it also needs to adapt to the conditions in the new environment. The poor shifts in breeding time also show that adaptation takes a long time and under adverse conditions this would be detrimental to the population. It is also interesting to note that it appears that this species and several others in South Africa are shifting westwards, which goes against climate change predictions.

As global temperatures continue to increase (Walther et al. 2002), all seasons will become warmer than they currently are. This will negatively impact all species which require low temperature in order to breed successfully. When this happens, breeding may be restricted to the few months with temperatures low enough to allow for breeding. This may therefore be predicted to result in reduced breeding success and productivity for this species.

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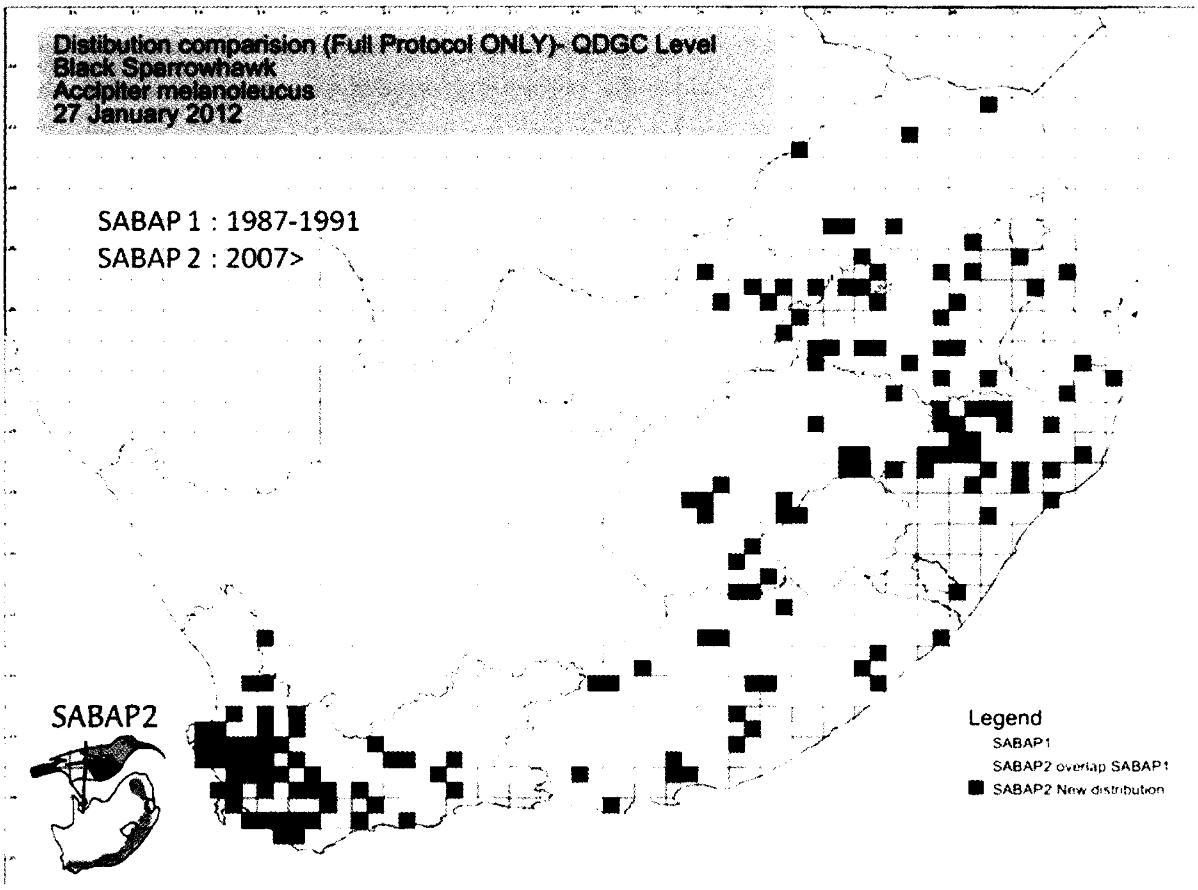
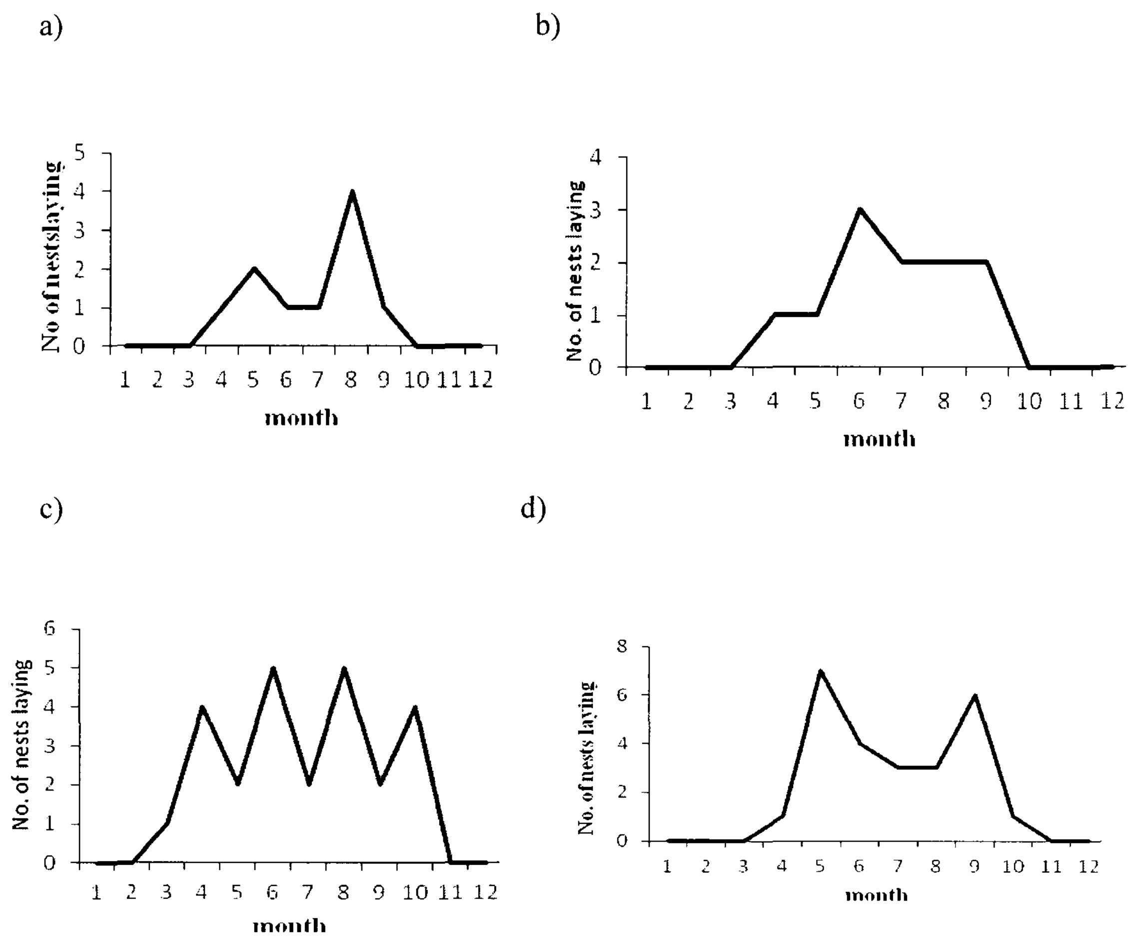
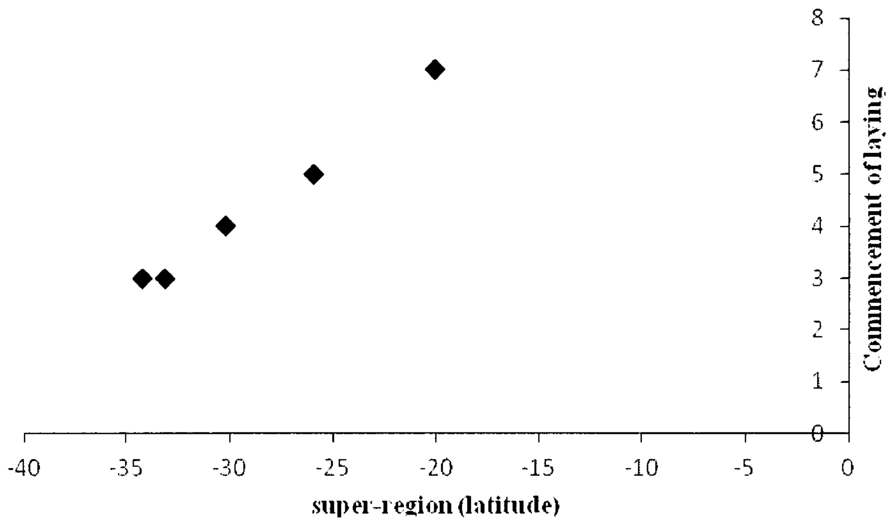
Appendices



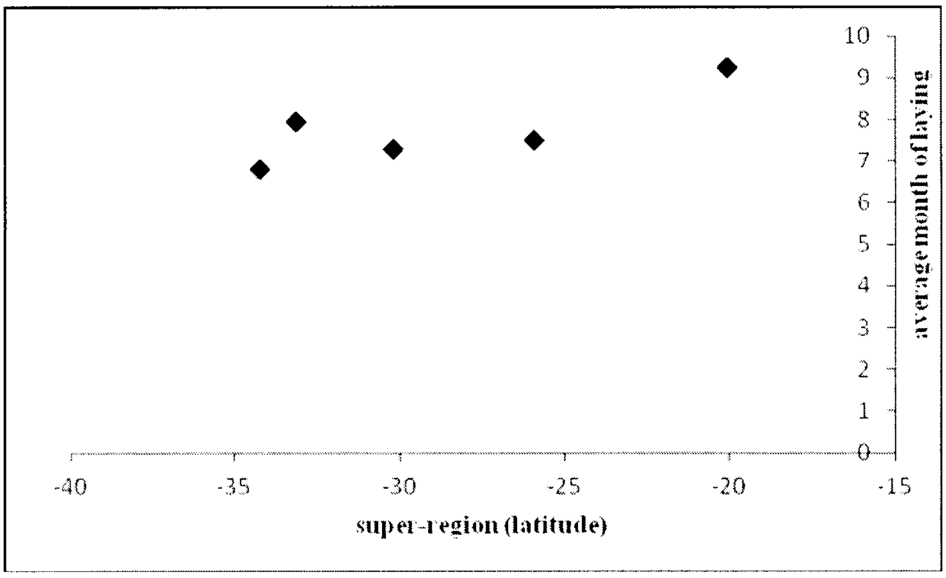
Appendix A. A comparison of Black Sparrowhawk distribution between two bird atlas projects (1987-1991 and 2007 - present), showing westwards range expansion in the species.



Appendix B. Annual variation in lay dates of Black Sparrowhawks on the Cape Peninsula. a) = 2006, b) = 2007 c) =2008 d) =2009.



Appendix C. The relationship between commencement of laying and latitude for Black Sparrowhawks. The latitudes represent the super-regions in their chronological order.

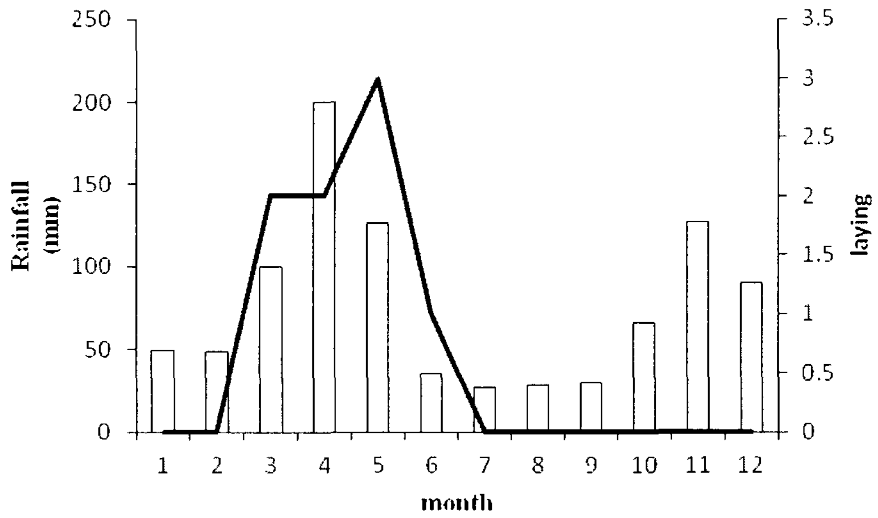


Appendix D. The relationship between altitude and timing of breeding in Black Sparrowhawks in South Africa. The latitudes represent the super-regions in their chronological order.

Appendix E. Parameters used in the population model in program Vortex – parameters and values in bold are different between the populations.

Parameter	**Input value**	
Model settings	Population 1 (without the shift in breeding time)	Population 2 (with the shift in breeding time)
Number of iterations	100	100
Number of years	20	20
Extinction definition	Only 1sex remains	Only 1sex remains
Number of populations	1	1
Inbreeding depression	No	no
Reproductive system		
Pair system	monogamous	monogamous
Age at first breeding (female)	2	2
Age at first breeding (male)	2	2
Maximum age of reproduction	15	15
Maximum number of broods/year	1	1

Maximum number of progeny/year	3	3
Sex ratio at birth (m/f)	50/50	50/50
Density dependent reproduction	No	no
% adult females breeding successful/year	**76**	**80**
EV in% adult females breeding successful/year	**24**	**15**
Mean number of offspring/female/year[1] (± SD)	**1.37 (±0.96)**	**1.5 (±0.98)**
Mortality rates		
% mortality from age 0-1 (juveniles) ± SD	62.5±4.7	62.5±4.7
% mortality from age 1-2 (sub-adults) ± SD	19.2±8.7	19.2±8.7
% mortality from age 1-2 (adults) ± SD	10.5±1.9	10.5±1.9
Initial population structure		
Initial population size	20	20
Stable age structure	Yes	yes
Carrying capacity	200	200



Appendix F. The relationship between rainfall and laying dates in East Africa (Brown 1980).

Appendix G. Breeding season of some Black sparrowhawk prey in the traditional and newly colonised areas.

Species	Traditional areas	Newly colonised areas (Western Cape)
Speckled pigeon	Data not found	September-January
Rock pigeon	throughout the year	September-January
Laughing dove	March-September	September-October
Cape Turtle dove	September-December	September-December
Helmeted Guinea fowl	September-November	September-November

Appendix H. The effect of individual female characteristics and territory on lay date determination. It also shows the effect of each one of these variables (female characteristics and territory) while controlling for the other variable to avoid the confounding effects.

	Df	Sum Sq	MeanSq	F value	AIC	Pvalue
Female	36	273.3	7.593	3.473	514.12	0.001
Territory	32	254.6	7.955	3.479	517.52	0.001
Female + Territory					508.18	
Female	36	273.34	7.593	3.74		0.001
Territory	7	29.22	4.175	2.057		0.0566
Territory + Female					508.18	
Territory	32	254.56	7.955	3.919		0.001
Female	11	48.01	4.365	2.15		0.05