



**WITS**  
UNIVERSITY

**The demography and ecology of  
the European Honey-buzzard  
(*Pernis apivorus*) in southern Africa**


**Caroline Grace Howes**  
909864

A dissertation submitted to the Faculty of Science,  
University of the Witwatersrand, Johannesburg,  
South Africa, in fulfilment of the requirements for  
the degree of Doctor of Philosophy

17 October 2019

# Declaration

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, South Africa. It has not been previously submitted for any degree or examination at any university.



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Caroline Grace Howes  
17 October 2019

**Supervisors:**

Prof. Craig T. Symes, University of the Witwatersrand, Johannesburg, South Africa  
Dr Patrik Byholm, Novia University of Applied Sciences, Ekenäs, Finland  
Dr Jolene Fisher, University of the Witwatersrand, Johannesburg, South Africa

# Abstract

Globally, there have been significant declines in long-distance migratory birds. Over the past three to four decades, this trend has been well documented in Palaearctic migrants, which breed in Europe and winter in Africa. In the case of Palaearctic migrants, there has been a strong research focus on the population trends and breeding statistics in Europe but relatively little research in the African non-breeding regions, particularly with regards to habitat loss and transformation. This is despite evidence from the Neotropics that indicates that the non-breeding season of migratory birds is critical to both their survival and breeding success. It is, therefore, essential to understand the non-breeding period of Palaearctic migrants in Africa to aid in their conservation.

European Honey-buzzard (*Pernis apivorus*) is a Palaearctic migrant that is declining globally but displays an increase in records in the southern African sub-region. Honey-buzzard is an unusual raptor species that specializes in preying upon Hymenoptera larvae. In addition, the species is also a forest specialist, breeding in mature woodland in Europe and spending the non-breeding season in tropical rainforest in Africa. In this thesis, I aimed to examine the causes and consequences of the apparent increase in European Honey-buzzards in southern Africa, in order to assess how both Palaearctic migrants and specialist species may be able to adapt to a rapidly changing world.

To begin (in Chapter 2), I examined the drivers of the increase in records in European Honey-buzzard in southern Africa. As there was no evidence of an increase in the breeding population in Eastern Europe and Russia (where tracked South African honey-buzzards bred), I addressed two hypotheses: i) the growth in birdwatching and citizen science effort in southern Africa was driving the increase in records, and ii) a loss of suitable habitat further north in the honey-buzzards non-breeding range was pushing honey-buzzards further south, and therefore, causing the proliferation of records in southern Africa. There was evidence that increased birdwatching effort accounted for a portion of the growth in European Honey-buzzard records but did not explain the majority of the increase. When assessing both southern African and East African honey-buzzard records, there was a positive correlation over time between forested area in East Africa and the number of East African honey-buzzard records, and a negative correlation between East African forested area and southern African honey-buzzard records. This indicates that with the loss of forest further north in Africa, European Honey-buzzards

have shifted their non-breeding range further south, and the population of honey-buzzards in southern Africa has grown.

In Chapter 3, I assessed the sex and age class ratios of the southern African European Honey-buzzard population over the period of its range shift. The southern African adult honey-buzzard population was overwhelmingly female (93.3%). This supports the *arrival time hypothesis* which predicts that the sex responsible for establishing the breeding territory (male in the honey-buzzard) will winter closer to the breeding grounds than the opposite sex (female in the honey-buzzard). The southern African population had a high proportion of juvenile and second year birds (41.6%). Young birds were more likely to be found in southerly and low elevation locations, likely due to the funnelling effect of Africa on migration. The high proportion of young birds may indicate that they are the drivers of the range shift.

In addition to age and sex ratios, I explored the colour morph ratios of the southern African European Honey-buzzard population in Chapter 4. There were significant differences in the colour morph ratios between ages and sexes. The differences between age classes support the hypothesis that there is temporal morph instability between age classes in European Honey-buzzard. Juvenile birds were disproportionately likely to be of the dark morph while adults were disproportionately likely to be of the dark intermediate morph. There may be a selective advantage for the dark morph for juvenile birds who spend a minimum of two years in Africa.

For Chapter 5, a large tracking dataset ( $n = 32$ ) of European Honey-buzzards was used to assess which habitats were preferred on the non-breeding grounds in Africa, and how the availability and fragmentation of these habitats affected honey-buzzard movement. Adult birds were found to have much higher site fidelity and fewer home ranges than juvenile birds, supporting the hypothesis that juvenile birds are likely to be driving the southwards range shift. As expected, honey-buzzards strongly favoured treed habitats over all other habitats. Lastly, honey-buzzards with a large patch of treed habitat had smaller home ranges than those with a smaller treed patch. At the same time, individuals with higher edge density (a measure of fragmentation) also had smaller home ranges. This may reveal that honey-buzzards have some tolerance for fragmented habitat if they have a large forest patch in which to roost and feed. While the birds are able to survive in these fragmented habitats, they may also be at greater risk of detection by predators, and greater daily energy expenditure due to longer daily flight distances between patches.

Lastly, European Honey-buzzard primary moult timing and location were assessed in Chapter 6, using stable isotope analysis. Photographs of honey-buzzards in southern Africa showed that outer five primaries (P6-P10) were commonly moulted in the sub-region. This

aligns with the period that tracked birds are found in southern Africa. The  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and  $\delta^2\text{H}$  values of the primary feathers were highly variable between the seven individuals tested. To begin, only two adult birds grew primaries in Europe (two and three feathers respectively). Between the outer two and seven of the adult birds' primaries appeared to be grown in southern Africa. All other primaries were grown in other parts of Africa, implying that southern African honey-buzzards are growing primaries while migrating, which may result in increased energy expenditure over this period as well as reduced flight efficiency.

In conclusion, the southwards range shift in European Honey-buzzards has highlighted the complexity of problems facing Palaearctic migrants during the non-breeding season. This specialist has adapted to a novel environment in southern Africa but there are costs involved including longer migration, increased fragmentation of non-breeding habitat, and mistiming of moult. Juveniles are likely driving the movement south; during their two or more years on the African non-breeding grounds, they range widely. This study emphasises the importance of studying migrants on their non-breeding grounds in order to better understand the causes of their declines as well as to develop potential conservation actions.

# Acknowledgements

This thesis has been a true labor of love and while I cannot say that I loved every single minute of it, I can certainly say that it has been a truly incredible (and usually enjoyable) adventure! None of this work would have been possible without an enormous number of people who have contributed their time, expertise, or funds to this project. First and foremost, I would like to thank my three supervisors, Craig Symes, Patrik Byholm, and Jolene Fisher, who have guided me through this process. Craig, your broad ornithological knowledge and keen editor's eye have helped me every step of the way. You have helped me become a better scientist and critical thinker. Patrik, thank you for bringing your incredible expertise on this species (and many others) and its life on the other end of the world. I have learned so much from you, and have thoroughly enjoyed showing you some of South Africa's incredible birds and places on your visits here. Jolene, thank you for stepping in and helping me through the end of this thesis. I truly appreciate your encouragement and input and I have loved being in your lab for the past year.

There are so many people at Wits who have kept me company throughout my time here. I would like to thank Francesca Parrini for her contributions on my research committee. I also have to thank all the tearoom "regulars" who have always kept my spirits up and made me consider new things each and every day. Lastly, I think I would have gone crazy were it not for my labmate, Stephanie Payne. Thank you for all the tea breaks, lunch breaks, coffee breaks, and more. Here's to many more chats in the tearoom and filled Okoa Coffee loyalty cards!

Tracking honey-buzzards from South Africa would have been impossible if not for the help of numerous people. I would like to acknowledge Wildlife Computers for their donation of a tracker to the project as well as the von Frenckell Foundation for its contribution for trackers. I am eternally grateful to the many wildlife rehabilitators, Lorna Stanton, Natasja Saunders of Raptor Rescue, Frith Douglas and Magdali Theron of Dullstroom Bird of Prey Centre, and Nicci Wright, Karin Lourens, and Penny Morkel of the Johannesburg Wildlife Vet, who have carefully rescued honey-buzzards and let us put trackers on them before release as well as donated carcasses to us for stable isotope analysis. I am so lucky to have gotten to meet all of these dedicated people. Lastly, I would like to thank Craig Natrass, a truly extraordinary ringer, who has helped me with tracker deployments and ringing of honey-buzzards.

Tracking data were just one piece of the puzzle and I would be remiss not to recognize all the people who have contributed record data and photographs to this project. First of all,

thank you to all Southern African Bird Atlas Project and Tanzania Bird Atlas contributors for going out collecting bird records. Every record counts and together, you have created a truly staggering database. A big thanks also goes to Trevor Hardaker, the devoted Southern African Rare Bird Newsletter collater. The data from these emails were a true treasure trove! I would also like to acknowledge BirdLife South Africa for the use of their extensive library and the National Rarity Committee database. Lastly, I would like to recognize Mike Butler and all the staff at the iThemba Laboratory for Accelerator Based Sciences' isotope facility for helping me analyse my many stable isotope samples.

To my parents, I cannot thank you enough for all that you have done for me over the course of my education. I know that it is not always easy having me so far away, but your support, encouragement, and reassurance have been invaluable through this entire process.

And last but certainly not least, I truly have to thank my incredible wife. Melissa, I am so grateful for all that you have done for me over the course of this degree. Throughout the last three years, you have joined me in celebrating the highs, and lifted me out of the lows. You have been a sounding board, talking through ideas and rewording titles during dinner and road trips. You have played photographer for every one of my satellite tag deployments and technical support for every one of my talks. I do not know if I can ever express how much your support means to me.

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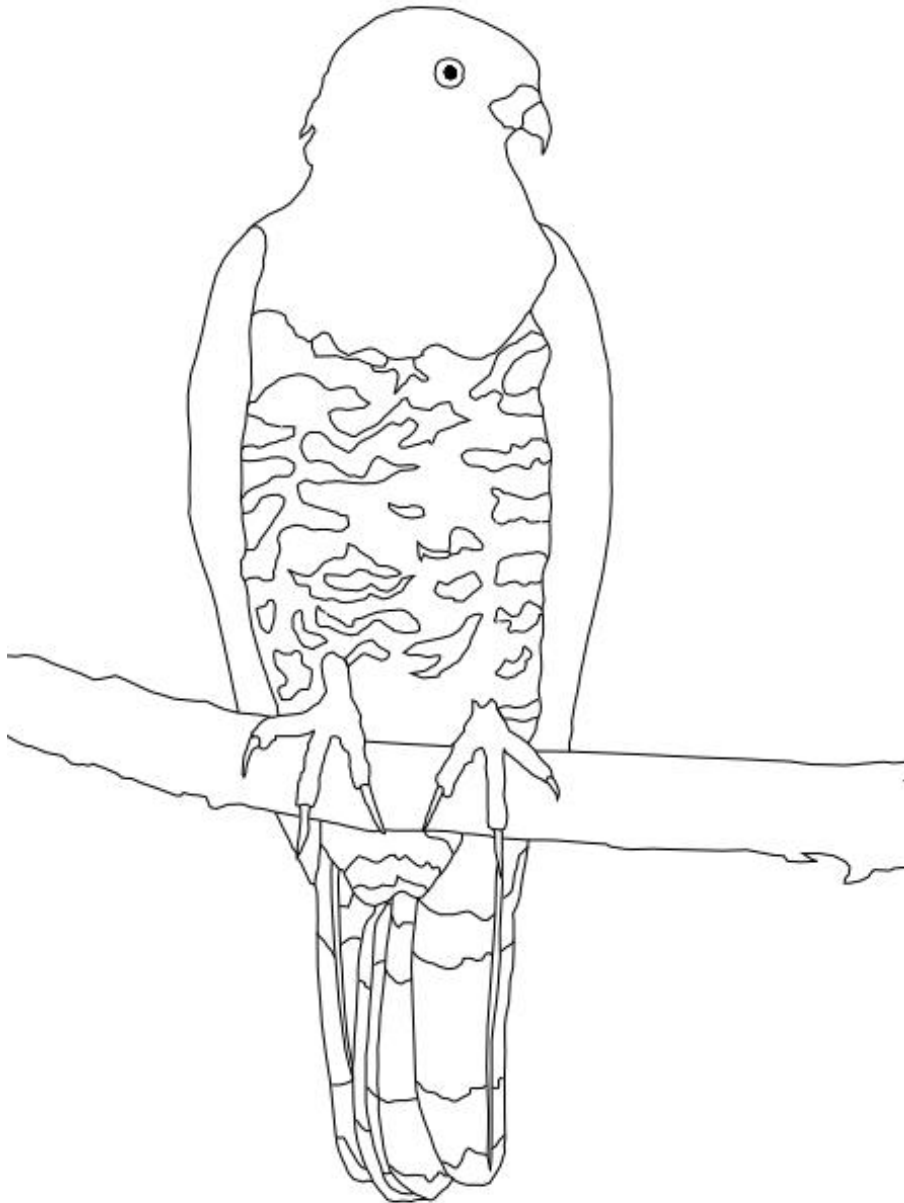
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## Papers arising from this thesis

The following manuscript was published before the submission of this thesis. This manuscript has multiple authors who contributed to the final product. C. Howes was the primary author, and as such, formulated research questions, collected and analysed all data, and wrote the manuscript. C.T. Symes and P. Byholm acted in supervisory roles. They provided guidance related to the theoretical ideas and data analysis of the manuscript, and commented on multiple drafts of the paper.

**Howes, C.,** Symes, C.T., and Byholm, P. 2019. Evidence of large-scale range shift in the distribution of a Palearctic migrant in Africa. *Diversity and Distributions*, 25: 1142-1155.

# **General Introduction**



## 1.1 Rationale

Migratory birds around the world are declining at a rapid rate due to human-caused mortality events, climate change, and habitat loss (Robbins et al. 1989, Sanderson et al. 2006, Thaxter et al. 2010, Vickery et al. 2014). Palaearctic migrants are no exception with many species decreasing by more than 50%, and some species decreasing by more than 80% over the past 30 years (Vickery et al. 2014). While substantial research has taken place on the European breeding grounds of many migrant species, relatively little has been performed on the African non-breeding grounds, leaving a substantial gap in the knowledge of these species (Vickery et al. 2014). This knowledge gap persists despite strong evidence from long-distance Neotropical and short-distance Palaearctic migrants that indicates that quality of non-breeding habitat plays a critical role in the survival and reproduction of migratory birds (Sherry and Holmes 1996, Norris et al. 2004, Gunnarsson et al. 2005, Holmes 2007, Reudink et al. 2009b). Understanding the role of non-breeding habitats on declining Palaearctic migrants is critical to identifying the mechanisms of decline, and in turn, providing conservation solutions to reduce or halt population losses.

Over the past three decades, there has been a surge in the number of records of European Honey-buzzard (*Pernis apivorus*) in southern Africa (Howes et al. 2019). This unique Palaearctic migrant has declined across much of its European breeding grounds despite appearing to increase in southern Africa (Bensusan et al. 2007, IUCN 2019). Honey-buzzard is unusual amongst Palaearctic migrant raptors in that it both breeds and winters in densely forested habitat (Strandberg et al. 2012, Gamauf et al. 2013). In addition, honey-buzzard subsists mainly on wasp and bee (Hymenoptera) larvae although it supplements its diet with birds, frogs, and reptiles (Itämies and Mikkola 1972). All of the factors above make European Honey-buzzard, and in particular the southern African population of honey-buzzard, a unique case study among Palaearctic migrants.

The global environment is currently experiencing change at an unprecedented rate. Species around the world are responding to global change in many ways including range expansion and contraction. As a specialist and a migrant species, the European Honey-buzzard presents a unique lens through which to view the effects of global change on a single species. Research on the honey-buzzard allows for a better understanding of how anthropogenic change on the African continent may be affecting Palaearctic migrants as a whole, as well as an understanding of how specialists may be able to adapt to a rapidly transforming world.

## 1.2 Background

Globally, almost one fifth (1817 species or 18.5% of all species) of all bird species migrate in some form (Rolland et al. 2014). Among these migrants are 97 species of raptors, almost a third (30.0%) of global raptor species, as well as 61.9% (26 species) of Palaearctic raptors (Newton 1998, IUCN 2019). These migrations vary in their scope from short altitudinal migrations of a few hundred kilometres to long trans-hemispheric migrations of tens of thousands of kilometres (Dingle and Drake 2007). Bird migration is often viewed as an adaptation to temporal changes in habitat quality, often seasonally in the case of Northern Hemisphere birds (Dingle and Drake 2007). Moving between suitable habitats on migration allows birds to exploit temporally variable resources on a greater spatial scale.

Migratory birds are found around the world but the highest diversity and proportion are found in the Northern Hemisphere, particularly between 20°N and 55°N (Somveille et al. 2013). Europe is included in this latitudinal band and hosts approximately 126 Afro-Palaearctic migrants (Somveille et al. 2013). These long-distance migrants breed in Europe, and then migrate, generally annually, to Africa. On the African continent, East Africa hosts the highest diversity of Palaearctic migrants with smaller hotspots in the Sahel region and the northern parts of southern Africa (Pearson and Lack 1992, Wisz et al. 2007, Barbet-Massin et al. 2009, Somveille et al. 2013). The majority of these species enter and leave Africa through major flyways in Spain, Italy and the Middle East (Pearson and Lack 1992).

### 1.2.1 Declines in Afro-Palaearctic migrants

Afro-Palaearctic migrant birds are declining more rapidly than short distance migrants or resident species (Sanderson et al. 2006, Heldjberg and Fox 2008, Hewson and Noble 2009, Thaxter et al. 2010). Some of the most common and widespread migrants have more than halved their population over the past 40 years, e.g. European Turtle Dove (*Streptopelia turtur*) (-69%) or Whinchat (*Saxicola rubetra*) (-67%) (Vickery et al. 2014). This trend is not limited to one taxonomic group but is documented in passerines (Passeriformes), raptors (Accipitriformes), doves (Columbiformes), shorebirds (Charadriiformes), and ducks (Anseriformes) (Thiollay 2007, Vickery et al. 2014, Debayle et al. 2017). Despite a large amount of evidence for these declines, there is relatively little understanding of the drivers of these changes (Vickery et al. 2014). Most data assessed have been from Europe, with an emphasis on Western Europe (Vickery et al. 2014). There have been few long-term monitoring

datasets that have examined trends in migrant bird populations in Africa (Vickery et al. 2014). The majority of African studies on migrant species have focused on arid habitats rather than humid woodlands and forest, leaving large gaps in the understanding of many species (Hewson and Noble 2009, Thaxter et al. 2010, Vickery et al. 2014).

The role of threats on the non-breeding grounds of Palaearctic migrants have only been investigated in 27% of all migrant species (Saino et al. 2004, Schaub et al. 2005, Mihoub et al. 2010, Vickery et al. 2014). Based on the current limited data, three main factors in Africa appear to be contributing to the decline in migrants: i) human-caused mortality events (pesticides, infrastructure collision, and hunting), ii) climate change, and iii) habitat transformation (Vickery et al. 2014, Brouchet et al. 2016).

It is well documented that Palaearctic migrants are hunted in large numbers during their passage through the Mediterranean, the Middle East, and North Africa (Baha el Din and Salama 1991, Boutin 2001, McCullough et al. 2009, Brouchet et al. 2016). In some species, hundreds of thousands of individuals are killed or captured annually, e.g. Common Quail (*Coturnix coturnix*), or European Turtle Dove (Baha el Din and Salama 1991, Boutin 2001, Brouchet et al. 2016). In addition, some species are hunted when they arrive on their non-breeding grounds (Debayle et al. 2017). Currently, it is still unclear how widespread hunting of migrants is in Africa (Vickery et al. 2014). Human infrastructure, such as wind turbines, radio masts, and electrical pylons, has also been raised as a possible issue for migrant species during migration and on the non-breeding grounds (Schaub and Pradel 2004, Newton 2006, Carrete et al. 2009). Egyptian Vultures (*Neophron percnopterus*) and White Storks (*Ciconia ciconia*) have both shown population-reducing mortality due to infrastructure (Schaub and Pradel 2004, Carrete et al. 2009). Lastly, pesticide use has been suggested as a mechanism of decline in migratory bird populations (Mullié and Keith 1993). This may be through direct poisoning, as well as through the indirect effect of reduced insect biomass, particularly in the Sahelian region (Mullié and Keith 1993, Byholm et al. 2018).

Climate change has been found to affect Palaearctic migrants in Africa in several ways: i) altering weather conditions during their migrations, ii) driving a phenological mismatch between breeding birds and their prey, and iii) shifting and/or shrinking suitable non-breeding ranges (Vickery et al. 2014). The changes in weather conditions along migratory routes have been shown to affect the timing and speed of migration (Ahola et al. 2004, Hüppop and Winkel 2006, Rubolini et al. 2007, Jones and Cresswell 2009, Robson and Barriocanal 2011). Warmer weather generally leads to earlier and faster migration, although this has not resulted in earlier breeding (Hüppop and Winkel 2006, Jones and Cresswell 2009, Robson and Barriocanal 2011).



This mismatch is likely because of the uneven spatial effects of climate change globally (Jones and Cresswell 2009). The complete effects of these phenological shifts on migration are not fully understood, but these phenological changes may result in discrepancies between peak prey availability and peak breeding efforts, or in changes in arrival times on the breeding grounds leading to lower breeding success (Both et al. 2006, Both et al. 2010, Ockendon et al. 2013).

Another effect of climate change that has been documented in Palaearctic migrants is the phenological mismatch between food requirements and food availability during breeding (Both et al. 2006, Both et al. 2010, Ockendon et al. 2013). This mismatch is driven by uneven change in climate globally; birds experience climatic conditions on the non-breeding grounds which signal them to return to the breeding grounds at an inopportune time (Both et al. 2006, Both et al. 2010, Ockendon et al. 2013). There is significant evidence that temperatures and other climatic conditions on the non-breeding grounds are important signs for birds to move north (Ahola et al. 2004, Newton 2008). Due to significant warming on the non-breeding grounds, birds leave for the breeding grounds early (Both et al. 2006, Both et al. 2010, Ockendon et al. 2013). This early departure from the non-breeding grounds causes birds to arrive earlier on the breeding grounds than is ideal for breeding. Declines in species that are phenologically mismatched are the most extreme in species that breed in more seasonal habitats as well as those with longer migrations, both of which create a narrower window of suitable breeding conditions (Both et al. 2010).

Because many Palaearctic migrants' current ranges in Africa are poorly known or documented, large variations exist in the predictions for range changes or reductions on the continent (Vickery et al. 2014). Distribution models of all Palaearctic migrant passerines predicted that 37 of the 64 species studied would experience a range reduction with 16 of these species showing a decline of 50% or greater (Barbet-Massin et al. 2009). In addition to range shrinkage, ranges (based on the range centroids) were also predicted to move an average of 500 kilometres away from their current range centroid (Barbet-Massin et al. 2009). A similar study of *Sylvia* warblers showed high variation in species responses to future climate change, although the distance between their breeding ranges and non-breeding ranges generally increased significantly (Doswald et al. 2009). The increased distance could have a profound impact on the energy expended during and the timing of migration for these warblers (Doswald et al. 2009). Longer migration distances due to southwards shifts in non-breeding ranges have already been demonstrated in two Palaearctic migrant species, Caspian Tern (*Hydroprogne caspia*) and Western Osprey (*Pandion haliaetus*) (Potvin et al. 2016). However, not all species

have increased their migration distances, some species have shown the opposite trend by spending the non-breeding season closer to their breeding grounds. One example of this would be the Barn Swallow (*Hirundo rustica*) which has shifted its African non-breeding grounds northwards at a rate of three to nine kilometres per year since 1912, bringing it closer to its breeding grounds (Ambrosini et al. 2011).

In addition to climate-driven range changes, habitat changes on the non-breeding grounds are another cause of decline in Afro-Palaeartic migrants due to widespread habitat degradation and fragmentation across Africa (Gonzalez 2001, Tappan et al. 2004, Gaiser et al. 2011, Oduori et al. 2011, Adams et al. 2014). In many parts of the West African Sahel, there has been a marked decline in savanna, woodland, and forest habitats due to clearing for crops and livestock, as well as wood harvesting for charcoal and firewood (Gonzalez 2001, Tappan et al. 2004, Gaiser et al. 2011 Oduori et al. 2011, Hansen et al. 2013). Similar trends have been documented in many of the African arid environments north of the Equator (Gonzalez 2001, Tappan et al. 2004, Gaiser et al. 2011 Oduori et al. 2011). These land cover changes, initially caused by increased human densities have been exacerbated by the effects of climate change (Gaiser et al. 2011). For Palaeartic migrant birds, the habitat quality of the non-breeding grounds is extremely important to the birds continued survival and reproduction (Pearson and Lack 1992, Saino et al. 2004, Schaub et al. 2005, Wilson and Cresswell 2006, Cresswell et al. 2007, Mihoub et al. 2010). Some species have proven relatively robust to the habitat changes on their non-breeding grounds (e.g. Common Whitethroat (*Sylvia communis*)) while other species (e.g. Subalpine Warbler (*S. cantillans*)) have declined in areas where they were previously abundant (Wilson and Cresswell 2006, Cresswell et al. 2007).

### 1.2.2 Importance of non-breeding habitat

High-quality non-breeding habitat increases the survival and breeding success of migrant birds (Sherry and Holmes 1996, Holmes 2007, Rushing et al. 2016). Birds occupying high-quality non-breeding territories with higher food availability gain greater body and fat mass, and have lower stress hormone levels over the non-breeding season (Marra and Holberton 1998, Studds and Marra 2007, Angelier et al. 2009). The advantages of high-quality non-breeding habitat continue on the breeding grounds with greater reproductive success for both male and female birds (Norris et al. 2004, Reudink et al. 2009b, Rushing et al. 2016).

The importance of non-breeding habitat to the survival and breeding of migrant birds has been best documented in Neotropical wood warblers, namely American Redstart

(*Setophaga ruticilla*), Black-throated Blue Warbler (*S. caerulescens*), and Ovenbird (*Seiurus aurocapilla*) (Sherry and Holmes 1996, Holmes 2007, Rushing et al. 2016). In the high-quality non-breeding habitats of American Redstarts, such as mangroves, there is a greater density of arthropods, which in turn allows individuals in these habitats to be fitter in a number of ways (Johnson and Sherry 2001, Brown and Sherry 2006). The high food availability allows birds to gain a greater amount of body and fat mass over the course of the winter (Marra and Holberton 1998, Studds and Marra 2007). In addition, redstarts in higher quality habitats are less prone to the effects of varying rainfall than those in poor habitats (Angelier et al. 2011). This allows individuals in high-quality habitat to remain in a single territory over the non-breeding season with a lower chance of mortality (Parrish and Sherry 1994). Similar trends have been documented in both the Black-throated Blue Warbler and the Ovenbird (Strong and Sherry 2000, Sillett and Holmes 2002, Brown and Sherry 2006). In the Ovenbird, slower flight feather growth has also been documented in birds in lower quality habitats with lower prey biomass (Strong and Sherry 2000).

The effect of non-breeding habitat conditions can impact the breeding fitness of individual migrants. Male American Redstarts in better non-breeding habitats had brighter tail feathers, a feature used in attracting mates (Reudink et al. 2009a). In addition, both male and female redstarts that had wintered in higher quality habitat had greater breeding success the following season (Norris et al. 2004, Reudink et al. 2009b, Rushing et al. 2016). Females were able to raise two extra young, and were able to fledge their young a month earlier (Norris et al. 2004). This is highly significant in a single-clutched species that generally raises only three to five young per breeding season (Norris et al. 2004). Male redstarts from high-quality non-breeding habitats were able to arrive back on the breeding grounds earlier which allowed them to reduce paternity loss to other males, and to increase their probability of multiple mates (Reudink et al. 2009b). This, in turn, allowed them to produce a greater number of offspring than birds that had wintered in poor habitats (Reudink et al. 2009b).

There are few long-term studies on the effects of non-breeding habitat on Palaearctic migrant survival and reproduction with most published work focusing on large-scale, remote sensing datasets (Schaub et al. 2011, Ockendon et al. 2014, Johnston et al. 2016). Sahelian rainfall has proven to be good estimator in terms of survival and return to the breeding grounds for many Palaearctic migrants (Peach et al. 1991, Ockendon et al. 2014, Johnston et al. 2016). The rainfall in the Sahel is likely related to food availability, as has been demonstrated by the trends in the Neotropics. Red-backed Shrikes (*Lanius collurio*) have higher reproductive output after Sahelian non-breeding seasons with higher vegetation greenness, indicated by normalized

difference vegetation index (NDVI) (Schaub et al. 2011). The Red-backed Shrike provides some evidence that improved non-breeding conditions for Palaearctic migrants have similar effects to those documented in Neotropical migrants. The effect of non-breeding habitat is not the same for all species. Blackburn and Cresswell (2015a) documented little effect on the survival of Whinchats (*Saxicola rubetra*) relative to territory quality in Nigeria. The Whinchats, however, were generalist in their habitat choice, perhaps explaining the lack of a habitat quality effect on survival (Blackburn and Cresswell 2015b). In addition, the non-breeding period was documented as a period of low mortality in general (Blackburn and Cresswell 2015a).

### 1.2.3 Southern African migrant birds

Southern Africa supports a large contingent of non-breeding Afro-Palaearctic migrants which make up 14.6% (113 species) of non-pelagic bird species in southern Africa. When vagrants are excluded, Palaearctic species still make up 9.2% (73 species) of regularly-occurring non-pelagic bird species in the sub-region. In the case of southern African raptors, Palaearctic migrants make up 21.5% (14 species) of the sub-region's raptor community. Despite the migrant diversity in southern Africa, Newton (1995) indicates that only 3% of European migrant bird species (six species in total) winter exclusively south of the Equator. This small group is made up of mostly small, insectivorous falcons: Amur Falcon (*Falco amurensis*), Red-footed Falcon (*F. vespertinus*), Sooty Falcon (*F. concolor*), and Eurasian Hobby (*F. subbuteo*), along with two other insectivores: Lesser Grey Shrike (*Lanius minor*), and Icterine Warbler (*Hippolais icterina*) (Newton 1995). Within the southern African sub-region, the highest diversity of Palaearctic migrants is in the northeast, which is made up of well-structured savanna and woodland habitats (Underhill et al. 1998). In contrast, many of the more open habitats, such as the arid Karoo in the west and the central highland grasslands, are less favoured, along with the denser forested habitats scattered throughout the region (Underhill et al. 1998).

Palaearctic migrants begin to arrive in southern Africa in mid-September, although the majority of individuals arrive from late October to December (Underhill et al. 1992). Migrant birds typically arrive in the northern and eastern parts of the sub-region first (Underhill et al. 1992). Most species remain in southern Africa until March or April (Underhill et al. 1992).

Many Palaearctic migrant species have been tracked from Europe to their non-breeding grounds in southern Africa including European Honey-buzzard, Lesser Spotted Eagle (*Clanga*

*pomarina*), European Nightjar (*Caprimulgus europaeus*), European Roller (*Coracias garrulus*), Red-backed Shrike, Barn Swallow, and Great Reed Warbler (*Acrocephalus arundinaceus*) (Meyburg et al. 2004, Tøttrup et al. 2012, Rodríguez-Ruiz et al. 2014, Liechti et al. 2015, Horns et al. 2016, Norevik et al. 2017). These migrants have come from a wide variety of breeding areas including Spain (European Roller), Switzerland (Barn Swallow), Sweden (Red-backed Shrike and European Nightjar), Finland (European Honey-buzzard), Slovakia (Lesser Spotted Eagle), and Turkey (Great Reed Warbler), and have wintered in Namibia, Botswana, Zimbabwe, Mozambique, and South Africa (Meyburg et al. 2004, Tøttrup et al. 2012, Rodríguez-Ruiz et al. 2014, Liechti et al. 2015, Horns et al. 2016, Norevik et al. 2017). Interestingly, these species have been recorded using all three major flyways: i) Gibraltar in Spain, ii) the Italian Peninsula, and iii) the Bosphorus Peninsula in Turkey. Following their Mediterranean and Sahara Desert crossings, almost all of the birds tracked to southern Africa have used stopover sites in the savannas and woodlands of the Sahel, indicating the important link between the vast majority of Palaearctic migrants and the Sahelian region (Meyburg et al. 2004, Tøttrup et al. 2012, Rodríguez-Ruiz et al. 2014, Horns et al. 2016, Norevik et al. 2017). Once these European migrants arrive in southern Africa, most species (with the exception of Great Reed Warbler and European Honey-buzzard) rely on the savannas and woodlands of the sub-region as indicated by Underhill et al. (1998).

#### 1.2.4 European Honey-buzzard biology

The European Honey-buzzard is a medium-sized, Palaearctic migratory raptor (Figure 1.1) (Hockey et al. 2005). It is both sexually dimorphic in size (male = 510-940 g, female = 530-1,050 g), and dichromatic (Forsman and Shirihai 1997, Hockey et al. 2005). In addition to its sexual dichromatism, it also has polymorphic plumage at all ages with chests, bellies, flanks, and underwings ranging from pure white to completely brown, with various mottled patterns in between (Forsman and Shirihai 1997, Hockey et al. 2005). Due to the extreme phenotypic variability of the species, they are often confused with *Buteo* buzzards, as well as other medium-sized brown raptors (Forsman and Shirihai 1997, Hockey et al. 2005). However, their pigeon-like heads, relatively small bills, and distinctive tail and wing barring separate them from other raptor species (Forsman and Shirihai 1997, Hockey et al. 2005).

The European Honey-buzzard breeds throughout Europe from Spain and the United Kingdom in the west to western Russia in the east, and from Scandinavia in the north to Italy, Spain, Greece and Turkey in the south (Roberts et al. 1999, Batten 2001, Hockey et al. 2005).

In Europe, they are generally found in densely wooded habitats ranging from entirely deciduous to completely coniferous forests (Forsman and Solonen 1984, Roberts et al. 1999, Gamauf et al. 2013). After breeding, honey-buzzards complete a trans-Saharan migration to mainly western and central Africa, where they spend the Northern Hemisphere winter (Strandberg et al. 2012). In these regions, they are found in tropical woodlands and forest (Strandberg et al. 2012). A minority of European Honey-buzzards spend their non-breeding season in East and southern Africa (Cramp and Simmons 1979).



*Figure 1.1:* An adult male, dark intermediate morph European Honey-buzzard (*Pernis apivorus*). Photo by Lukas Pich.

Currently, the population estimate of the European Honey-buzzard is between 280,000 and 420,000 mature individuals (IUCN 2019). However, this is likely an underestimate as approximately 500,000 birds migrate through Batumi, Georgia, annually (Batumi Raptor Count 2017). Globally, the European Honey-buzzard is a species of Least Concern due to its relatively large population and wide range (IUCN 2019). However, it is experiencing declines in many European breeding populations (Bensusan et al. 2007, IUCN 2019). A total of thirteen European countries have assessed its conservation status using IUCN criteria with another two nations using alternate methods. Of the thirteen countries, one lists the species as Critically Endangered, two list it as Endangered, three list it as Vulnerable, three list it as Near Threatened, three list it as Least Concern, and one lists it as Insufficiently Known. The declines in the species have been attributed to various threats including habitat loss on its breeding and

non-breeding grounds, increases in nest predators such as Northern Goshawk (*Accipiter gentilis*), intensification in the use of pesticides, and persecution (particularly on its migration) (Kostrzewa 1987, Löhmus 2005, Gamauf et al. 2013, Byholm et al. 2018, IUCN 2019).

#### 1.2.4.1 Feeding ecology of European Honey-buzzard

The vast majority of European Honey-buzzard diet is made up of Hymenoptera insects (Lack 1946, Itämies and Mikkola 1972, Kostrzewa 1989, Gamauf 1999). When nine honey-buzzard gizzards were dissected, nearly 100% of the contents were Hymenoptera (Itämies and Mikkola 1972). In Austria, 81.8% of the species diet was made up of Hymenoptera (76.4% wasps and 5.4% bumble bees) (Kostrzewa 1989). Honey-buzzards eat both larval and adult wasps and bees (Itämies and Mikkola 1972). However, they disproportionately target wasps, particularly the genus *Vespula*, whilst avoiding *Vespa* and *Polistes* species (Itämies and Mikkola 1972). In South Africa (on their non-breeding grounds), they have been recorded feeding on invasive *Vespula* wasps as well as bird nestlings (Oettle 2014, C. Howes pers. obs.). Not only do the adults eat wasps but the majority of the chicks' diet also is made up of wasps (Itämies and Mikkola 1972, Kostrzewa 1989, Gamauf 1999). Because of this, the breeding success of European Honey-buzzards is linked to wasp availability, which in turn is controlled by climatological factors (Kostrzewa 1989). Honey-buzzards are able to avoid competition with many of the other forest bird species due to their specialized diet (Lack 1946).

In addition to feeding on Hymenoptera, European Honey-buzzards also supplement their diet with a variety of vertebrate prey (Lack 1946, Itämies and Mikkola 1972). In an Austrian study of nest remains, 7.5% of individual honey-buzzard prey was frogs (generally Common Frog (*Rana temporaria*)), 1.1% was lizards, and 6.3% was birds (Gamauf 1999). No mammal remains were recorded (Gamauf 1999). Nests were more likely to contain other prey remains early in the breeding season, perhaps because wasps and bees had not yet emerged (Itämies and Mikkola 1972). The European Honey-buzzard has been observed eating a wide variety of bird species (mostly nestlings). These species include Common Wood-pigeon (*Columba palumbus*), Willow Warbler (*Phyllocopus trochilus*), Eurasian Golden Oriole (*Oriolus oriolus*), Eurasian Jay (*Garrulus glandarius*), and several species of *Turdus* thrushes (Itämies and Mikkola 1972, Gamauf 1999). Honey-buzzards are accomplished nest robbers, eating not only nestlings but also occasionally eggs (Itämies and Mikkola 1972, Gamauf 1999).

#### *1.2.4.2 Breeding biology of the European Honey-buzzard*

The European Honey-buzzard breeds exclusively in the forests of the Palaearctic region (Forsman and Solonen 1984, Roberts et al. 1999, Gamauf et al. 2013). Their exact breeding habitat is variable depending on the region in which they are located (Forsman and Solonen 1984, Roberts et al. 1999, Gamauf et al. 2013). Nesting habitat preferences have been best described in Germany, Estonia, and Sweden with some smaller studies being conducted in Britain and Finland (Forsman and Solonen 1984, Kostrzewa 1987, Amcoff et al. 1994, Roberts et al. 1999, Hakkarainen et al. 2004, Löhmus 2005, Gamauf et al. 2013). In Germany, the biggest driver of nest site selection was Northern Goshawk presence with European Honey-buzzards tending to avoid breeding near goshawk nests (likely in an effort to avoid nest predation) (Kostrzewa 1987). However, in Finland, there was no effect of goshawks on honey-buzzard nest selection, perhaps due to a lower goshawk population density, and therefore, a lower chance of goshawk encounter in Finland in comparison with Germany (Hakkarainen et al. 2004).

In addition to choosing areas far from goshawks, European Honey-buzzards in Germany and Sweden tended to select for wider woodland areas, but did not avoid areas of human disturbance (Kostrzewa 1987, Amcoff et al. 1994). The lack of effect of human disturbance was also documented in Estonia, where breeding pairs were not affected directly by human presence but were affected by poor forest management (i.e. management that caused large-scale forest change) (Löhmus 2005). This relationship was also reflected in honey-buzzards' preference for old growth forests over plantations and younger forests (Löhmus 2005). However, in some parts of their range, honey-buzzards showed little habitat preference, and were found in a wide variety of forests ranging from natural deciduous forests to plantation coniferous forests, perhaps indicating some flexibility in their habitat selection (Roberts et al. 1999). The density of breeding pairs varies across the European continent and between years with values of 0.8-1.9 pairs per 100 km<sup>2</sup> recorded in one German study, 8-9 pairs per 100 km<sup>2</sup> and 26 pairs per 100 km<sup>2</sup> in two regions in a second German study (Kostrzewa 1989), and 9-11 pairs per 100 km<sup>2</sup> in Finland (Forsman and Solonen 1984). There have not been any estimates of honey-buzzard breeding densities published more recently, and therefore, the current densities of breeding birds may be substantially different than previously documented.

Once European Honey-buzzards have selected their territory, they defend the area from other pairs (Cramp and Simmons 1979). They perform a unique wing display over their forest patches to advertise their presence (Cramp and Simmons 1979). Nest building begins quickly



as the birds have little time on their breeding grounds, only 110-135 days per year (Cramp and Simmons 1979). European Honey-buzzards build their own twig nest and regularly line it with greenery during the breeding cycle (Cramp and Simmons 1979). The nest-building process takes between ten and fifteen days (Cramp and Simmons 1979). After the nest is built, the female honey-buzzard lays one to three (usually two) eggs and incubates them for 30-35 days (Cramp and Simmons 1979). When the chicks hatch, the female broods and feeds them for the first seven to ten days, while the male hunts for food (Cramp and Simmons 1979). Once the young are older, both parents forage, and deposit food at the nest for the chicks (Figure 1.2) (Cramp and Simmons 1979). The chicks fledge at 40-44 days and are fed by the parents for another ten to fifteen days after leaving the nest (Cramp and Simmons 1979). The total breeding period ranges from 105-119 days (Cramp and Simmons 1979).



Figure 1.2: A male European Honey-buzzard (*Pernis apivorus*) on its nest with two nestlings. Photo by Stanislav Harvancik.

Fledging rate is highly variable across the birds' breeding range. The lowest success rates were recorded by Kostrezwa (1989) in Germany with values ranging from 0.1 fledglings per breeding attempt in poor years and 1.1 fledglings per attempt in good years. Generally, there is only one breeding attempt per season. Sweden had a particularly low average of 0.30 fledglings per breeding attempt (Tjernberg and Ryttman 1994). Another study in Germany

recorded of 1.17 fledglings per attempt and 1.23 fledglings per attempt in two separate regions (Batten 2001). The highest success recorded was 1.66 fledglings per attempt in the United Kingdom (Roberts et al. 1999). The spring weather plays a role in honey-buzzard nesting success (Kostrzewa 1989). In years where spring was particularly cold or wet (likely delaying the emergence of wasps and bees), honey-buzzard nesting success declined significantly (Kostrzewa 1989).

#### *1.2.4.3 European Honey-buzzard migration*

European Honey-buzzards migrate from their European breeding grounds to their African non-breeding habitats. Adults do so annually while juvenile birds usually remain in Africa for at least two years before returning for their first breeding attempt (Strandberg et al. 2012). Adult birds have high site fidelity to both their breeding and non-breeding locations, as well as their migration routes (Hake et al. 2003, Strandberg et al. 2012). Adults and juveniles show very different migration strategies (Hake et al. 2003, Agostini 2004, Strandberg et al. 2009). Adults tend to take longer routes with shorter sea crossings while juveniles take more direct paths with longer sea crossings (Hake et al. 2003). In addition, the juvenile birds leave later than the adults, fly shorter distances per day, and take longer to arrive at the non-breeding areas (Hake et al. 2003). Juvenile birds are also strongly influenced by the wind patterns which push them longitudinally, and strongly affect where in sub-Saharan Africa they initially arrive (Vansteelant et al. 2017). Adults took an average of 42 days to complete their migration from southwestern Sweden to West Africa, while juveniles took 64 days (Hake et al. 2003). Adults moved 163 km per day on migration, while juveniles travelled 104 km per day (Hake et al. 2003). Juveniles are less likely to have been migrating with the prevailing winds, and more likely to spend time using energy-inefficient flapping during long water crossings (Hake et al. 2003, Agostini 2004).

When migrating, the majority of adult honey-buzzards take one of four major migratory routes (the Gibraltar, Italian, and Bosphorus peninsulas, and the east coast of the Black Sea), each of which passes through a bottleneck (Figure 1.3) (Agostini et al. 1994, Bruderer et al. 1994, Agostini and Panuccio 2005, Agostini et al. 2005, Agostini et al. 2007a, Agostini et al. 2007b, Bensusan et al. 2007, Batumi Raptor Count 2017). The adults also perform a loop migration, which means that they do not take the same route when migrating southwards as they do when migrating northwards (Hake et al. 2003). The less experienced juveniles generally do not use the typical migration routes of the adults (Hake et al. 2003).



*Figure 1.3: A flock of European Honey-buzzards (*Pernis apivorus*) migrating through Eilat, Israel. Photo by Jonathon Meyrav.*

#### *1.2.4.4 European Honey-buzzard non-breeding behaviour*

Currently, very little is known about European Honey-buzzards' non-breeding behaviour in Africa. Few papers have been published on honey-buzzard movements during the Palaearctic winter, and have examined only juvenile behaviour (Strandberg et al. 2012, Vansteelant et al. 2017). However, many migration tracking papers do note that adult birds tend to have high site fidelity to their non-breeding territory, and that they move very little on their non-breeding grounds (Hake et al. 2003, Strandberg et al. 2009, Strandberg et al. 2012). Juveniles have a contrasting strategy with much greater movement (Strandberg et al. 2012). They begin by crossing the Sahara Desert in northern Africa (well after adult honey-buzzards) before stopping in the Sahelian savanna zone in order to feed and regain body condition (Strandberg et al. 2012). After their initial stopover, they head directly south to the coastal zones of West Africa before moving east and settling in a foraging range (Strandberg et al. 2012). They remain in Africa for at least two years before returning to Europe to breed (Strandberg et al. 2012, Vansteelant et al. 2017). The juveniles' ranging behaviour may relate to three factors according to Strandberg et al. (2012). The first hypothesis is that the change in

weather over the year drives juveniles' movements; they are hypothesized to be following the rain as it moves east. The second idea is that their ranging is a prospecting behaviour with the young birds choosing the best location for future non-breeding territories. The final hypothesis is that this behaviour is due to lack of appropriate habitat because of massive deforestation in the region (Strandberg et al. 2012). The adults have already occupied the best feeding areas leaving the young birds to be pushed between them. In all likelihood, it is a combination of all three hypotheses (Strandberg et al. 2012).

### *1.3 Aims and Objectives*

The aim of this study was to examine the causes and consequences of range change on the African non-breeding grounds of a specialist Palaearctic migrant, the European Honey-buzzard (*Pernis apivorus*), by examining its demographics, migratory origins, habitats, and movement behaviours.

The objectives were as follows:

1. To examine the apparent increase in the European Honey-buzzard population in southern Africa using citizen science data, and to assess whether the growth in records was due to: i) an intensification of birdwatching and citizen science in the sub-region, or ii) changes further north in the honey-buzzards range that have driven a southwards range shift in the species.
2. To assess the sex, age class, and colour morph ratios of the southern African European Honey-buzzard population in order to better understand the species sex and age class segregation, and colour morph adaptations on the non-breeding grounds and how these demographics may be affecting or driving the apparent range shift of the species.
3. To determine which habitat types are preferred by European Honey-buzzard on the non-breeding grounds, and how the availability of this habitat and its fragmentation may affect the movement patterns of this specialist species.
4. To establish the spatiotemporal patterns of primary moult in the migratory European Honey-buzzard using stable light isotopes, and to evaluate what these patterns indicate about the species migration and non-breeding movements.

#### 1.4 Thesis organisation and products

The five research chapters of this thesis were each written as standalone scientific papers. Due to this, there is repetition between these chapters, particularly in their introductions. The third data chapter (Chapter 4) was written as a short communication as it was split from the second data chapter (Chapter 3) during the journal submission and review process. An introduction chapter, with a literature review, presents and contextualises the thesis, and a concluding synthesis chapter assesses the drivers of the range shift in European Honey-buzzard, and discusses how this knowledge can be applied to other Palaeartic migrant bird species. The five research chapters are as follows:

1. Evidence of large-scale range shift in the distribution of a Palaeartic migrant in Africa (published in *Diversity and Distributions*; IF: 4.092)
2. Highly skewed sex and age ratios of European Honey-buzzard in southern Africa (revised and resubmitted to *Journal of Ornithology*; IF: 1.472)
3. Temporal morph instability in European Honey-buzzard (*Pernis apivorus*) (for submission to *Bird Study*; IF: 1.124)
4. Forest availability and fragmentation drive movement behaviour of non-breeding European Honey-buzzard (*Pernis apivorus*) in Africa (submitted to *Ardea*; IF: 1.125)
5. Evidence of primary moult during the extended migration of a Palaeartic raptor using stable isotope analyses (for submission to *Ibis*; IF: 1.994)

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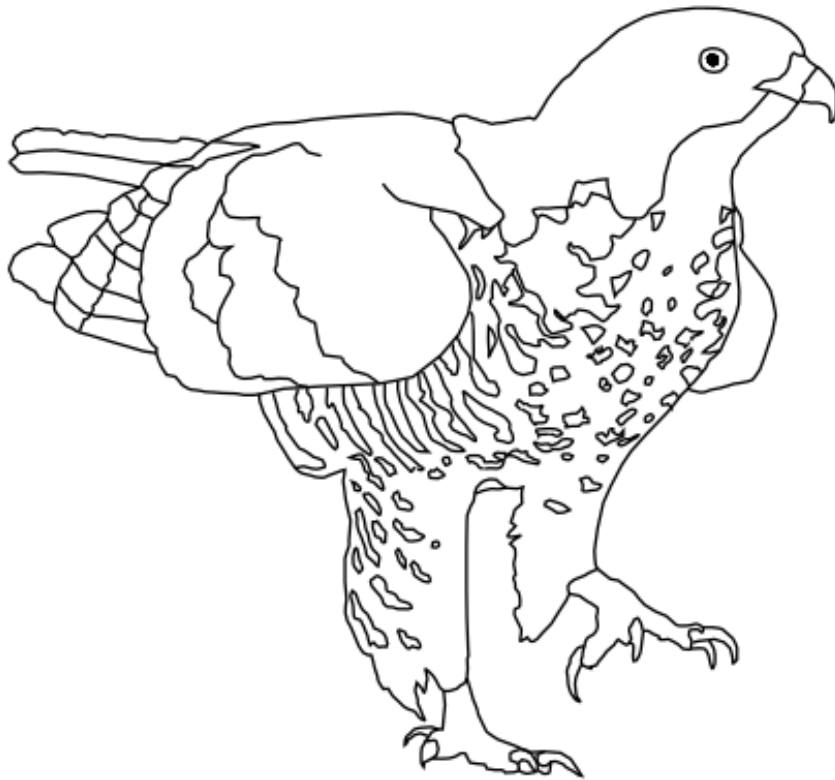


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# Evidence of large-scale range shift in the distribution of a Palaeartic migrant in Africa



## *Abstract*

Long-distance Palaearctic migrant birds are declining at a faster rate than short-distance migrant or resident species. This is often attributed to changes on their non-breeding grounds and along their migratory routes. The European Honey-buzzard (*Pernis apivorus*) is a scarce migrant in southern Africa that is declining globally. This study assessed the distribution and abundance of honey-buzzards in southern Africa over the past four decades, and compared it to trends in the East African population to examine possible drivers of population expansion in southern Africa. European Honey-buzzard reporting data from southern and East Africa were collected from a variety of sources including citizen science databases (1983-2017). In addition, records of all other southern African vagrants (including ten other regularly occurring species) were gathered to account for changes in birdwatching effort in the sub-region. To assess the effect of forest loss on honey-buzzard abundance, rolling correlations were performed using forest cover in East Africa, and number of honey-buzzard records in both sub-regions. European Honey-buzzard records in southern Africa have increased over five times more than other regularly occurring vagrant species, and almost 40 times more than honey-buzzard in Tanzania where the population has remained stable. Loss of forested area in East Africa was correlated with an increase in European Honey-buzzard records in southern Africa. We suggest that the shift in European Honey-buzzard wintering range may be driven by a decline in suitable habitat further north in Africa amongst other possible reasons. This effect may have been amplified by an increase in appropriate habitat across southern Africa brought about by anthropogenic changes to vegetation such as increased tree cover in urban areas. This study further highlights the importance of using African distributional data banks to understand the effects of global change on Palaearctic migrant bird species.

*Keywords:* birdwatching, citizen science, forest loss, European Honey-buzzard, *Pernis apivorus*, population shift, range change, range expansion, southern Africa

## *2.1 Introduction*

It is important that migratory birds select non-breeding sites beneficial to both their breeding success and survival (Norris et al. 2003, Saino et al. 2004, Gunnarsson et al. 2005). Given this, the low migratory connectivity (birds breeding in close proximity in Europe migrating to vastly different locations in Africa) of many Palaearctic migrant bird species

indicates that multiple factors affect where birds migrate post-fledging or post-breeding (Thorup et al. 2003, Finch et al. 2017).

Previous research has shown that wind patterns *en route* and habitat quality affect where migrating birds establish non-breeding territories (Richardson 1990, Norris et al. 2003, Thorup et al. 2003, Saino et al. 2004, Gunnarsson et al. 2005, Vansteelant et al. 2017). Adult birds are more able to account and correct for the effects of wind, but inexperienced juveniles, who are likely not navigating to a specific location, are not as able to rectify their direction (Thorup et al. 2003). The direction and strength of the wind is likely to have a large effect on where young birds initially arrive in sub-Saharan Africa (Vansteelant et al. 2017). However, it is not clear how this may affect where they eventually settle.

Habitat quality in the non-breeding season has also been shown to have strong effect on both survival and breeding success in Neotropical and Palaearctic migrants (Norris et al. 2003, Saino et al. 2004, Gunnarsson et al. 2005). For example, more productive non-breeding territories have been shown to correlate with earlier arrival and better breeding territories in American Redstart (*Setophaga ruticilla*) (Norris et al. 2003). The same is true for Icelandic Black-tailed Godwits (*Limosa limosa*); individuals that spent the non-breeding season in more productive coastal habitats had higher quality breeding sites and better breeding success than those that selected less productive inland non-breeding locations (Gunnarsson et al. 2005). Once a productive site is located, many adult migratory birds, particularly long-lived species such as raptors and waterbirds, return to the same non-breeding site year after year (Cresswell 2014). It is believed that returning to known suitable sites benefits long-term survival by reducing mortality risk during the non-breeding season (Cresswell 2014). These sites are likely to be located during juvenile exploratory movements earlier in life, which allow the bird to find more suitable locations (Cresswell 2014).

Long-distance Palaearctic migrant bird species are declining at a faster rate than both short-distance migrant and resident species (Sanderson et al. 2006, Thaxter et al. 2010, Vickery et al. 2014). This is believed to be due to change in climate and habitat degradation on both the breeding and wintering grounds as well as mortality during migration. A study of British migrant birds reflected this trend with Afrotropical migrants declining more rapidly than species spending their winters in the United Kingdom or other parts of Europe (e.g. residents and short-distance migrants) (Thaxter et al. 2010). From 1986-2006, species that spent the non-breeding season in the humid West African forest and savanna declined at a greater rate than those in the more arid northern zone of Africa (Thaxter et al. 2010). This may be due to large-

scale habitat loss and fragmentation from forest clearing, and intensification of agriculture in this region (Thaxter et al. 2010).

The European Honey-buzzard (*Pernis apivorus* Linnaeus 1758) is a Palearctic raptor that migrates annually from its breeding grounds in Europe to its non-breeding grounds in Africa (Cramp and Simmons 1979). This dietary specialist breeds in dense forest where it feeds mostly on wasps and bees (Hymenoptera) with frogs (Anura) as an important alternate prey (Itämies and Mikkola 1972, Gamauf 1999). Following breeding (or fledging in the case of juvenile birds), honey-buzzards migrate south *en masse* (Cramp and Simmons 1979). It is thought that the vast majority of birds spend the Northern Hemisphere winter in the tropical rainforests of west and central Africa with a small proportion migrating to East and southern Africa (Bruderer et al. 1994, Hake et al. 2003, Agostini et al. 2007).

While the European Honey-buzzard is listed as a species of Least Concern by the IUCN, it has declined across Western Europe and Scandinavia over the past 30 years (Kostrzewa 1987, Löhmus 2005, Benusan et al. 2007, IUCN 2019). This may be due to habitat transformation and loss on both the breeding grounds in Europe as well as the non-breeding grounds in Africa (Kostrzewa 1987, Löhmus 2005, Benusan et al. 2007). Persecution during migration also plays a role in the decline (Brochet et al. 2016). Migration counts at Gibraltar in Spain and Batumi in Georgia show stable or declining numbers of honey-buzzards passing annually (Benusan et al. 2007, Batumi Raptor Count 2017).

The European Honey-buzzard is generally considered a scarce migrant to southern Africa (Cramp and Simmons 1979, Hockey and Ryan 2005). Over the past three decades, the number of reported records of this species has appeared to increase. This study aimed to examine the drivers of the apparent increase in the European Honey-buzzard population in southern Africa using citizen science data. We assessed two hypotheses: i) the growth in records was due to an intensification of birdwatching and citizen science in the southern African sub-region, and ii) the changes further north in the honey-buzzards range (e.g. habitat loss) have driven the range shift in the European Honey-buzzard, and have consequently caused an expansion in the southern African population.

## 2.2 Methods

### 2.2.1 Southern African rarity record collection

European Honey-buzzard records in southern and East Africa were collected from a variety of sources. East African records were selected for comparison based on tracking data which indicate that most southern African honey-buzzards migrate from the eastern portion of their breeding range and travel through East Africa on their way to and from southern Africa (Howes, Byholm, and Symes, unpubl. data).

To begin, eight museums were surveyed to determine if they had European Honey-buzzard specimens from southern and East Africa. These museums were: i) American Museum of Natural History (New York, NY, U.S.A.), ii) Ditsong Museums of South Africa (Pretoria, South Africa), iii) Field Museum (Chicago, IL, U.S.A.), iv) Iziko Museums (Cape Town, South Africa), v) Museum für Naturkunde (Berlin, Germany), vi) Royal Museum for Central Africa (Tervuren, Belgium), vii) Smithsonian National Museum of Natural History (Washington D.C., U.S.A.), and v) Natural History Museum at Tring (Tring, U.K.). Only records with spatial and temporal information were included.

Southern African honey-buzzard records were collected from the three following sources. The Southern African Rare Bird Newsletter (SARBN), which covered from July 2008 to July 2017, contributed the greatest number of southern African records. This is a bi-weekly email list-server which informs birdwatchers about rare bird species in the southern African sub-region. A total of 2,320 emails were examined in the SARBN Google Group. The second source was the National Rarity Committee (NRC), which assesses and records rarities in southern Africa. It provided records from January 1982 to December 2002. Records were also sourced from the Zest for Birds website which covered January 2002 to December 2010. This site documents photos and information on rare species in southern Africa, and spans the time gap between NRC and SARBN coverage.

In addition to European Honey-buzzard records, southern African rarity records for all sub-region rarities were also collected from SARBN, the NRC, and the Zest for Birds website. Pelagic rarities were excluded. The total number of rarity records provided a measure of observer effort over the study period. The ten most regularly occurring migrant rarities were assessed to examine whether records of all vagrant species were increasing due to increased observer skill and effort in the sub-region. Each of the ten occurred at a rate of above one record per season. They included one migrant raptor species, Western Marsh-harrier (*Circus*



*aeruginosus*), and nine migrant shorebird species: American Golden Plover (*Pluvialis dominica*), Pacific Golden Plover (*Pluvialis fulva*), Black-tailed Godwit (*Limosa limosa*), Red-necked Phalarope (*Phalaropus lobatus*), Red Phalarope (*Phalaropus fulicarius*), Common Redshank (*Tringa totanus*), Green Sandpiper (*T. ochropus*), Eurasian Oystercatcher (*Haematopus ostralegus*), and Pectoral Sandpiper (*Calidris melanotos*).

### 2.2.2 Southern African Bird Atlas data collection

The Southern African Bird Atlas Project (SABAP) is a collection of bird distribution data collected by citizen scientists (SABAP 2 2018). It is divided into two parts, SABAP 1 and SABAP 2, which use different protocols and spatial scales. SABAP 1 occurred from 1987-1991, while SABAP 2 is ongoing since 2007. SABAP 1 was collected by quarter degree grid cell (QDGC) and SABAP 2 is collected by pentad (Bonnievie 2011). A pentad is one ninth of a QDGC, and is a 15-minute by 15-minute grid (approximately 9 km by 9 km). SABAP 1 had sampling periods of two to seven days in a QDGC during which all bird species heard or seen were recorded (Bonnievie 2011). All SABAP 1 data were used. SABAP 2 has three classes of data of which we used only full protocol data. A full protocol atlas card for SABAP 2 is a minimum of two hours and a maximum of five days in a given pentad. Every bird species seen or heard during this period is recorded. Cards are then submitted, and the reporting rate of each species is calculated using the total number of species records divided by the total number of full protocol cards for each pentad. The data for European Honey-buzzard were downloaded by species as SABAP 1 vs. SABAP 2 reporting rates at a QDGC level in August 2017.

In addition, SABAP 1 vs. SABAP 2 data for Forest Buzzard (*Buteo trizonatus*) were also downloaded for the same period. This species appears to have similar habitat requirements to European Honey-buzzard, as well as presenting a challenging identification to many birdwatchers. Therefore, it is the ideal species to compare with European Honey-buzzard in terms of range expansion in order to provide a quality check of the atlas data.

### 2.2.3 Tanzanian Bird Atlas data collection

For East Africa, European Honey-buzzard records from the Tanzania Bird Atlas were obtained on 15 October 2017 (TBA 2017). Tanzania Bird Atlas data were selected due to their long time series and generally good spatial cover. Only records from 1983 to 2017 were included in analyses, corresponding to the time scale of the southern African dataset.

#### 2.2.4 European Honey-buzzard record analysis

For all records of European Honey-buzzard from southern Africa and East Africa, the date and location were recorded and catalogued. Repeat records, based on date and location, were removed from analysis. The records were then plotted spatially in ArcGIS 10.3. A QDGC grid was plotted over the records, and the records were extracted to the grid to understand the distribution of honey-buzzards spatially and temporally. The data were grouped seasonally from July to June to include the full non-breeding season of the European Honey-buzzard. Total records per season were compared for each sub-region over time.

To examine the effect of observer effort on the number of southern African records, the total number of European Honey-buzzard records per season was divided by the total number of rarity records per season. This was then plotted to assess whether observer effort accounted for changes in the number of records over time.

#### 2.2.5 Southern African rarity record analysis

Records of the other ten southern African vagrant species examined were similarly plotted over seasons (July-June), a period covering an entire Austral summer period. In addition, the annual number of records for each species, as well as European Honey-buzzard, was compared before and after SARBN using a Wilcoxon rank sum test to determine the effect of increased birdwatching effort and communication on reporting rate.

In order to assess whether trends in European Honey-buzzard numbers differed significantly from other vagrant species, a generalised linear mixed model for number of annual vagrant records was created. Species was the random variable. The fixed variables were year, *perapi*, a binomial variable indicating whether or not the species was European Honey-buzzard, and an interaction term between year and *perapi*. The model was created using the 'glmer' function (with a Poisson distribution) from the package 'lme4' in R. The function 'confint' was used to determine 95% confidence intervals for all fixed variables. Confidence intervals that did not overlap with zero were taken to be significant.

#### 2.2.6 Southern African Bird Atlas data analysis

For both European Honey-buzzard and Forest Buzzard in South Africa, the number of QDGCs in each reporting rate change category (SABAP 1 only, decrease in SABAP 2, increase

in SABAP 2, and SABAP 2 only) was compared using a  $\chi^2$  test to determine whether the two species showed similar changes in range and reporting rate between the two periods. Only South Africa was assessed as Forest Buzzard does not occur in the other southern African countries.

### 2.2.7 Global Forest Change data collection and analysis

Global Forest Change 2000-2016 data layers were downloaded for East Africa (Burundi, Kenya, Rwanda, Tanzania, and Uganda), where there is a large amount of suitable habitat for the European Honey-buzzard (Hansen et al. 2013). The two datasets included in these analyses were the forest cover for the year 2000, and the year of gross forest loss. Pixels (30 m by 30 m) were defined as forest if there was over 30% cover, as was defined in the forest loss layer (Hansen et al. 2013). The total area of forest for the sub-region was calculated, and the amount of forest loss annually was subtracted from previous year's total forest area.

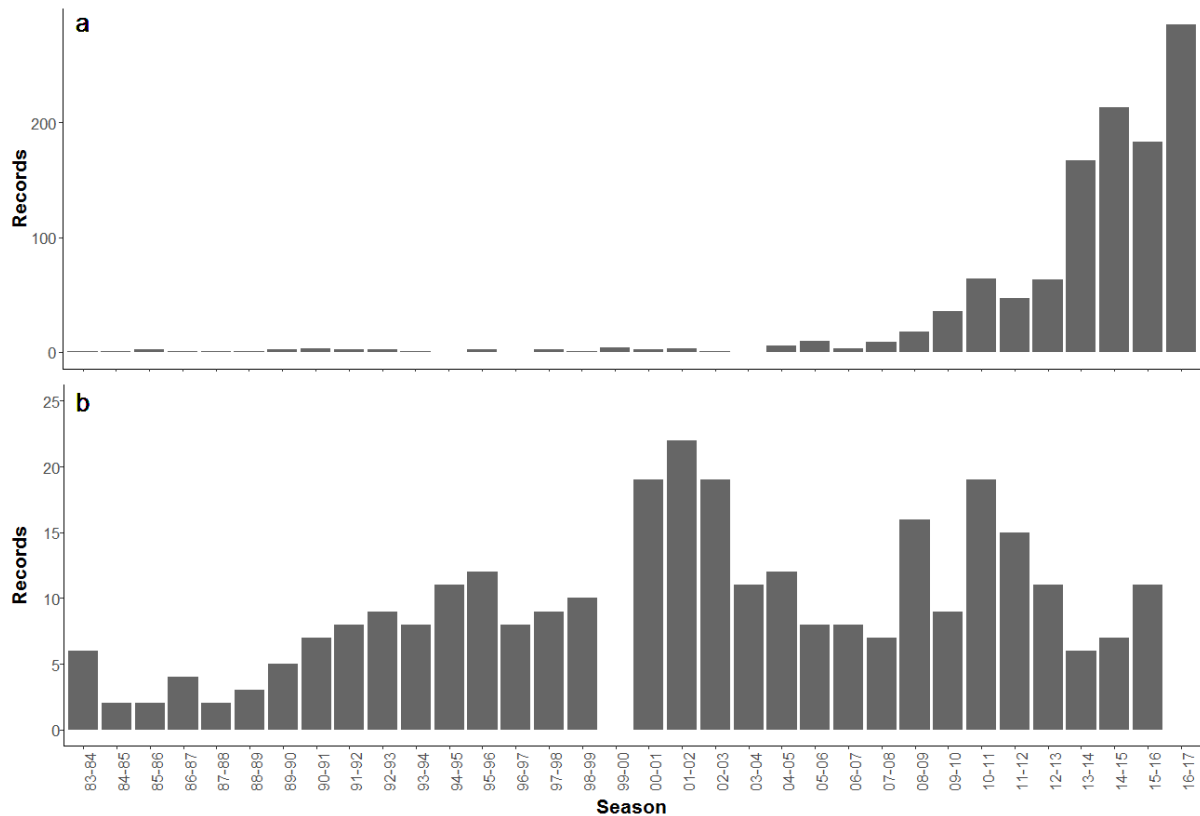
Rolling correlations were created for the relationship between the annual number of honey-buzzard records in southern Africa and the annual number of honey-buzzard records in Tanzania to assess the relationship between the two populations over time. Rolling correlations were also calculated for: i) the relationship between the annual number of Tanzanian honey-buzzard records with the total forested area in East Africa, and ii) the annual number of southern African honey-buzzard records with the total forested area in East Africa. Lastly, rolling correlations for the association of the total forested area in East Africa with the proportion of southern African rarity records that were European Honey-buzzards were computed in order to assess how observer effort affected the relationship. A rolling correlation is a time series analysis which uses a moving window (in this case time) to assess the correlation of two variables during that window. This was used to determine how the relationships between the two populations as well as the two populations and habitat availability may have changed over time. The rolling correlations were calculated, using the R package 'roll', for seven different intervals ranging from three years (the minimum number of points for a correlation) to nine years. Different intervals were used because a species response to altered habitat, particularly that of a habitat specialist, is not usually immediate (Uezu and Metzger 2016). For all time intervals, a minimum of three points was required to include a correlation value. The  $R^2$  values for each window were plotted for the last year of that window.

### 2.3 Results

Nine southern African European Honey-buzzard specimens were found in three of the eight museums (Supplementary Information Table S2.1). These specimens were collected as early as 1894. Six specimens were from South Africa, and three were from Zimbabwe. Eight specimens from three museums were from East Africa. The first specimen was collected between 1895 and 1897. Six specimens were from Kenya, and three were from Tanzania.

A total of 1,136 records of European Honey-buzzard in southern Africa were obtained from three different sources from December 1983 to May 2017. The majority of records (91% or 1,030 records) were collected from SARBN, followed by 7% (78 records) from the Zest for Birds website, and 2% (28 records) from NRC documents. Over the same period, the Tanzania Bird Atlas collected 306 records for Tanzania.

There has been a notable increase in the number of European Honey-buzzard records in southern Africa with sharp increases in the 2005-2006 (67% increase from the previous season), 2010-2011 (78% increase), 2013-2014 (165% increase), and 2016-2017 (56% increase) seasons (Figure 2.1a). The greatest number of honey-buzzard records in Tanzania was in the 2001-2002 season (Figure 2.1b). There were not sharp increases in the Tanzanian records over the study period.



*Figure 2.1:* The number of European Honey-buzzard (*Pernis apivorus*) records from birdwatching sources (South African Rare Bird Newsletter, Zest for Birds, National Rarity Committee, and Tanzania Bird Atlas) in: a) southern Africa and b) Tanzania between December 1983 and May 2017. Note the different y-axis scales.

The number of QDGCs with a European Honey-buzzard record has also increased in southern Africa over the past 30 years (Figure 2.2; Supporting Information Figure S2.1). The number of QDGCs with honey-buzzard records increased in Tanzania until the 2000s before it declined in the 2010s. In the 1980s and 1990s, honey-buzzards occurred in 0.1% ( $n = 6$ ) and 0.3% ( $n = 16$ ) of southern African QDGCs respectively. In these same periods, European Honey-buzzard was reported in 1.0% ( $n = 14$ ) and 3.0% ( $n = 41$ ) of Tanzanian QDGCs. In the 2000s in southern Africa, this increased to 0.9% ( $n = 45$ ) of QDGCs followed by an increase to 5.8% ( $n = 291$ ) of QDGCs in the 2010s. In Tanzania, the number of QDGCs with honey-buzzards peaked with 5.3% ( $n = 72$ ) in the 2000s, and then dropped to 2.8% ( $n = 38$ ) in the 2010s.

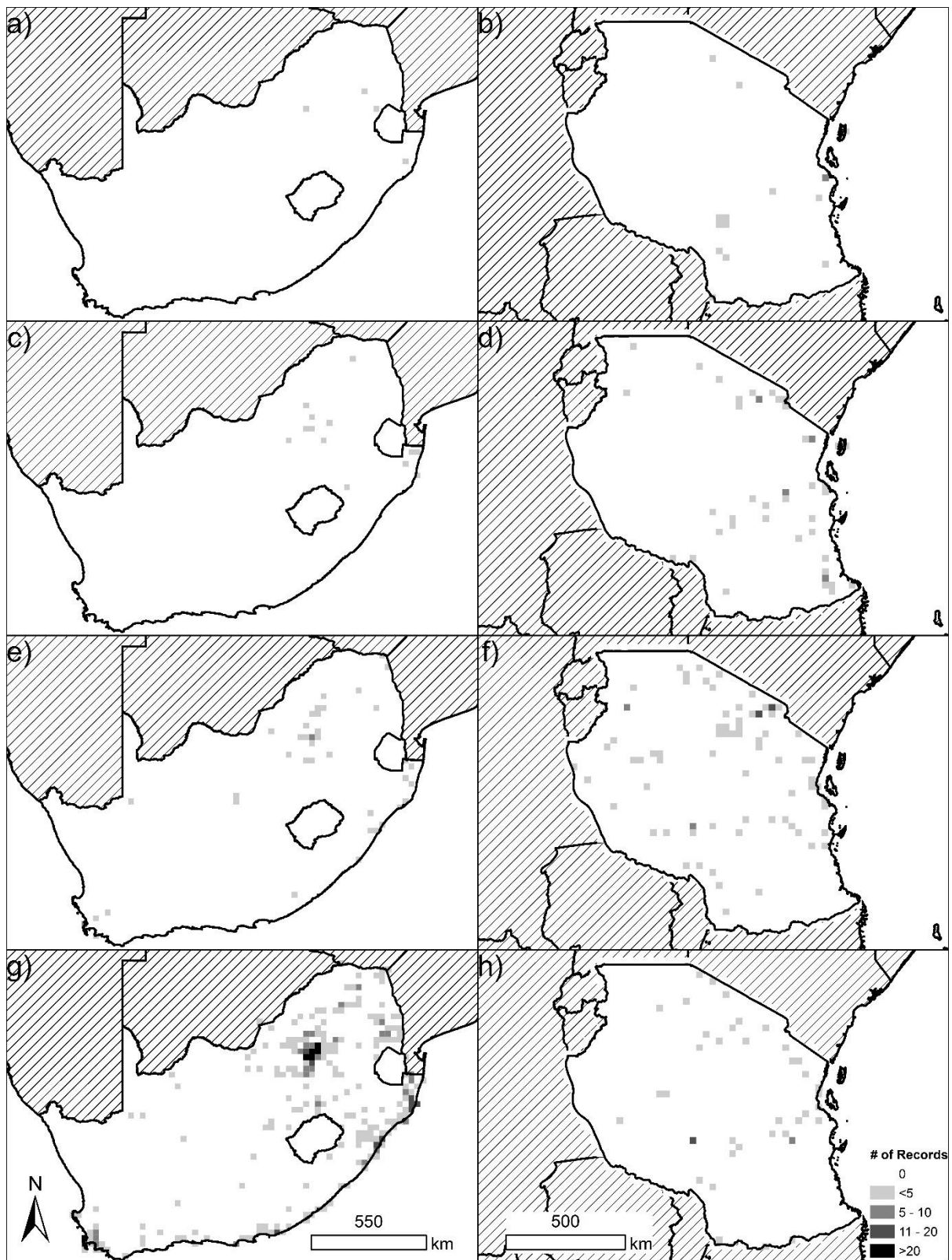


Figure 2.2: The number of European Honey-buzzard (*Pernis apivorus*) records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) in quarter degree grid cells (QDGCs) in South Africa during: a) 1983-1989 (5 QDGCs, 0.3%), c) 1990-1999 (15 QDGCs, 0.8%), e) 2000-2009 (40 QDGCs, 2.0%), and g) 2010-2017 (229 QDGCs, 11.6%), and in Tanzania in: b) 1983-1989 (14 QDGCs, 1.0%), d) 1990-1999 (41 QDGCs, 3.0%), f) 2000-2009 (72 QDGCs, 5.4%), and h) 2010-2017 (38 QDGCs, 2.8%).

A total of 2,517 sub-region rarity records of 87 species were assessed (Supporting Information Table S2.2). The three most common species were European Honey-buzzard ( $n = 1,094$ ), Green Sandpiper ( $n = 179$ ), and Pectoral Sandpiper ( $n = 96$ ). The annual number of rarity records has consistently increased over time with the greatest number of records documented in the 2016-2017 season ( $n = 433$ ) (Figure 2.3a). The proportion of European Honey-buzzard records has also increased over time with a similar pattern to the total number of honey-buzzard records (Figure 2.3b).

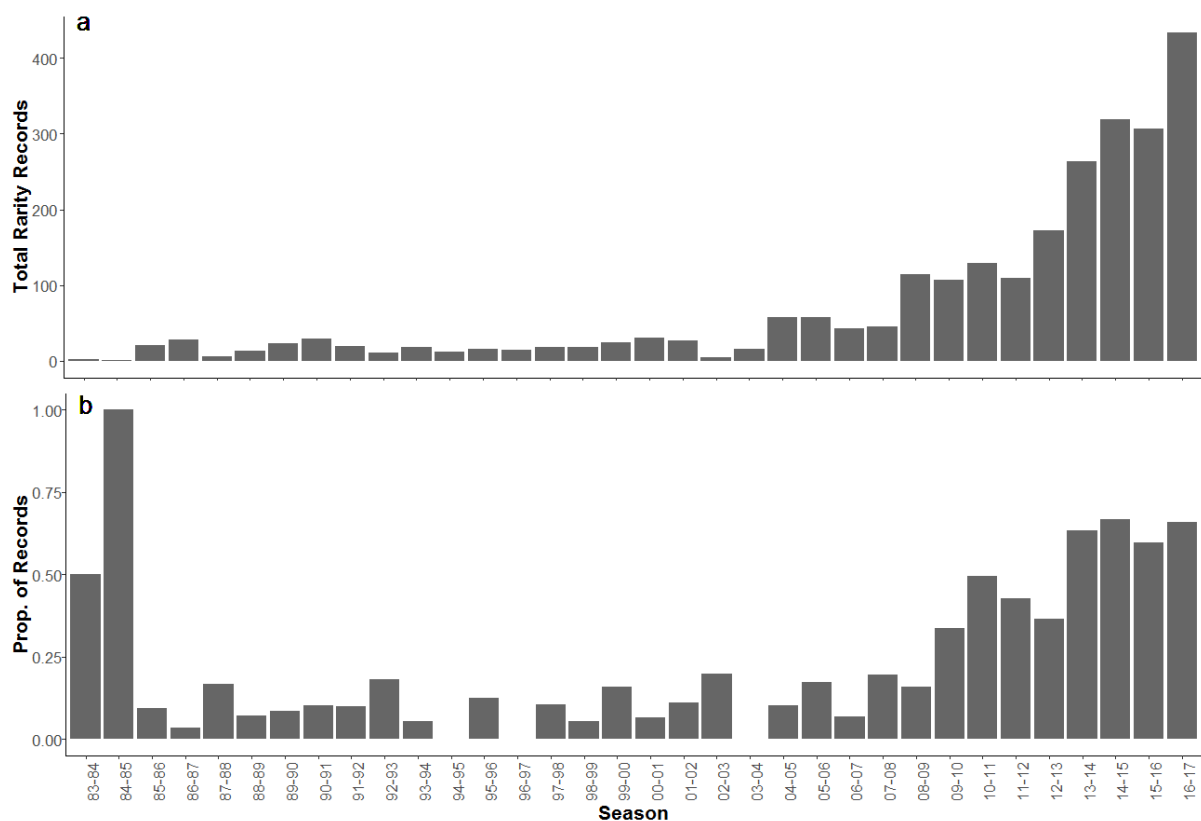


Figure 2.3: The: a) total number of sub-region rarity records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee), and b) the proportion of European Honey-buzzard (*Pernis apivorus*) records out of the total number of rarity records between December 1983 and May 2017.

### 2.3.1 Comparison of European Honey-buzzard and other rare bird species in southern Africa.

Of the rare species examined, all eleven showed a significant increase in southern Africa between the annual number of records before and after the introduction of SARBN (Table 2.1). There was no significant difference in the Tanzanian honey-buzzard records. European Honey-buzzard in southern Africa showed the greatest increase of the species examined, followed by Green Sandpiper and Red Phalarope. Western Marsh-harrier (the

species that is most phylogenetically similar to European Honey-buzzard, and with the most similar life history and distribution) showed only a modest increase in comparison to honey-buzzard.

*Table 2.1:* Eleven “vagrant” southern African bird species as well as European Honey-buzzard (*Pernis apivorus*) in Tanzania with the total number of accepted records, the average number of annual records ( $\pm$  standard error) before (August 1982-July 2007) and after (August 2007-July 2017) the Southern African Rare Bird Newsletter, and the increase factor (i.e. how many times the average annual number of records has increased post-SARBN). Kruskal-Wallis test p-values of pre-SARBN average annual records vs. post-SARBN average annual records: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

Species	Total records (1982-2017)	Avg. annual records (pre-SARBN)	Avg. annual records (post-SARBN)	Increase factor
European Honey-buzzard (Southern Africa)	1,133	2.31 $\pm$ 0.49	119.22 $\pm$ 31.29	51.66***
Green Sandpiper ( <i>Tringa ochropus</i> )	202	1.73 $\pm$ 0.37	17.44 $\pm$ 1.97	10.08***
Red Phalarope ( <i>Phalaropus fulicarius</i> )	78	0.77 $\pm$ 0.28	6.44 $\pm$ 0.88	8.38***
Eurasian Oystercatcher ( <i>Haematopus ostralegus</i> )	66	0.84 $\pm$ 0.18	4.89 $\pm$ 0.67	5.78***
Pectoral Sandpiper ( <i>Calidris melanotos</i> )	101	1.35 $\pm$ 0.27	7.33 $\pm$ 2.04	5.45***
Western Marsh-harrier ( <i>Circus aeruginosus</i> )	77	1.23 $\pm$ 0.29	5.00 $\pm$ 0.53	4.06***
American Golden Plover ( <i>Pluvialis dominica</i> )	50	0.85 $\pm$ 0.19	3.11 $\pm$ 0.61	3.68***
Red-necked Phalarope ( <i>Phalaropus lobatus</i> )	43	0.77 $\pm$ 0.27	2.56 $\pm$ 0.38	3.32***
Pacific Golden Plover ( <i>Pluvialis fulva</i> )	45	0.85 $\pm$ 0.28	2.56 $\pm$ 0.69	3.02**
Black-tailed Godwit ( <i>Limosa limosa</i> )	52	1.04 $\pm$ 0.26	2.78 $\pm$ 0.66	2.67*
Common Redshank ( <i>Tringa totanus</i> )	72	1.50 $\pm$ 0.26	3.67 $\pm$ 0.47	2.44***
European Honey-buzzard (Tanzania)	302	8.51 $\pm$ 1.19	11.22 $\pm$ 1.52	1.32

Two of the three fixed variables in the rarity record generalised linear mixed effects model had confidence intervals that did not overlap with zero: i) year, and ii) the interaction term between year and the binary variable (*perapi*) that indicates if the species is European Honey-buzzard (Table 2.2). Both Western Marsh-harrier and Green Sandpiper showed a longer and less drastic increase over time than European Honey-buzzard over the same period as is indicated by the interaction term (Figure 2.4).



Table 2.2: Generalised linear mixed model selection results for number of rarity records in southern Africa for eleven bird species from December 1983 to May 2017. The model includes species as the random effect and all fixed variables are scaled. Estimate = variable slope, SE = standard error, and 95% CI = 95% confidence interval. See methods for definitions of model covariates.

Variable	Estimate	SE	95% CI
Intercept	0.32	0.14	0.03 to 0.62
as.factor( <i>perapi</i> )	0.42	0.45	-0.53 to 1.39
scale(year)	0.90	0.04	0.82 to 0.99
as.factor( <i>perapi</i> ):scale(year)	2.01	0.10	1.82 to 2.21

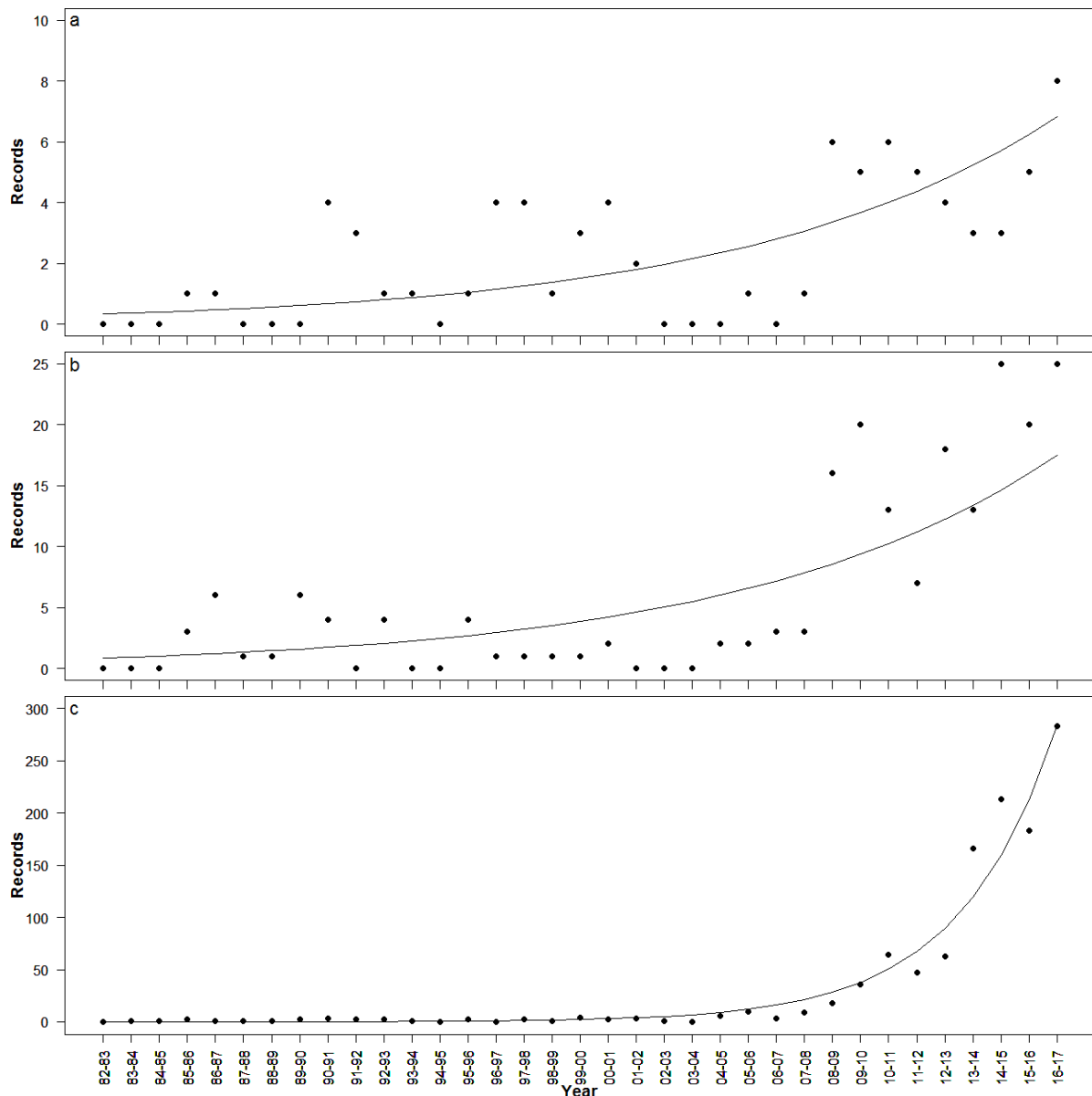


Figure 2.4: The annual number of records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) for three bird species in southern Africa: a) Western Marsh-harrier (*Circus aeruginosus*), b) Green Sandpiper (*Tringa ochropus*), and c) European Honey-buzzard (*Pernis apivorus*) from August 1982 to May 2017. Lines represent the generalised linear mixed model (described in Table 2.2) for each species. Note the different y-axis scales for each species.

### 2.3.2 Comparison of European Honey-buzzard and Forest Buzzard SABAP data

The European Honey-buzzard had a significantly greater proportion of pentads with an increase between SABAP 1 and SABAP 2 than the Forest Buzzard ( $\chi^2(3) = 155.16, p < 0.01$ ). The majority (80%) of QDGCs with European Honey-buzzard were new in SABAP 2 while Forest Buzzard had smaller percentage (25%) of new QDGCs (Supporting Information Figure S2.2).

### 2.3.3 Correlations of European Honey-buzzard records in southern Africa and Tanzania

The five-year interval rolling correlation between southern African and Tanzanian records showed the strongest negative correlation during the 1980s, and the strongest positive correlation during the 2010s (Figure 2.5). The 1990s and 2000s showed very weak correlations. The trends were similar for rolling correlation intervals ranging from five to nine years (Supporting Information Figure S2.3).

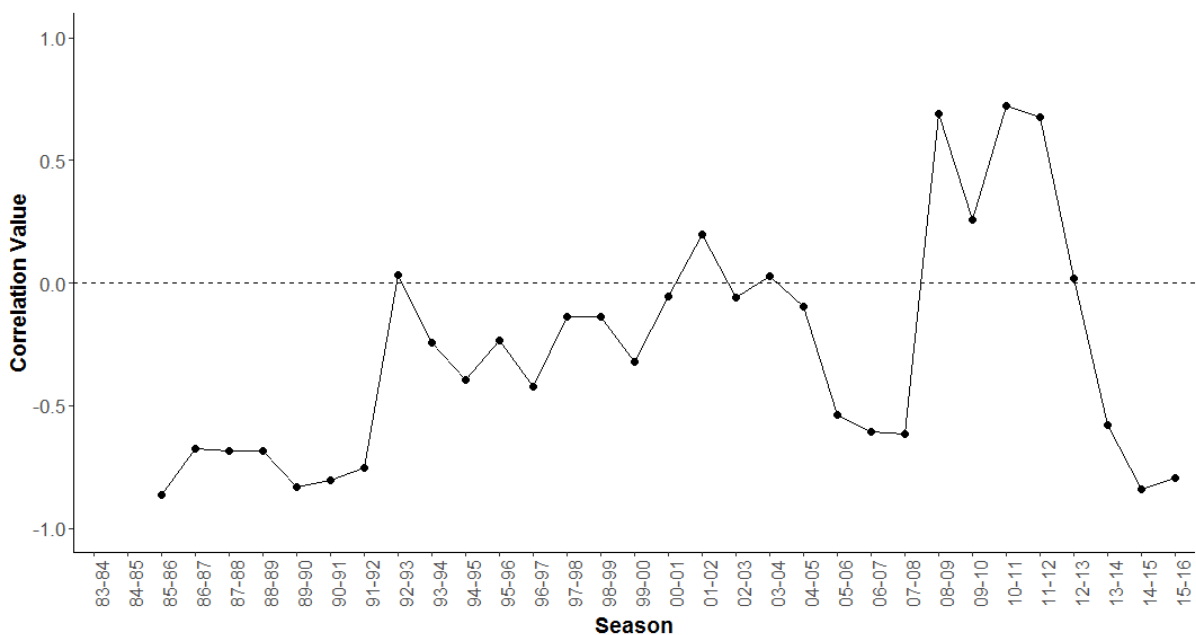


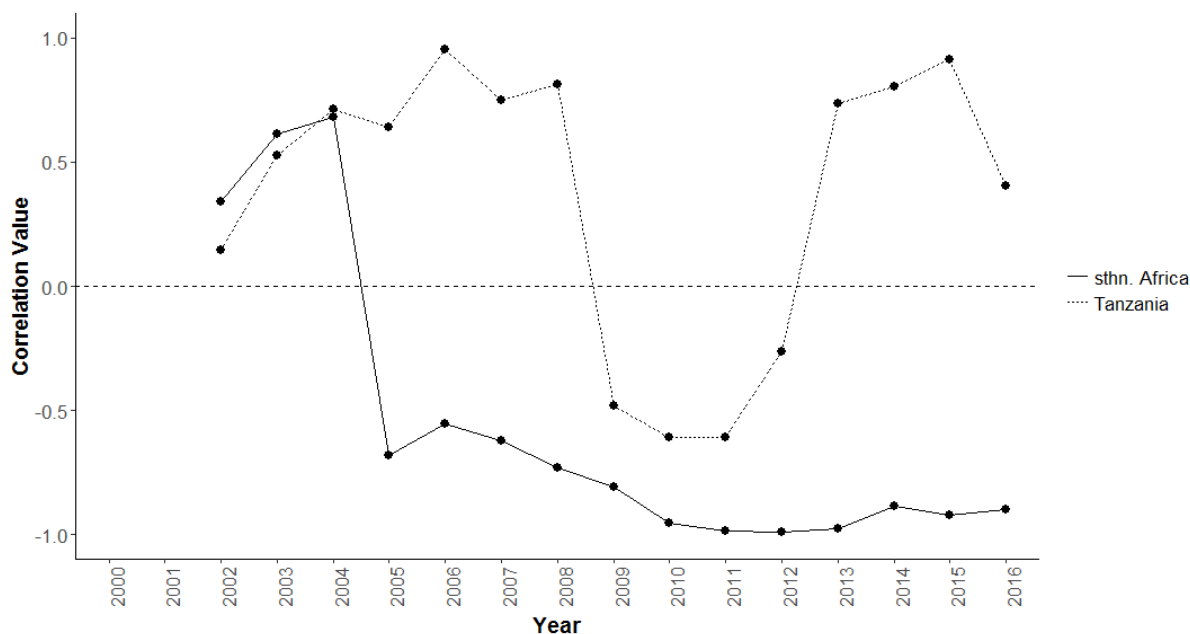
Figure 2.5: The relationship between European Honey-buzzard (*Pernis apivorus*) records in southern Africa and Tanzania from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, National Rarity Committee, and Tanzania Bird Atlas) showing a five-year rolling correlation between the number of southern African records and the number of Tanzanian records per season.

Over the 16 years assessed, there was an 11.6% (46,367.0 km<sup>2</sup>) loss of forest area in East Africa (Table 2.3). The majority of the forest loss (66.2%) was in Tanzania.

*Table 2.3:* The total area of forest in East Africa in 2000 and 2016 along with the total forest area loss and the percent forest change during this period. The percent of regional loss indicates what proportion of the total forest area loss in the region occurred in that country/countries. URB = Uganda, Rwanda, and Burundi.

Country	Forest area 2000 (km <sup>2</sup> )	Forest area 2016 (km <sup>2</sup> )	Forest area loss (km <sup>2</sup> )	% forest change	% of regional loss
Tanzania	264,597.3	233,912.0	30,685.3	-11.6	66.2
Kenya	90,093.9	81,611.9	8,432.0	-9.4	18.2
URB	45,558.4	38,308.7	7,249.7	-15.9	15.6
<b>Total</b>	<b>400,249.6</b>	<b>353,882.6</b>	<b>46,367.0</b>	<b>-11.6</b>	<b>100</b>

Southern African honey-buzzard records showed a strong negative correlation with forest coverage in East Africa, starting in 2005 (Figure 2.6). Tanzanian honey-buzzard records generally showed a strong positive correlation with East African forest cover except from 2009 to 2012. The trends for both regions were similar for intervals ranging from five to nine years (Supporting Information Figures S2.4-S2.5). The proportion of southern African rarity records that were European Honey-buzzards, had a strong negative correlation with East African forest coverage beginning in 2008 (Figure 2.7). The trend was similar for intervals ranging from five to nine years (Supporting Information Figure S2.6).



*Figure 2.6:* A five-year rolling correlation between square kilometres of forest in East Africa from Global Forest Change and the number of European Honey-buzzard (*Pernis apivorus*) records in both southern Africa and Tanzania from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, National Rarity Committee, and Tanzania Bird Atlas).

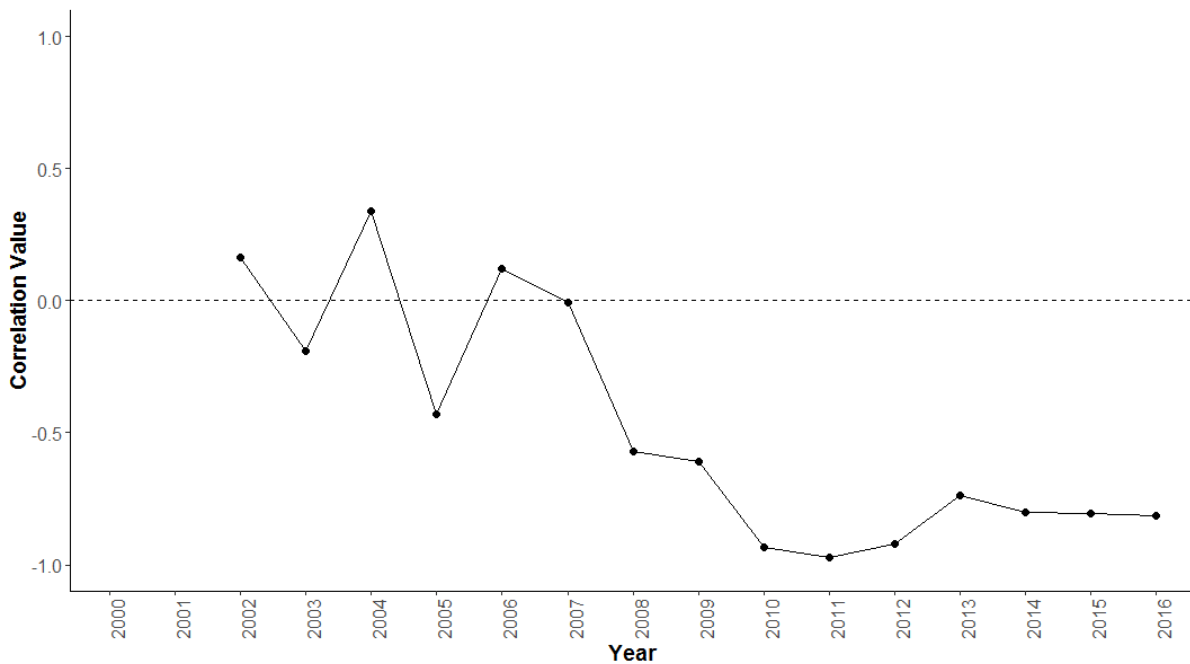


Figure 2.7: A five-year rolling correlation between square kilometres of forest in East Africa and the proportion of all rarity records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) in southern Africa that are European Honey-buzzard (*Pernis apivorus*) records.

## 2.4 Discussion

From the records collected for European Honey-buzzard from multiple sources, it is unquestionable that there has been an increase in both the abundance and distribution of the species in southern Africa over the 34 years for which data were analysed. This massive increase more likely reflects an actual increase in the number of birds migrating to the sub-region, rather than an artefact of increased birdwatcher effort in the area. Over the period of largest expansion in southern African honey-buzzards, there was a small decline in Tanzania.

### 2.4.1 Increase in European Honey-buzzard

All species examined, including the European Honey-buzzard, have shown a sharp increase in southern Africa since the advent of SARBN. This includes two species that are listed as Near Threatened by the IUCN due to population declines, the Eurasian Oystercatcher and Black-tailed Godwit. While all the species did increase, none of the species increased to the same extent as European Honey-buzzard. European Honey-buzzard showed a five times greater increase than the species with the next greatest increase, the Green Sandpiper. Interestingly, the Green Sandpiper is also one of only two species assessed that is regarded as

increasing along with the Western Marsh-harrier, which may similarly explain the sandpiper's large increase (IUCN 2019). In the case of the European Honey-buzzard, the enormous increase in a species that is declining in many parts of its range indicates that there are other factors contributing to the increase in records (Ottvall et al. 2009, Bijlsma et al. 2012, IUCN 2019).

In addition to the greater increase in European Honey-buzzard records, the timing of the increase also differed from similar species. While most species (including Green Sandpiper and Western Marsh-harrier) showed increases immediately following the introduction of SARBN, European Honey-buzzard showed the greatest increase much later in the 2012-2013 season rather than in the 2008-2009 season (when SARBN began). This suggests that there may be different drivers for this increase in records, e.g. climatological or habitat changes, rather than increased observer effort. This is further supported by similar trends in the number of European Honey-buzzard records, regardless of standardization for observer effort.

There is also the argument that birdwatchers have simply become more adept at identifying European Honey-buzzards, and therefore, the species reporting rate has increased. This seems unlikely considering that other difficult to identify vagrant species did not show a significant increase over the same period despite being equally challenging to identify. For example, Western Marsh-harrier is superficially very similar to the more common African Marsh-harrier (*Circus ranivorus*), and Green Sandpiper is comparable to the regularly occurring Wood Sandpiper (*Tringa glareola*) (Hockey and Ryan 2005). These two species have shown a much smaller increase over the period examined, as have other easier to identify species such as Eurasian Oystercatcher and Common Redshank.

Like elsewhere, e.g. the United States of America and United Kingdom, southern Africa has clearly shown an increase in the numbers of birdwatchers, although it is difficult to define the extent of this increase in the sub-region (Connell 2009, Rogerson et al. 2013). The number of rarity records submitted annually to SARBN, as well as SABAP 2 effort, have both increased annually since the 2008-2009 season (SABAP 2 2018). In addition, SABAP 2 now covers a greater number of pentads than ever before due to an increase in participants (SABAP 2 2018). The best records for the number of southern African birdwatchers come from the South African Ornithological Society (SAOS) which became BirdLife South Africa (BLSA) in 1996. In 1986, there were a total of 5,416 members to SAOS, which is greater than the 4,129 members BLSA currently holds. The number of members of BLSA has remained fairly steady over the past decade (pers. comm. Mark Anderson, CEO, BirdLife South Africa). This may indicate that the number of birdwatchers has not increased significantly, which may signify that more efficient

communication and documentation of rare birds may have a greater effect on the increase in European Honey-buzzard than the overall change in the number of birdwatchers.

#### 2.4.2 Explanations for the population increase

Based on the evidence detailed above, the European Honey-buzzard has truly increased in abundance and distribution in southern Africa, and this is not merely a reflection of increased reporting. While other species have also increased, none have increased to the same extent, and the number of honey-buzzard records appears to have increased disproportionately to the overall birdwatching effort. This brings to the forefront the question of what has caused this seemingly sudden increase in a species that is declining, particularly in Western Europe (Ottvall et al. 2009, Bijlsma et al. 2012, IUCN 2019).

One possible explanation for the increase in European Honey-buzzards is the large-scale change in habitat further north in Africa, which could in turn result in driving birds further south where they seek suitable overwintering habitat. The correlations between forest cover and honey-buzzard records support this hypothesis. As forest area has declined in East Africa, there has been a concurrent increase in the number of honey-buzzards reported in southern Africa. This trend began in the mid-2000s, and has remained the same since then, which may indicate that a forest loss threshold for the honey-buzzards was reached at this time. At the same time, there is a positive relationship between Tanzanian honey-buzzard records and forest cover with the exception of 2009 to 2012, an extreme drought period across much of East Africa (Hassan et al. 2014, Awange et al. 2016). This may indicate that European Honey-buzzards have been driven further south due to the loss of habitat in East Africa (Hansen et al., 2013). The extreme drought may have exacerbated the effect of forest loss, and caused a reduction in honey-buzzard prey availability (Hassan et al. 2014, Awange et al. 2016). This hypothesis is further supported by the slight decline in Tanzanian honey-buzzard records over the same period as well as the small contraction of its range.

It is important to note that there are limitations to the large-scale correlative methods used in this study. This study highlights a broad pattern in the shifts of the European Honey-buzzard, but further research examining the finer-scale relationships between the migratory bird populations of the two regions is needed, as well as more evidence on how honey-buzzards select and establish their non-breeding home ranges. By understanding more about these factors, we can better model how both regions' populations may be affected by habitat loss.

In addition to the above limitations, we have also not assessed the large-scale alteration of habitat and change in climate in southern Africa during this period (Buitenwerf et al. 2011). Many of the areas that honey-buzzards frequent in the sub-region are urban areas that have experienced increased afforestation, e.g. the Cape Peninsula, Gauteng province, and Windhoek, Namibia (Hockey and Midgley 2009, Hockey et al. 2011, Symes et al. 2017). These forested habitats may be attracting or supporting a larger population of European Honey-buzzard than was possible in previous decades.

Lastly, while non-breeding habitat may be driving the change in honey-buzzard numbers in southern Africa, we have not evaluated how changes in the breeding population or breeding success of the species could also be contributing to the increased abundance of the species in the sub-region. Four European Honey-buzzards tracked from South Africa to their breeding grounds have migrated to Finland (one individual) and Russia (three individuals) (Howes, Byholm, and Symes, unpubl. data). Based on these data, it is likely that many of the southern African honey-buzzards are migrating from the east of their breeding range, particularly Russia. The Russian population of European Honey-buzzards has not been well studied, and so, the population trend in this region is unclear. However, migration counts in Batumi, Georgia, a bottle-neck for European Honey-buzzards migrating from the east of the species range, have not shown any measurable change (Batumi Raptor Count 2018). A better understanding of the trends in the Russian honey-buzzard population could improve our understanding of the population increase on the southern African non-breeding grounds.

Migrating significantly further south may put European Honey-buzzards at greater risk regarding breeding success. A longer migration from southern Africa may lead to a later arrival on the breeding grounds. It has been demonstrated in many migratory species that late-arriving individuals are likely to have less productive breeding habitats and lower breeding success (Aebischer et al. 1996, Smith and Moore 2005, Fulin et al. 2009). This could have long-term consequences for the species if the southern African population continues to grow.

Many migrant bird species have been shown to be changing their migration timing and patterns in response to global change (Jones and Cresswell 2009, Both 2010, Moussus et al. 2010, Stanley et al. 2012, Gill et al. 2014). It has been suggested that this is as a result of plasticity within individuals, but plasticity within individual migrants has rarely been observed (Gill et al. 2014). It has been shown that new recruits to the population are more likely to arrive earlier, perhaps due to earlier hatching subsequently facilitating earlier migrations to and from the breeding grounds (Gill et al. 2014). These recruits are likely to be driving changes in population-level migration patterns (Gill et al. 2014). In the case of the European Honey-

buzzard, it seems likely that juvenile birds would be the drivers of the southwards overwintering range shift based on tracking studies of the species. Adults have high site fidelity, and are unlikely to change their non-breeding grounds, while juvenile birds wander widely in Africa for at least three years, presumably to find the most suitable non-breeding territory (Strandberg et al. 2012). This pattern strongly supports the *serial residency hypothesis* which predicts that a proportion of juvenile birds will find suitable non-breeding habitat that can be used as an adult, allowing for overall population resilience to large-scale change in the species' environment (Cresswell 2014).

This study documents the response of one migrant species, the European Honey-buzzard, to changes on its non-breeding grounds. We show that the apparent increase in southern Africa is a real expansion of the population in the sub-region, and hypothesise that it is new recruits that are driving this southwards shift. This shows remarkable flexibility for a specialist species, but may have negative long-term consequences for the species due to decreased breeding success of late arriving individuals. A southwards shift is in contrast to many previous studies of Palaearctic migrants which have predicted or documented a northwards shift (closer to the breeding grounds) in response to climate change (Barbet-Massin et al. 2009, Visser et al. 2009, Ambrosini et al. 2011). This may be because the focus of past studies has been on climatological factors rather than habitat variables. With a likely increase in the collection of bird distribution data across Africa due to new and repeat atlas projects in Kenya and Nigeria, as well as throughout southern Africa, we will be able to better answer questions regarding how both climate and habitat changes are affecting migrant birds on the non-breeding grounds at a finer scale. With much of the current understanding of Palaearctic migrant birds' response to global change based on European data, we emphasize the importance of better using these African distribution data resources to increase our understanding of shifts in non-breeding ranges, phenology, and more for migrant bird species.



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## 2.6 Supplementary Information

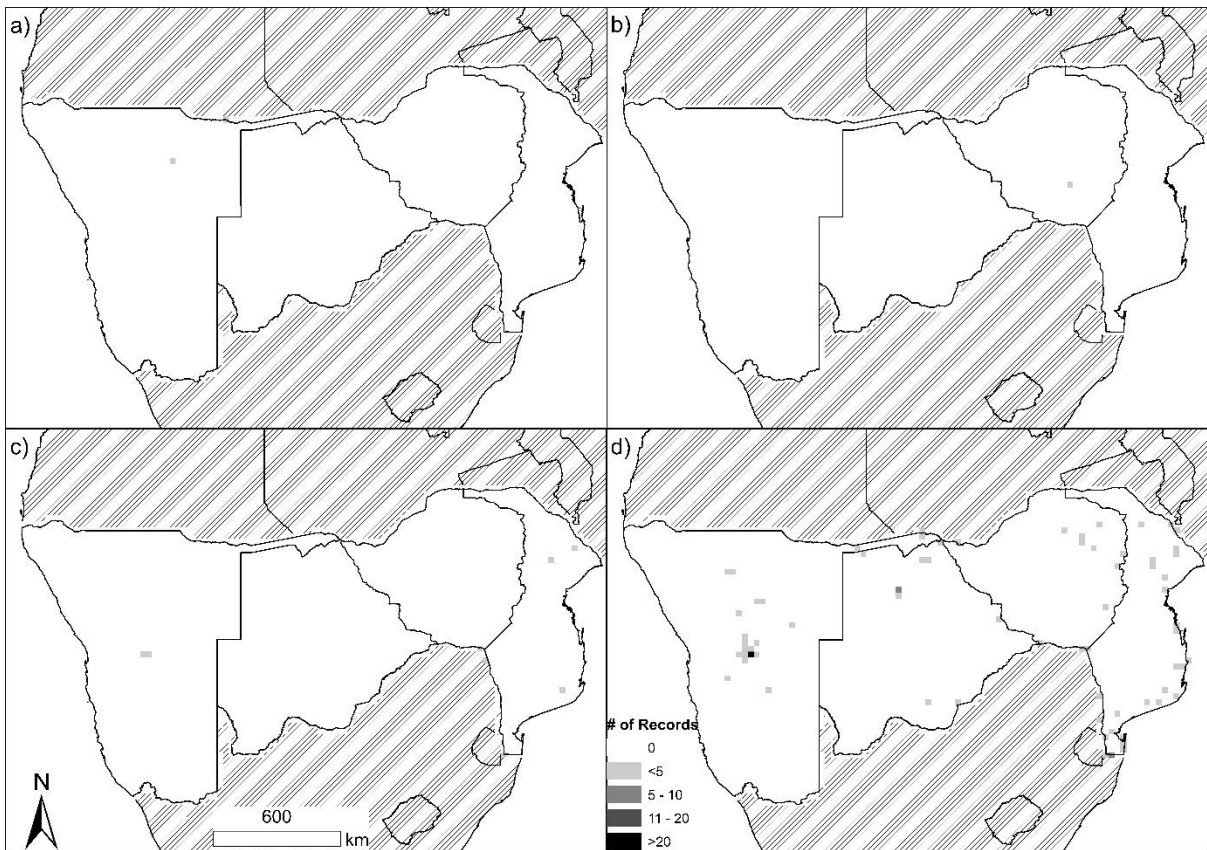
Table S2.1: European Honey-buzzard (*Pernis apivorus*) museum specimens collected from southern and East Africa from three out of eight museums that were investigated.

<b>Catalogue ID</b>	<b>Location</b>	<b>Year</b>	<b>Museum</b>
1894.6.16.345	Camperdown, Umlaas, Upper Shongweni, South Africa	1894	Natural History Museum at Tring
1900.2.20.5	Harare, Salisbury, Rhodesia	1900	Natural History Museum at Tring
1907.12.22.42	Harare, Salisbury, Rhodesia	1907	Natural History Museum at Tring
SKIN 196909	Bulawayo, Rhodesia	1908	American Museum of Natural History
9691	333 Mare St., Pretoria, Pretoria, South Africa	1912	Ditsong Museums of South Africa
15157	Mokeetsi, Limpopo, South Africa	1929	Ditsong Museums of South Africa
18000	Vryburg Zoetvlei, South Africa	1932	Ditsong Museums of South Africa
1955.6.N.20. 1042	Natal, South Africa	1955	Natural History Museum at Tring
76999	Potchefstroom, South Africa	1995	Ditsong Museums of South Africa
2000.29568	Lindi, Lindi, Tanzania	1895-1897	Museum für Naturkunde
2000.29558	Magogonia, Ruvu River, Morogoro, Tanzania	1911	Museum für Naturkunde
102905	Kiomosi, Kenya	1913	Royal Museum for Central Africa
192303	North Kavirondo: Yala Bridge, Kenya	1913	Field Museum
192301	North Kavirondo: Yala Bridge, Kenya	1915	Field Museum
192302	Mt Elgon, Kenya	1916	Field Museum
102906	Nairobi, Kenya	1920	Royal Museum for Central Africa

Table S2.2: The 87 southern African rarities assessed along with number of records per species (n = 2,517) from December 1983 to May 2017. Records were collected from the Southern African Rare Bird Newsletter, National Rarity Committee, and Zest for Birds site.

Common name	Scientific name	Records
European Honey-buzzard	<i>Pernis apivorus</i>	1,094
Green Sandpiper	<i>Tringa ochropus</i>	179
Pectoral Sandpiper	<i>Calidris melanotos</i>	96
Red Phalarope	<i>Phalaropus fulicarius</i>	75
Western Marsh Harrier	<i>Circus aeruginosus</i>	75
Franklin's Gull	<i>Leucophaeus pipixcan</i>	71
Common Redshank	<i>Tringa totanus</i>	65
Caspian Plover	<i>Charadrius asiaticus</i>	61
European Oystercatcher	<i>Haematopus ostralegus</i>	58
Red-necked Phalarope	<i>Phalaropus lobatus</i>	56
Lesser Black-backed Gull	<i>Larus fuscus</i>	54
Black-tailed Godwit	<i>Limosa limosa</i>	48
Pacific Golden Plover	<i>Pluvialis fulva</i>	41
Black-headed Gull	<i>Chroicocephalus ridibundus</i>	38
American Golden Plover	<i>Pluvialis dominica</i>	36
Grey Wagtail	<i>Motacilla cinerea</i>	36
Spotted Crake	<i>Porzana porzana</i>	33
Gull-billed Tern	<i>Gelochelidon nilotica</i>	30
Egyptian Vulture	<i>Neophron percnopterus</i>	24
Broad-billed Sandpiper	<i>Calidris falcinellus</i>	19
Greater Sheathbill	<i>Chionis albus</i>	19
Buff-breasted Sandpiper	<i>Calidris subruficollis</i>	14
Elegant Tern	<i>Thalasseus elegans</i>	14
Basra Reed Warbler	<i>Acrocephalus griseldis</i>	13
Golden Pipit	<i>Tmetothylacus tenellus</i>	13
White-throated Bee-eater	<i>Merops albicollis</i>	13
Eurasian Reed Warbler	<i>Acrocephalus scirpaceus</i>	12
Bridled Tern	<i>Onychoprion anaethetus</i>	11
Northern Rockhopper Penguin	<i>Eudyptes moseleyi</i>	11
White-rumped Sandpiper	<i>Calidris fuscicollis</i>	11
Wilson's Phalarope	<i>Phalaropus tricolor</i>	11
Whinchat	<i>Saxicola rubetra</i>	10
Eurasian Blackcap	<i>Sylvia atricapilla</i>	9
Madagascar Cuckoo	<i>Cuculus rochii</i>	9
Rüppell's Vulture	<i>Gyps rueppelli</i>	9
Northern Wheatear	<i>Oenanthe oenanthe</i>	8
Red-necked Buzzard	<i>Buteo auguralis</i>	8
Eleanora's Falcon	<i>Falco eleonorae</i>	7
Garganey	<i>Spatula querquedula</i>	7
Hudsonian Godwit	<i>Limosa haemastica</i>	7
Citrine Wagtail	<i>Motacilla citreola</i>	6
European Turtle Dove	<i>Streptopelia turtur</i>	6

Common name	Scientific Name	Records
Great Knot	<i>Calidris tenuirostris</i>	6
Purple Gallinule	<i>Porphyrio martinicus</i>	6
Dunlin	<i>Calidris alpina</i>	5
King Penguin	<i>Aptenodytes patagonicus</i>	5
Lesser Cuckoo	<i>Cuculus poliocephalus</i>	5
Lesser Yellowlegs	<i>Tringa flavipes</i>	5
Little Blue Heron	<i>Egretta caerulea</i>	4
Isabelline Wheatear	<i>Oenanthe isabellina</i>	3
Malagasy Pond Heron	<i>Ardeola idae</i>	3
Red-necked Stint	<i>Calidris ruficollis</i>	3
Royal Tern	<i>Thalasseus maximus</i>	3
Snowy Egret	<i>Egretta thula</i>	3
Spur-winged Lapwing	<i>Vanellus spinosus</i>	3
Temminck's Stint	<i>Calidris temminckii</i>	3
Western Reef Heron	<i>Egretta gularis</i>	3
Baird's Sandpiper	<i>Calidris bairdii</i>	2
Black-naped Tern	<i>Sterna sumatrana</i>	2
Grasshopper Buzzard	<i>Butastur rufipennis</i>	2
Macaroni Penguin	<i>Eudyptes chrysolophus</i>	2
Mascarene Martin	<i>Phedina borbonica</i>	2
Ortolan Bunting	<i>Emberiza hortulana</i>	2
Pied Wheatear	<i>Oenanthe pleschanka</i>	2
Red-throated Pipit	<i>Anthus cervinus</i>	2
Rose-coloured Starling	<i>Pastor roseus</i>	2
Angola Swallow	<i>Hirundo angolensis</i>	1
Asiatic Dowitcher	<i>Limnodromus semipalmatus</i>	1
Black Skimmer	<i>Rynchops niger</i>	1
Cardinal Quelea	<i>Quelea cardinalis</i>	1
European Pied Flycatcher	<i>Ficedula hypoleuca</i>	1
Gentoo Penguin	<i>Pygoscelis papua</i>	1
Herring Gull	<i>Larus argentatus</i>	1
Irania	<i>Irania gutturalis</i>	1
Little Crake	<i>Porzana parva</i>	1
Little Penguin	<i>Eudyptula minor</i>	1
Little Ringed Plover	<i>Charadrius dubius</i>	1
Magellanic Penguin	<i>Spheniscus magellanicus</i>	1
Northern Shoveler	<i>Anas clypeata</i>	1
Red-rumped Swallow	<i>Cecropis daurica</i>	1
Red-tailed Shrike	<i>Lanius phoenicuroides</i>	1
Red-throated Cliff Swallow	<i>Petrochelidon rufigula</i>	1
Ross's Turaco	<i>Musophaga rossae</i>	1
Rufous-tailed Scrub Robin	<i>Cercotrichas galactotes</i>	1
Slender-billed Gull	<i>Chroicocephalus genei</i>	1
Southern Rockhopper Penguin	<i>Eudyptes chrysocome</i>	1
White-cheeked Tern	<i>Sterna repressa</i>	1



*Figure S2.1:* The number of European Honey-buzzard (*Pernis apivorus*) records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) in quarter-degree squares (QDSs) in southern Africa excluding South Africa, Swaziland, and Lesotho during: a) 1983-1989 (2 QDSs, 0.1%), b) 1990-1999 (2 QDSs, 0.1%), c) 2000-2009 (9 QDSs, 0.3%), and d) 2010-2017 (71 QDSs, 2.2%).

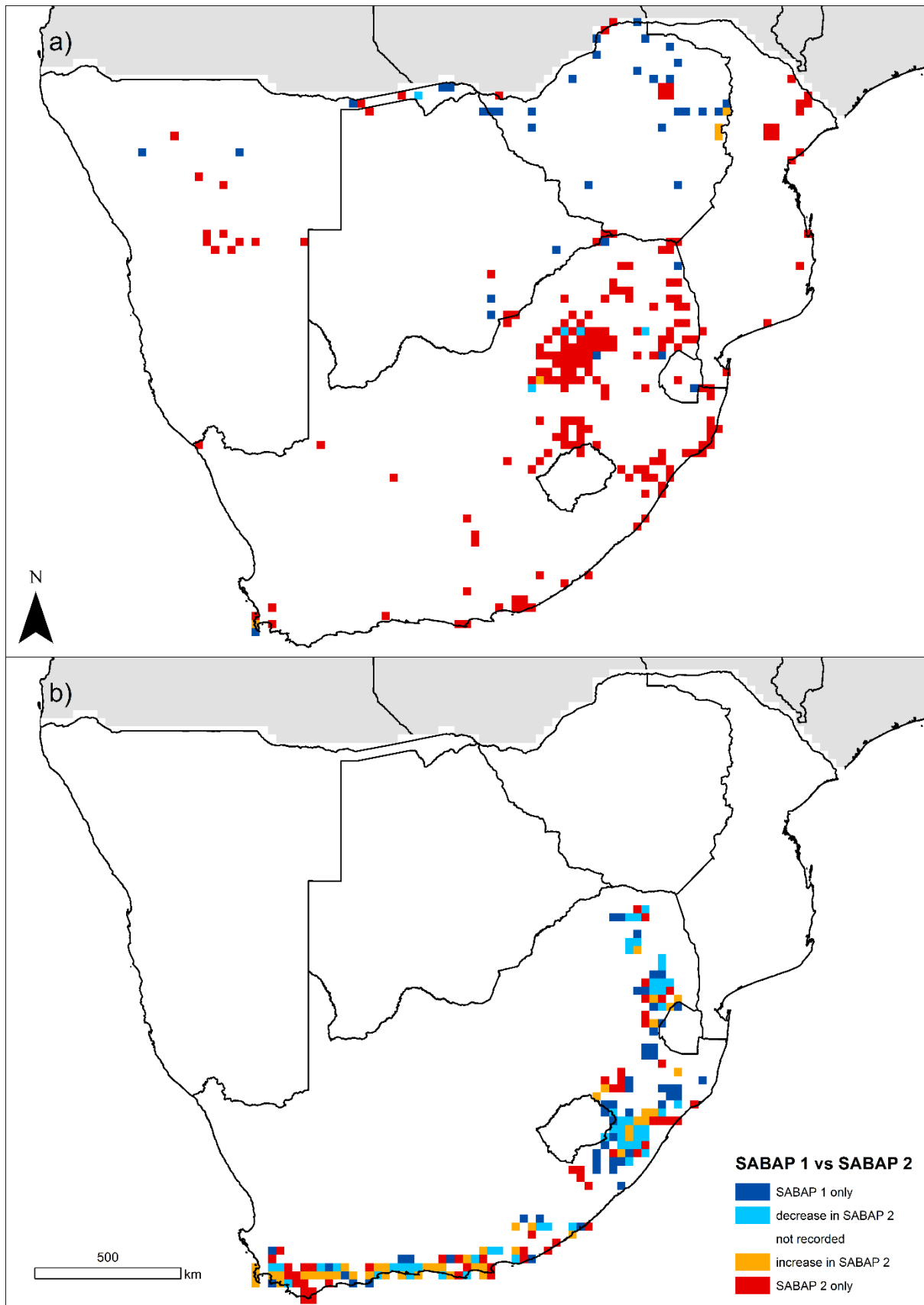


Figure S2.2: The change in reporting rate between Southern African Bird Atlas Project (SABAP) 1 (1987-1991) and SABAP 2 (2007-2017) for: a) European Honey-buzzard (*Pernis apivorus*), and b) Forest Buzzard (*Buteo trizonatus*).



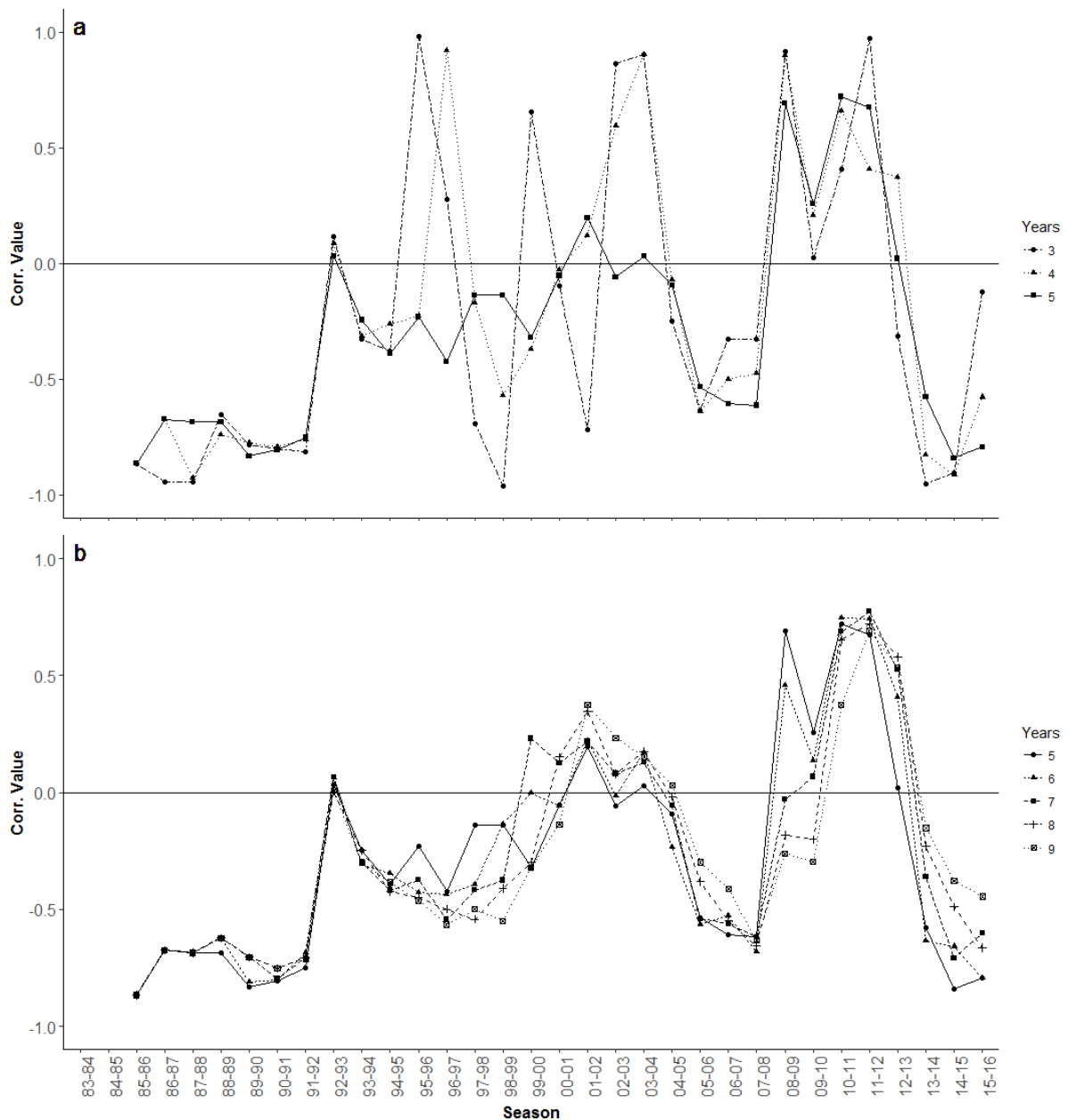


Figure S2.3: Rolling correlations between the number of southern African and Tanzanian European Honey-buzzard (*Pernis apivorus*) records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, National Rarity Committee, and Tanzania Bird Atlas) per season with different time windows of: a) three, four, and five seasons, and b) five, six, seven, eight, and nine seasons. Note the reduced variability with greater time windows.

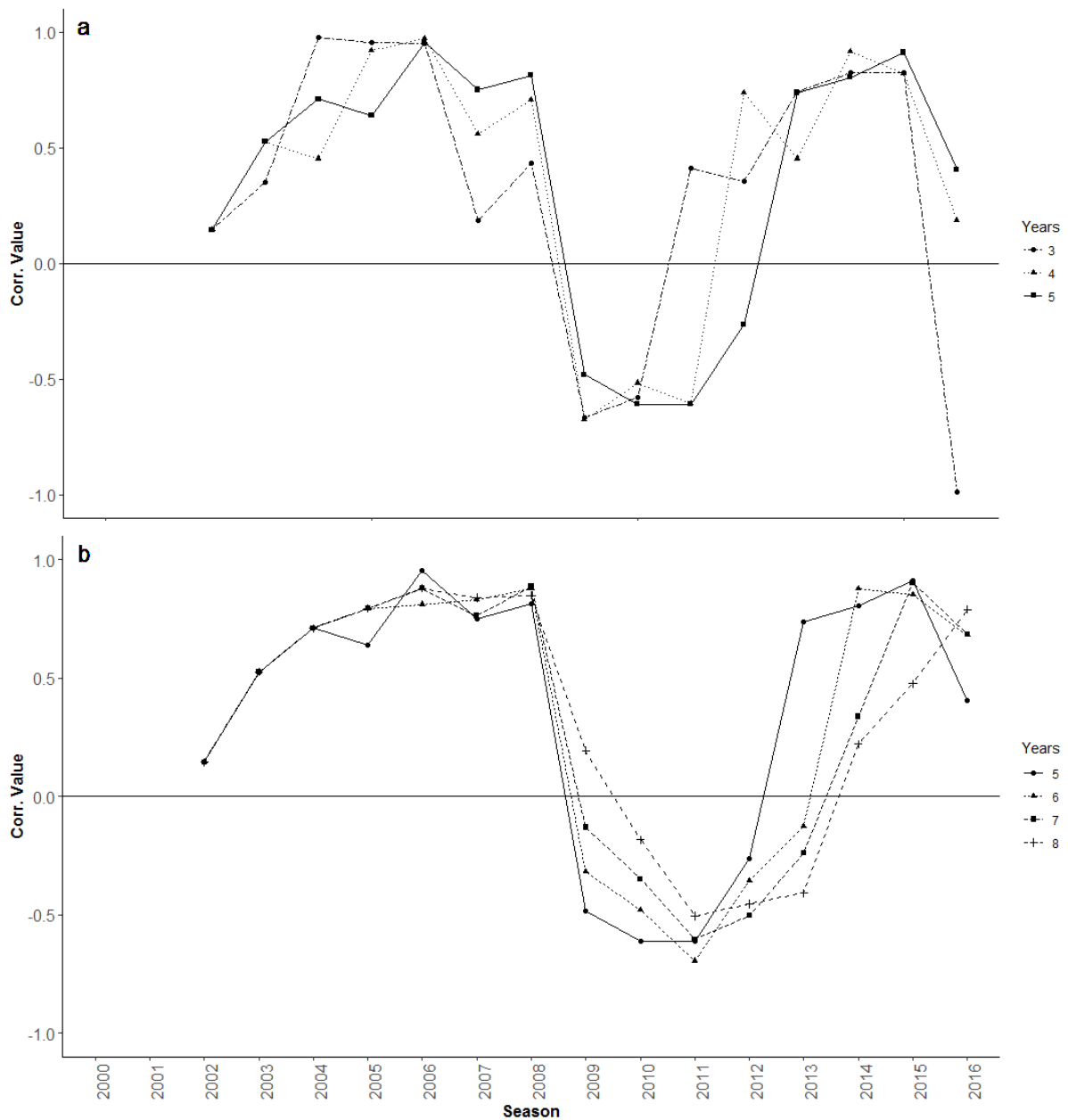


Figure S2.4: Rolling correlations between square kilometres of forest in East Africa and the number of Tanzanian European Honey-buzzard (*Pernis apivorus*) records from the Tanzania Bird Atlas per year with different time windows of: a) three, four, and five years, and b) five, six, seven, eight, and nine years. Note the reduced variability with greater time windows.

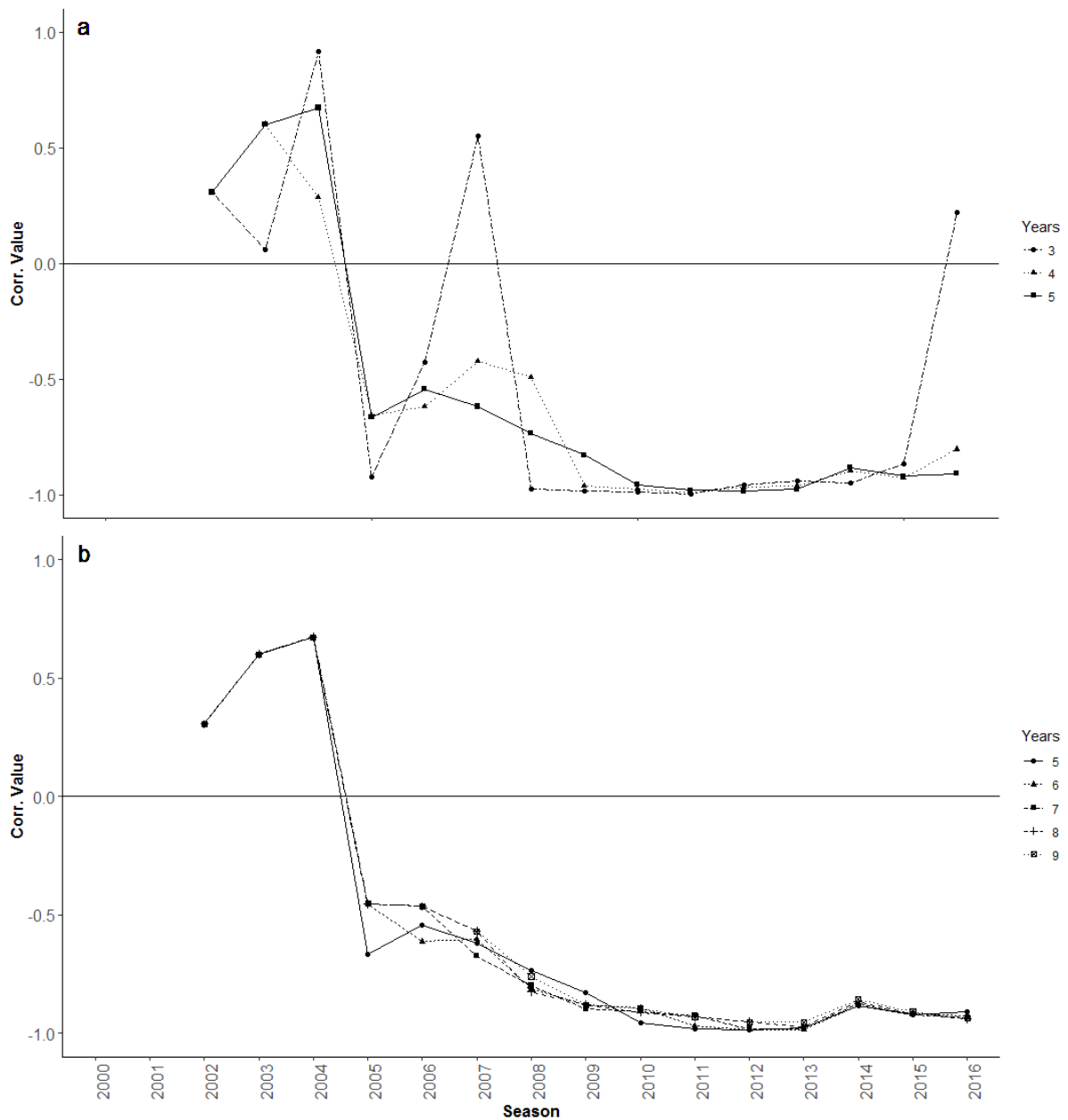


Figure S2.5: Rolling correlations between square kilometres of forest in East Africa and the number of southern African European Honey-buzzard (*Pernis apivorus*) records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) per year with different time windows of: a) three, four, and five years, and b) five, six, seven, eight, and nine years. Note the reduced variability with greater time windows.

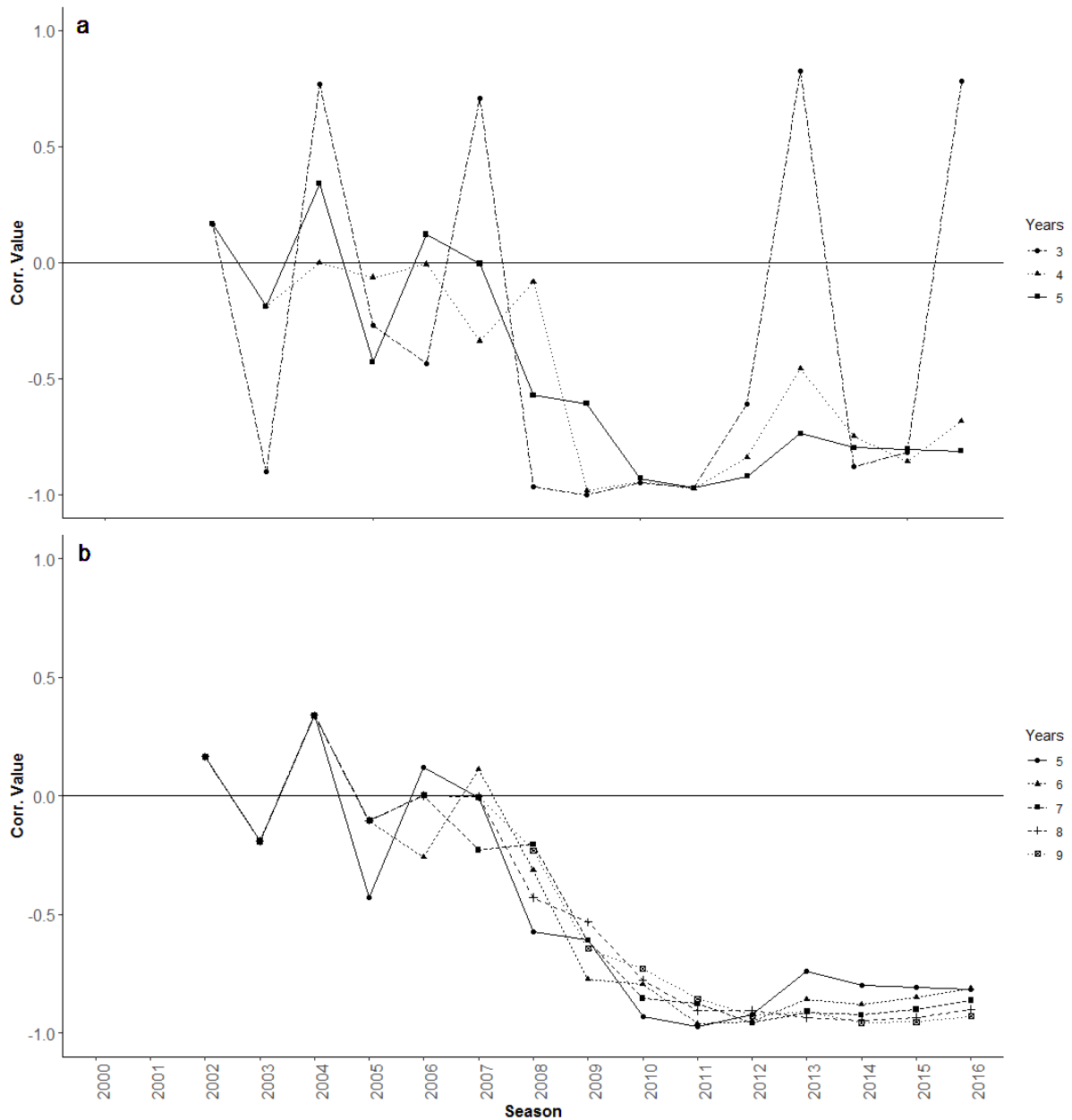
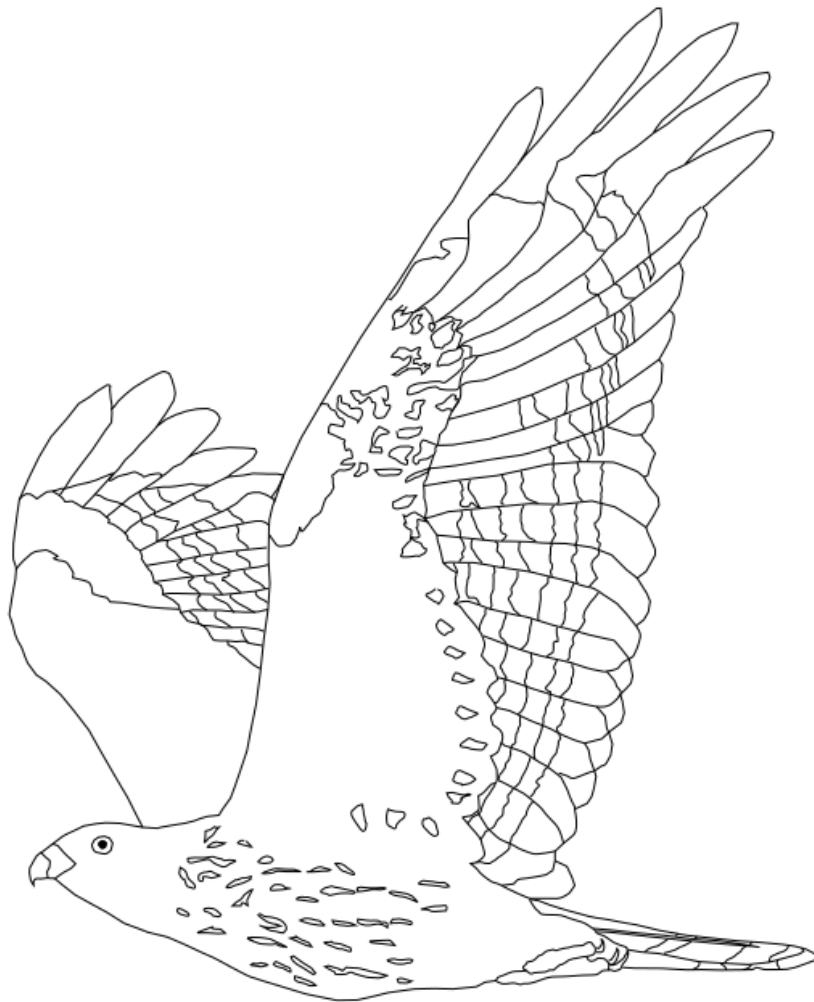


Figure S2.6: Rolling correlations between square kilometres of forest in East Africa and the proportion of rarity records from birdwatching sources (Southern African Rare Bird Newsletter, Zest for Birds, and National Rarity Committee) in southern Africa that were European Honey-buzzard (*Pernis apivorus*) records per year with different time windows of: a) three, four, and five years, and b) five, six, seven, eight, and nine years. Note the reduced variability with greater time windows.

# Highly skewed sex and age ratios of European Honey-buzzard in southern Africa



## *Abstract*

Sex and age segregation on the non-breeding grounds is common in raptor species. We studied the European Honey-buzzard (*Pernis apivorus*) on its southern African non-breeding grounds to examine changes in sex and age ratios over a period of recent population expansion (2002-2017). Photographs from multiple open sources were analysed. The adult population was found to be overwhelmingly female (93.3%) with no significant variation over months, years, or latitudes. This supports the *arrival-time hypothesis*, which states that the sex responsible for establishing the breeding territory (the male in honey-buzzard) will spend the non-breeding period closest to the breeding grounds, allowing them to reduce intrasexual competition for breeding territories. Juvenile and second year birds (41.6% of the population) were more common at lower elevations, as well as further south in the sub-region. This is likely due to a funnelling effect of inexperienced juvenile birds further south and to coastal zones. In addition, juvenile birds do not return to the breeding grounds for at least two years, so may be more likely to migrate further south. Lastly, second year birds increase later in the austral summer. This may be a result of both juvenile birds moulting into more adult plumage, and a southwards intra-continental movement of young honey-buzzards in Africa.

*Keywords:* demographics, European Honey-buzzard, *Pernis apivorus*, population structure, sex ratio

### *3.1 Introduction*

Many vertebrates display age and sex segregation with respect to migration timing, and non-breeding range and habitat. These behaviours have been examined in numerous taxa including fish, ungulates, and birds (Seghers 1973, Cristol et al. 1999, Bonenfant et al. 2004). Several hypotheses have been proposed to explain the change in age and sex ratios across latitudes or habitat types, particularly in Palaearctic migrant birds (Cristol et al. 1999). The *arrival-time hypothesis* proposes that the sex which is responsible for establishing a breeding territory will winter the closest to the breeding grounds in order to gain an advantage in the competition for breeding territories by arriving back earlier (Ketterson and Nolan 1976). The *dominance hypothesis* states that more dominant animals, often larger or older individuals, monopolize the ideal habitats in areas closest to their breeding grounds during the non-breeding season, forcing weaker individuals further from the breeding areas (Gauthreaux 1978). This

has been documented in Rough-legged Buzzard (*Buteo lagopus*), where adults are more common on northern non-breeding grounds, and the majority of these adults are larger females (Kasprzykowski and Cieśluk 2011). Large adult females are not only likely to be the most dominant birds but are also likely to be able to endure colder temperatures during winter (Kasprzykowski and Cieśluk 2011). The final hypothesis, the *migration constraints hypothesis*, asserts that younger birds do not have the physiological resources to survive long migrations from the northern hemisphere, and therefore, spend the non-breeding season closer to the breeding grounds than adults (Prescott and Middleton 1990). For instance, juvenile Western Marsh-harriers (*Circus aeruginosus*) are more likely to winter in Europe than adult harriers, perhaps indicating an inability to survive a taxing trans-Saharan migration (Strandberg et al. 2008, Agostini and Panuccio 2010).

In this study, we examined sex and age class ratios in the expanding population of European Honey-buzzard (*Pernis apivorus*) in the southern African sub-region (Howes et al. 2019). The European Honey-buzzard is a migratory raptor that breeds in the forests of the northern Palaearctic from the United Kingdom in the west to western Russia in the east (Cramp and Simmons 1979). It is a specialist in habitat and diet, generally found in nutrient-rich, mature forests where it feeds almost exclusively on Apoidea larvae (Itämies and Mikkola 1972, Gamauf 1999). Post-breeding, the European Honey-buzzard migrates south into Africa where it spends the Northern Hemisphere winter (Cramp and Simmons 1979). The majority of birds overwinter in Central and West Africa with a minority of individuals spending the non-breeding season in southern and East Africa (Cramp and Simmons 1979). Both sexes of adult honey-buzzard leave the breeding grounds at the same time (Cramp and Simmons 1979, Kjellén 1992, Hake et al. 2003). Juveniles depart later in the autumn and follow different migration routes (Kjellén 1992, Hake et al. 2003, Vansteelant et al. 2017). Juvenile birds do not return to Europe to breed for approximately three years (Hake et al. 2003, Strandberg et al. 2012, Vansteelant et al. 2017). During this period, young honey-buzzards move widely around the African continent (Strandberg et al. 2012, Vansteelant et al. 2017). Adult birds of both sexes return annually to their breeding territories during the Northern Hemisphere summer (Cramp and Simmons 1979, Hake et al. 2003).

The honey-buzzard population in southern Africa is the furthest south of the African non-breeding populations, and has increased in numbers over the past three decades despite the species' global decline (Kostrezewa 1987, Löhms 2005, Benusan et al. 2007, Howes et al. 2019). Prior to approximately 2004, the honey-buzzard was an exceptionally rare vagrant in the southern African sub-region (e.g. 1-2 records annually) (Howes et al. 2019). However,

since 2014, the species has become much more common (e.g. 200-300 records annually) (Howes et al. 2019). Southern Africa provides a unique setting to understand sex and age segregation in the migratory European Honey-buzzard due to both its distance from the European breeding grounds, as well as the species recent expansion in the region. Additionally, the honey-buzzard is sexually dimorphic and exhibits age class specific plumage, allowing for identification of these traits without capture (Cramp and Simmons 1979, Forsman and Shirihai 1997).

To understand patterns in the sex and age class ratios of the southern Africa sub-region and how these ratios relate to the migration and non-breeding season behaviours of the honey-buzzard, we investigated both temporal and spatial elements. From a temporal perspective, we assessed both changes from year to year in the demographic ratios over the period of population expansion (2002-2017), as well as from month to month over the austral summer season. Due to the differences in migration timing and speed between adult and juvenile honey-buzzards, it seems likely that adult birds arrive earlier than juvenile birds to southern Africa (Hake et al. 2003).

From a spatial perspective, we assessed where different sexes and age classes were found, and what variables may be driving any differences in their distribution. Due to the southern African sub-region's distance from the European Honey-buzzard breeding grounds, if the *arrival time hypothesis* applies to the species, there should be a greater number of adult female honey-buzzards than adult male honey-buzzards, due to the fact that males are responsible for establishing breeding territories in the species (Cramp and Simmons 1979). Meanwhile, if the *dominance hypothesis* affects individuals' distribution, there is likely to be a greater proportion of smaller male honey-buzzards (and young honey-buzzards) further south than larger females (Gauthreaux 1978, Cramp and Simmons 1979). If the *dominance hypothesis* applies to this species, adults, especially adult females, would also be likely to be in the highest quality habitats in the sub-region, particularly if they arrive earlier than younger birds. Lastly, if the *migration constraints hypothesis* explains the distribution of non-breeding honey-buzzards, there would likely be a low proportion of juvenile birds in the southern African sub-region, due to the extensive migration required to get there (Prescott and Middleton 1990).

To assess the sex and age ratios of the southern African sub-region, we collected photographs of European Honey-buzzard from the southern African sub-region over a period of fifteen years. By understanding the spatial and temporal changes in this particular population's demographics, we aimed to evaluate how these demographics may be affecting



or driving the recent non-breeding range expansion of this specialist species, as well as to better understand the sex and age class segregation of the migratory European Honey-buzzard on its non-breeding grounds.

### *3.2 Methods*

#### 3.2.1 Photograph attainment

European Honey-buzzard is considered a rarity in southern Africa, and therefore, is documented on the rarity-reporting platforms in the sub-region (Howes et al. 2019). Photographs of European Honey-buzzards in southern Africa were collected from: i) the Zest for Birds website, ii) the Southern African Rare Bird Newsletter (SARBN), iii) the Animal Demography Unit's Virtual Museum, and iv) two Facebook groups (BirdLife South Africa and SA Rare Birds). Zest for Birds is a website documenting rarities in southern Africa from January 2002 until December 2010. SARBN is an email list-server that is used to disseminate information on rarities in the sub-region. Records used from SARBN spanned from July 2008 until July 2017. The Animal Demography Unit's Virtual Museum showcases photographs uploaded by citizen scientists. No colour photograph records were found from before January 2002. All photographs were downloaded, and databased with the date, location, photographer, and source.

#### 3.2.2 Photograph analysis

Two variables were assessed on each photograph: i) age class, and ii) sex. Three age classes were identified: i) juvenile, ii) second year, and iii) adult birds. Four characteristics were used to assign each honey-buzzard to an age class: i) eye colour, ii) bill and cere colour, iii) secondary feather barring, and iv) primary feather pattern (Cramp and Simmons 1979, Forsman and Shirihai 1997). A bird was identified as a juvenile if it had: i) dark eyes, ii) a black bill with a yellow cere, iii) secondary feathers with more than three bands, and/or iv) all dark outer primaries. A honey-buzzard was classified as an adult if it had: i) bright yellow eyes, ii) a black bill with a dark cere, iii) pale secondaries with three or fewer bands, and/or iv) outer primaries with a small black tip. Second year birds had: i) pale brown or dark yellow eyes, ii) a black bill with a yellow cere, iii) pale secondaries with three or fewer bands, and/or iv)

primaries that were a mix of adult and juvenile feathers. At least two characteristics were used to age all individuals.

Sex was only identified in adult European Honey-buzzards as it is not possible to sex juveniles using plumage characteristics (Cramp and Simmons 1979, Forsman and Shirihai 1997). Three traits were used to identify the sex of each bird: i) secondary feather pattern, ii) tail feather pattern, and iii) head colour (Cramp and Simmons 1979, Forsman and Shirihai 1997). A honey-buzzard was assigned as male if it had: i) primaries with broad gaps between the subterminal and next proximal band (only one band visible in flight), ii) tail feathers with a broad area between the subterminal and next proximal band, and/or iii) a grey head. A bird was identified as female if it had: i) secondaries with a narrow gap between the subterminal and next proximal band (two bands visible in flight), ii) tail feathers with a narrow area between the subterminal and next proximal band, and/or iii) a brown head. One of these characteristics was sufficient to sex an individual (Cramp and Simmons 1979).

### 3.2.3 Statistical analysis

In order to assess possible drivers of sex and age class segregation in European Honey-buzzard, the location of each photographed individual was plotted in ArcGIS 10.3. BioClim (vers. 2.0) rasters were obtained for elevation (m), average monthly precipitation (mm), and temperature (°C) at approximately 1 km<sup>2</sup> resolution (Fick and Hijmans 2017). The total precipitation and the average temperature for the austral summer season (November-April) were calculated. Land cover values were obtained from the European Space Agency Climate Change Initiative 20 m Land Cover Map of Africa (ESA 2018). This layer included ten classes: i) tree cover area, ii) shrub cover area, iii) grassland, iv) cropland, v) aquatic or regularly flooded vegetation, vi) sparse vegetation, vii) bare area, viii) built-up area, ix) snow or ice, and x) open water. Elevation, precipitation, temperature, and land cover values were extracted for each photographed individual. These values were included along with the month and year of the photograph, and the latitude of the sighting. All continuous variables were scaled using the ‘scale’ function in R. This function subtracts the mean and divides that value by the standard deviation for each value within a variable.

A binomial logistic generalised linear model (GLM) was used to assess the relationship between sex, and month, year, and latitude. Fully nested models were built with month, year, and latitude, as well as interactions between each variable. A null model was also included. Models were assessed based on their Akaike information criterion scores (AICc). An AICc

value is an AIC value that has been corrected for sample size relative to the number of parameters being estimated (K). The best models were selected using AICc differences ( $\Delta\text{AICc}$ ), as well as evidence ratios (ER). When more than one model was appropriate, model averaging was applied. The 95% confidence intervals for the coefficients in the final model were calculated. All modelling was performed in R version 3.5.0 (R Core Development Team 2018). The ‘MuMIn’ package was used for model selection criteria as well as model averaging.

To assess temporal patterns in age classes, we tested for differences in occurrence of each age class between months and years using a  $\chi^2$  test. Only austral summer months (as defined above) were used due to a low number of records outside the summer season. In order to model the data using a binomial logistic GLM, second year and juvenile birds were combined into a single category, sub-adults. Adults were assigned 0s while sub-adults were assigned 1s. A total of 16 binomial GLMs were built. Age class models were assessed and averaged in the same manner as sex models.

The date of the first photographed arrival (arrival date) for each age class was recorded from 2009 to 2016, except second year birds which were recorded from 2012 to 2016 due to a small sample size of photographs of this age class from 2009 to 2011. The date was only used if it was during the Southern Hemisphere spring, which was assumed to be 1 September to 31 December. The number of days from 1 September was counted, and the average arrival dates were tested with a Kruskal-Wallis test.

### *3.3 Results*

A total of 498 individual European Honey-buzzards were photographed over the study period. There was an average of  $1.4 \pm 1.1$  photos per individual. The majority of individuals photographed were in South Africa ( $n = 432$ ), followed by Namibia ( $n = 26$ ), Mozambique ( $n = 18$ ), Zimbabwe ( $n = 8$ ), and Botswana ( $n = 7$ ) (Figure 3.1).

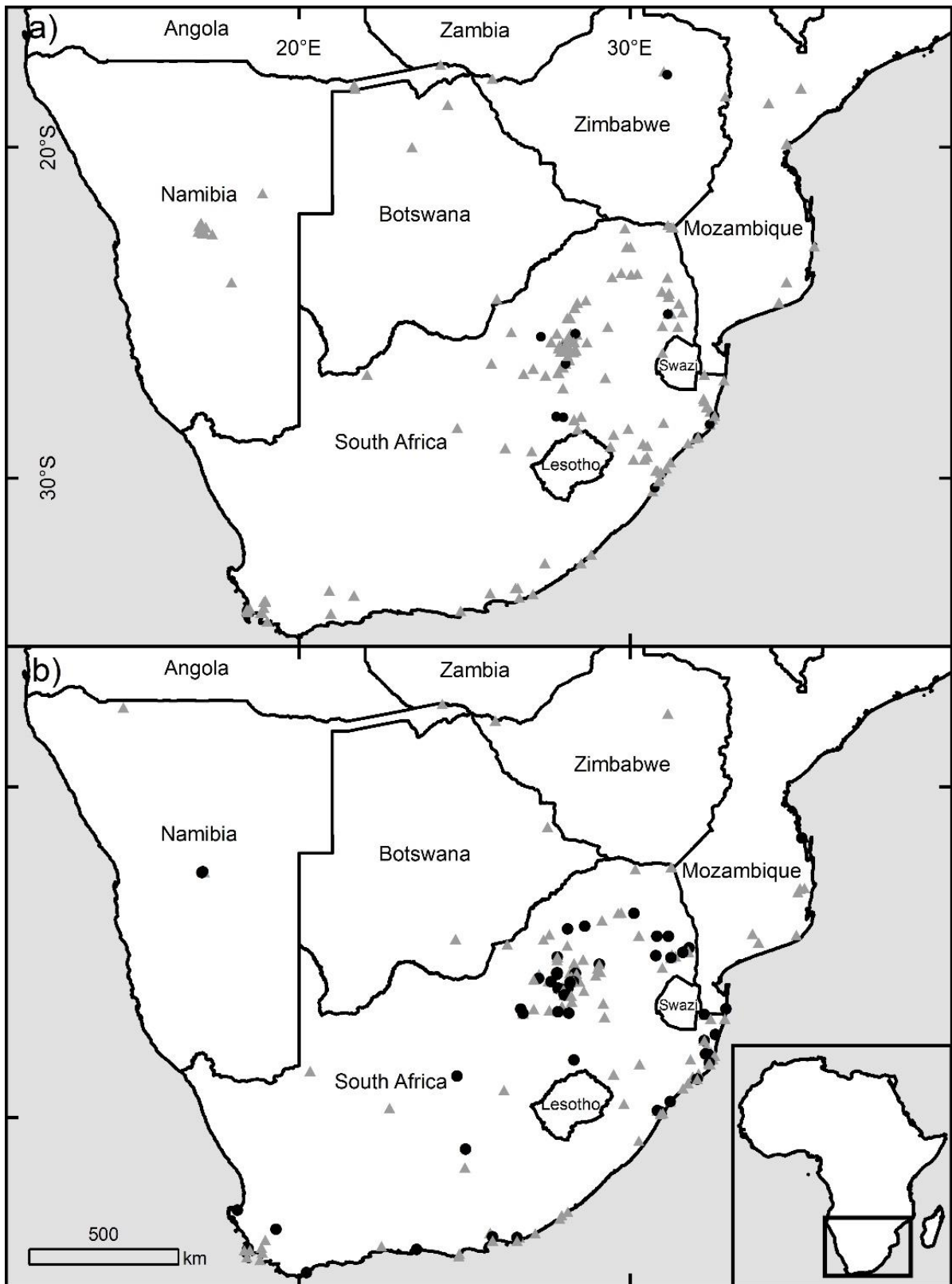


Figure 3.1: Locations of: a) adult European Honey-buzzard (*Pernis apivorus*) photographs with grey triangles representing females and black circles representing males, and b) second year and juvenile European Honey-buzzard photographs with black circles representing second year birds and grey triangles representing juveniles in southern Africa from January 2002 to July 2017.

### 3.3.1 European Honey-buzzard sex distribution

Of the 289 adult honey-buzzards photographed, 285 were identified to sex. Only four adult birds could not be identified as male or female. A total of 93.3% (n = 266) of identified honey-buzzards were female, and 6.7% (n = 19) were male. None of the binomial logistic GLMs using year, month, and latitude had AICc values significantly greater ( $\Delta\text{AICc} < 2.0$ ) than the null model. This indicates that there were no differences in the likelihood of male or female honey-buzzards occurring in relation to year, month, or latitude. The lack of latitudinal effect within the sub-region may be due to the limited sample of male individuals.

### 3.3.2 European Honey-buzzard age distribution

A total of 495 European Honey-buzzards were classified into age classes. Of these birds, 58.4% (n = 289) were adults, 12.1% (n = 60) were second years, and 29.5% (n = 146) were juveniles.

There was no significant difference in European Honey-buzzard age class proportions across years ( $\chi^2 = 4.51$ , df = 6, p = 0.61). There was high variation in the proportions of age classes from year to year (Figure 3.2). The age class proportions of honey-buzzard differed significantly between months ( $\chi^2 = 21.22$ , df = 10, p = 0.02) (Figure 3.3). The proportion of second year birds increased over the austral summer season while the proportion of juveniles dropped over the same period. There was, however, a slight increase in the proportion of juveniles in April.

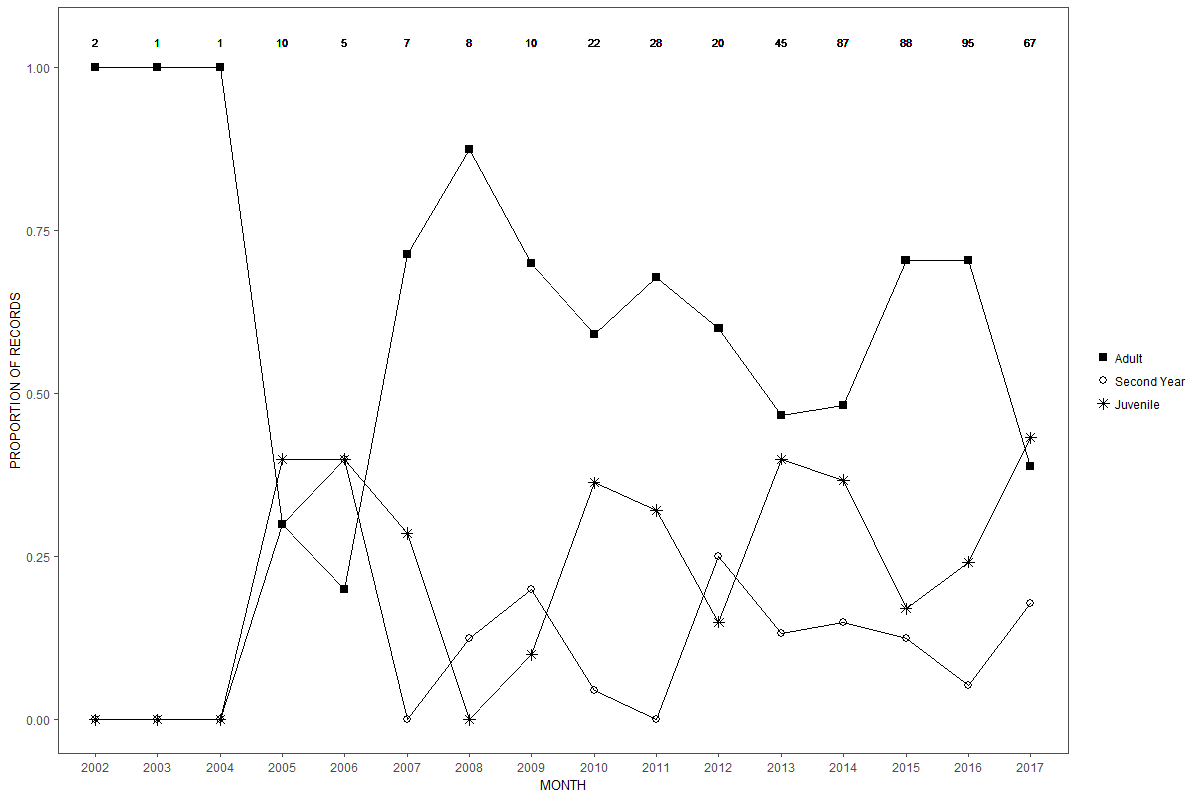


Figure 3.2: The proportion of adult ( $n = 289$ ), second year ( $n = 60$ ), and juvenile ( $n = 146$ ) European Honey-buzzards (*Pernis apivorus*) in southern Africa annually over the austral summer season from January 2002 to April 2017. The numbers above the lines indicate the total number of individuals analysed from each year.

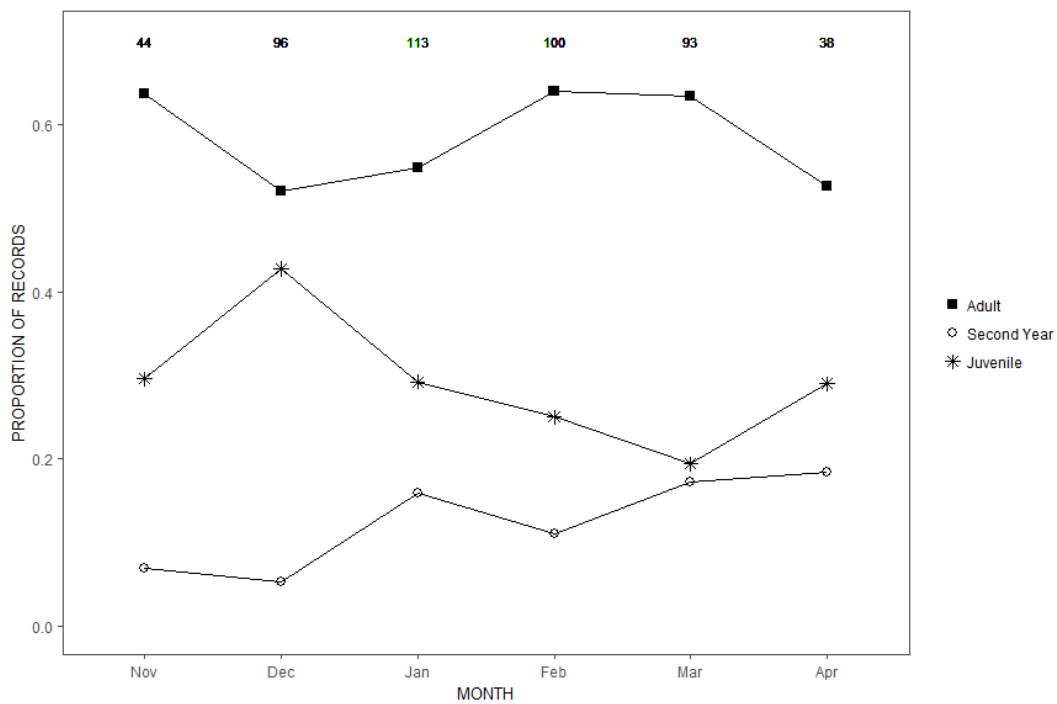


Figure 3.3: The monthly proportion of adult ( $n = 289$ ), second year ( $n = 60$ ), and juvenile ( $n = 146$ ) European Honey-buzzards (*Pernis apivorus*) in southern Africa over the austral summer season from January 2002 to April 2017. The numbers above the lines indicate the total number of individuals analysed from each month.

The three best fitting age class models included: i) latitude and elevation, ii) elevation, and iii) latitude, elevation, and the interaction between latitude and elevation (Table 3.1). The top model (latitude and elevation) had 43% of the support, while the second model (elevation) had 33%, and the third model (latitude, elevation, and interaction) had 16%. Based on the  $\Delta\text{AICc}$  ( $< 2.0$ ) and ER values, there was far less support for all other models. Model averaging resulted in a coefficient for elevation with confidence intervals that did not overlap zero (Table 3.2). There was less support for the coefficients for latitude, and the interaction between latitude and elevation; both coefficients had confidence intervals that overlapped zero. Based on the model, sub-adult birds were more likely to be found at lower elevations (Figure 3.4). There was less support for sub-adult birds being more likely to be found further south in the sub-region (Figure S3.1).

*Table 3.1:* The results of the binomial logistic generalised linear models assessing the relationship between the likelihood of occurrence for sub-adult versus adult European Honey-buzzards (*Pernis apivorus*) in relation to the following environmental variables: Month = month recorded, Year = year recorded, Lat = latitude of record, Ele = elevation (m), Precip = total austral summer precipitation (mm), Temp = average austral summer temperature ( $^{\circ}\text{C}$ ), Veg = land cover type. \* indicates an interaction between variables. The table includes: number of parameters (K), the AICc difference between the model and the highest ranked model ( $\Delta\text{AICc}$ ), the AICc weight ( $w_i$ ), and the evidence ratio (ER). The models used for model averaging to create the final model are in bold.

Model	K	Log likelihood	$\Delta\text{AICc}$	$w_i$	ER
<b>Lat + Ele</b>	<b>3</b>	<b>-275.21</b>	<b>0.00</b>	<b>0.425</b>	
<b>Ele</b>	<b>2</b>	<b>-276.49</b>	<b>0.54</b>	<b>0.325</b>	<b>1.31</b>
<b>Lat + Ele + Lat*Ele</b>	<b>4</b>	<b>-275.16</b>	<b>1.94</b>	<b>0.161</b>	<b>2.02</b>
Lat	2	-278.50	4.56	0.043	7.47
Lat + Ele + Precip + Temp + Veg	11	-269.37	4.90	0.037	8.88
Lat + Ele + Precip + Temp + Veg + Month + Year	13	-269.04	8.50	0.006	> 20
Precip + Temp + Precip*Temp	4	-279.70	11.02	0.002	> 20
Precip	2	-282.38	12.32	0.001	> 20
Temp + Precip	3	-281.91	13.41	0.001	> 20
Null Model	1	-284.49	14.52	0.000	> 20
Temp	2	-284.33	16.21	0.000	> 20
Month	2	-284.33	16.22	0.000	> 20
Year	2	-284.48	16.52	0.000	> 20
Month + Year + Month*Year	4	-282.79	17.20	0.000	> 20
Month + Year	3	-284.31	18.20	0.000	> 20
Veg	7	-281.27	20.34	0.000	> 20

Table 3.2: The parameter estimates for the final model average of the top three models from Table 3.1. The 95% confidence intervals and the relative importance of the variable are included.

Variable	Parameter estimate	Confidence intervals		Relative importance
		2.5%	97.5%	
Intercept	-0.413	-0.622	-0.204	1
Ele	-0.339	-0.579	-0.100	1
Lat	-0.116	-0.431	0.069	0.64
Lat*Ele	0.008	-0.239	0.330	0.18

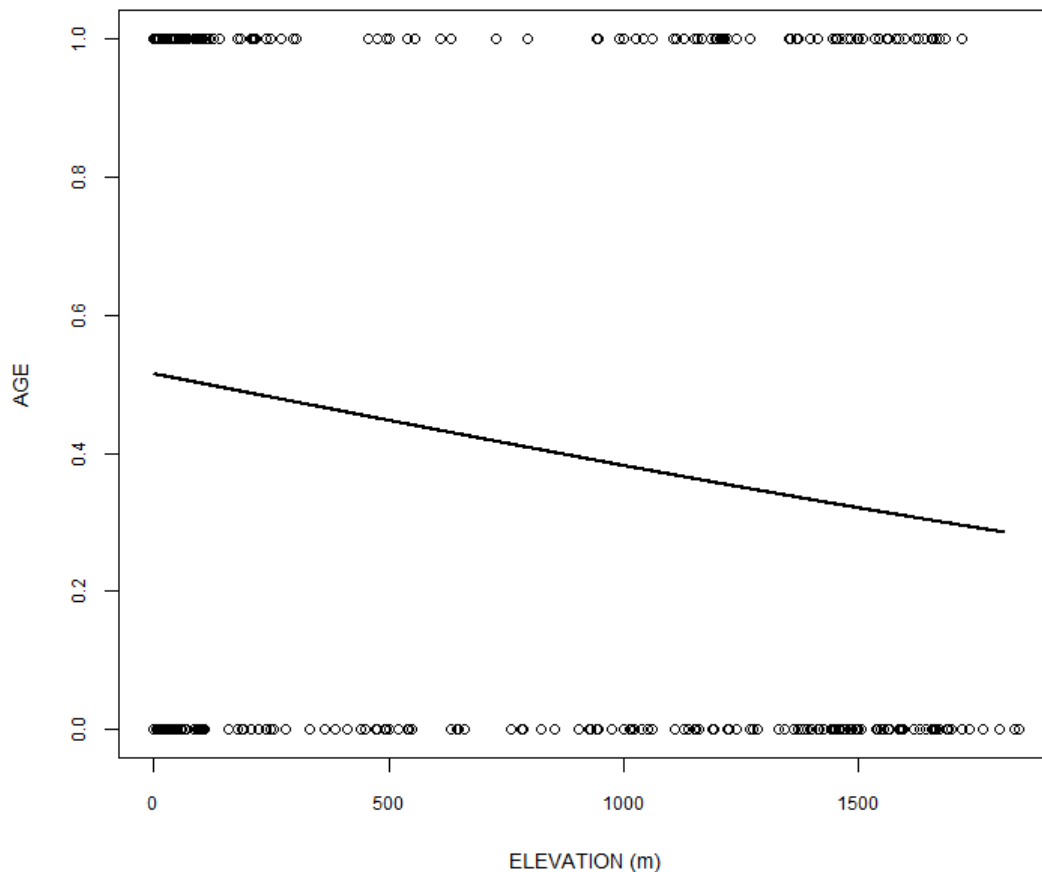


Figure 3.4: The likelihood of sub-adult European Honey-buzzard (*Pernis apivorus*) occurrence relative to elevation in southern Africa based on the model detailed in Table 3.2. Circles represent records of individuals while the line represents the predicted likelihood. 0 = adult bird, 1 = sub-adult bird.

Adult birds arrived in southern Africa earlier than second year birds. There was a statistically significant difference between the arrival date of adult and second year birds ( $H(2) = 7.61, p = 0.02$ ). The average first arrival date for adults was 29 October  $\pm 4.1$  days while the average first arrival date for juveniles was 12 November  $\pm 9.1$  days. Second years first arrived on average on the 11 December  $\pm 10.4$  days.



### 3.4 Discussion

Sex ratios in the adult European Honey-buzzard population of southern Africa are highly skewed towards females. Over the past fifteen years, only nineteen males (6.7% of adult birds) were identified in the sub-region. This contrasts with the nearly even sex ratios of adults (51% males, 49% females) migrating through Falsterbo, Sweden, indicating that this does not reflect a skewed sex ratio on the breeding grounds (Kjellén 1992, 1998). The evidence suggests that the best explanation for this pattern is the *arrival time hypothesis* (Ketterson and Nolan 1976). Male European Honey-buzzards are responsible for establishing a pair's breeding territory (Cramp and Simmons 1979). If a male does not arrive back in time, it is at risk of losing both its territory and mate, as has been documented in many migratory species including European Honey-buzzard (Kokko et al. 2006, Byholm, pers. obs.). Spending the non-breeding season closest to the breeding grounds is one of the few options that could allow for male honey-buzzards to arrive on the breeding grounds earlier as the species does not shorten their migration route or reduce stopover lengths to cut its spring migration time (Vansteelant et al. 2015). Therefore, the long trip to southern Africa, rather than central Africa, is not worth the compromise of an unsuccessful breeding season for male birds. However, in order to confirm this hypothesis, more data need to be collected on spring arrival times in the species as well as information about the sex ratios across the African continent. It is important to note that females are also exposed to the risk of missing a breeding season if they arrive late. The Northern Hemisphere breeding period is very short for European Honey-buzzard, approximately 115 days, meaning there is a narrow window for the birds to breed (Cramp and Simmons 1979). At least one tracked female honey-buzzard with a non-breeding territory in South Africa has failed to breed four out of five seasons, likely due to its late arrival back from Africa (Byholm, unpubl. data).

An alternate explanation for this imbalance in the sex ratios of the southern African honey-buzzard population may relate to the delay of sexual maturity displayed by females of some raptor species (Blas and Hiraldo 2010). In the case of the Black Kite (*Milvus migrans*), young adult male birds showed hormonal levels similar to that of adult males (regardless of whether they were breeding), while young adult females did not (Blas and Hiraldo 2010). Young female kites appeared to reduce their physiological costs by delaying ovarian maturation until they found a mate and were ready to breed, and therefore, had a higher chance of reproductive success (Blas and Hiraldo 2010). This may afford them more flexibility in where they spend their winters. If this applies to European Honey-buzzard, it is possible that

young adult females (third and fourth years) may be more likely to winter further from the breeding grounds due to the fact that they return to Europe later in their life than young male birds.

The southern African population of European Honey-buzzard is made up of 29.5% juvenile birds and 12.1% second year birds, a total of 41.6% sub-adult birds. This appears to be a slightly elevated proportion of juveniles based on the breeding success rates of the honey-buzzard as well as the mortality of juvenile birds on migration and during their exploratory movements on the African continent. The breeding success of European Honey-buzzard is highly variable between populations and years. In a single German population, the reproductive output of the population varied between 0.1 fledglings/pair during poor years, and 1.1 fledglings/pair during good years (Kostrzewa 1989). Similar variation was recorded by Bijlsma et al. (2012) in The Netherlands with an average reproductive rate of 0.74 fledgling/pair over the three-decade study period ending in 2005. This variation from year to year may be reflected in the variable proportions of juvenile and second year birds recorded year to year in southern Africa over the course of the study period. The mortality of the juvenile birds also appears to be high. Strandberg et al. (2009) documented an approximately 30% mortality rate in juvenile migratory raptors on their first autumn migration. In addition, Bijlsma et al. (2012) calculated a survival rate for first year (juvenile) honey-buzzards of 62.5%, which indicates a similarly high mortality rate. Given these values, the expected proportion of juvenile birds would likely be around 20%, which is lower than the proportion observed in this study.

The high proportion of sub-adult honey-buzzards in the sub-region, combined with the fact that sub-adult birds are more common further south and at low elevations (often along the coast), may be driven by a few factors. The first is that juveniles are strongly driven by wind and geography on their first outbound migration (Vansteelant et al. 2017). They are likely not migrating to specific locations like adults but rather just moving southwards (Strandberg et al. 2012, Vansteelant et al. 2017). This naivety combined with the funnelling effect of Africa, meaning that they are drawn from a wide range of natal longitudes and concentrated in the south of the continent, likely explains the high proportion of young birds in southern Africa (Newton 1995, Symes and Woodborne 2010). This effect may be exacerbated by the juveniles' late arrival on the non-breeding grounds, after adults have already established territories, which could press juveniles to continue migrating south (Strandberg et al. 2012). This could partially support the *dominance hypothesis* (Ketterson and Nolan 1976).

Another possible reason for the high proportion of juveniles, particularly in the south of the sub-region, is the *arrival time hypothesis* (Ketterson and Nolan 1976). Juvenile European

Honey-buzzards spend at least three years in Africa before returning to their breeding grounds (Strandberg et al. 2012). This is supported by tracking data, as well as spring migration counts, which indicate that very few second year birds migrate north (Forsman and Shirihai 1997, Hake et al. 2003, Strandberg et al. 2012). Juvenile birds have little pressure to return timeously to the breeding grounds, and therefore, can migrate further south to southern Africa.

Lastly, the higher likelihood of juveniles in lower elevation areas may be a result of their documented exploratory behaviours. Adult European Honey-buzzards have high site fidelity to their non-breeding territory (Strandberg et al. 2012). Juvenile and second year birds are much more likely to wander into novel habitats, potentially testing different sites for their future, more permanent adult non-breeding territories (Strandberg et al. 2012, Cresswell 2014). Juveniles are, therefore, more likely to be in areas that adults have not selected. Strandberg et al. (2012) also noted that juvenile honey-buzzards moved southwards towards the coast before beginning more extensive intra-African movements.

The case of the second year honey-buzzards is less clear. They are the last to arrive but may be arriving from somewhere within Africa rather than Europe due to their long sub-adult period on the continent (Cramp and Simmons 1979, Strandberg et al. 2012). They are, however, unlikely to be individuals that have spent the Northern Hemisphere summer in southern Africa, as there are few records from June to August (austral winter) in the sub-region (eight over the past 40 years) (Howes, Byholm, and Symes, unpubl. data). This late arrival may actually reflect juvenile birds beginning their transition into second year plumage rather than late arriving individuals. This is further supported by the increased proportion of second year birds later in the austral summer season. An alternate hypothesis for the increase in second year individuals later in the season is that there is intra-African movement of young birds southwards during the austral summer. This could potentially be in response to an influx of adult birds further north in their African range, resulting in juveniles being pushed out of their austral winter territories (Strandberg et al. 2012). Alternatively, this movement could be as a result of changes in environmental conditions over the course of the austral summer, which cause southern Africa to become a more attractive foraging area for honey-buzzards (Strandberg et al. 2012).

In this study, we assumed an equal chance of detection and identification of all ages and sexes of European Honey-buzzards by birdwatchers in southern Africa. However, there are known differences between the movement patterns of adult and sub-adult honey-buzzards in Africa with juveniles travelling far more widely than adults (Strandberg et al. 2012). This may mean young birds are more likely to be detected as they move through more open landscapes between denser woodland patches. There may, similarly, be differences between

the movement behaviours of male and female honey-buzzards on the non-breeding grounds that have yet to be assessed. The trends documented in this study will need to be further confirmed using the ample tracking data of this species.

The southern Africa population of European Honey-buzzard appears to be expanding in range and population size, which makes it an important population to understand in terms of demographics (Howes et al. 2019). As has been mentioned, this population has a sex ratio that is strongly biased towards females, and has a relatively large proportion of juvenile birds. There has been no change in these ratios over the expansion period of this species in the sub-region. Due to low recruitment of juveniles to the breeding population (Bijlsma et al. 2012), the southern African population may be particularly important due to its slightly larger proportion of juveniles. To further understand the migratory timing and behaviour of adult European Honey-buzzards, monitoring of the migratory bottlenecks could better record the sexes of birds, particularly during spring migration, to determine any differences in the arrival periods of male and female birds. In addition, further tracking of second year individuals, especially birds from southern Africa, could help elucidate the intra-African movements of young honey-buzzards to determine if there are any predictable patterns in the north-south movement of sub-adult European Honey-buzzards.

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3.6 Supplementary Information

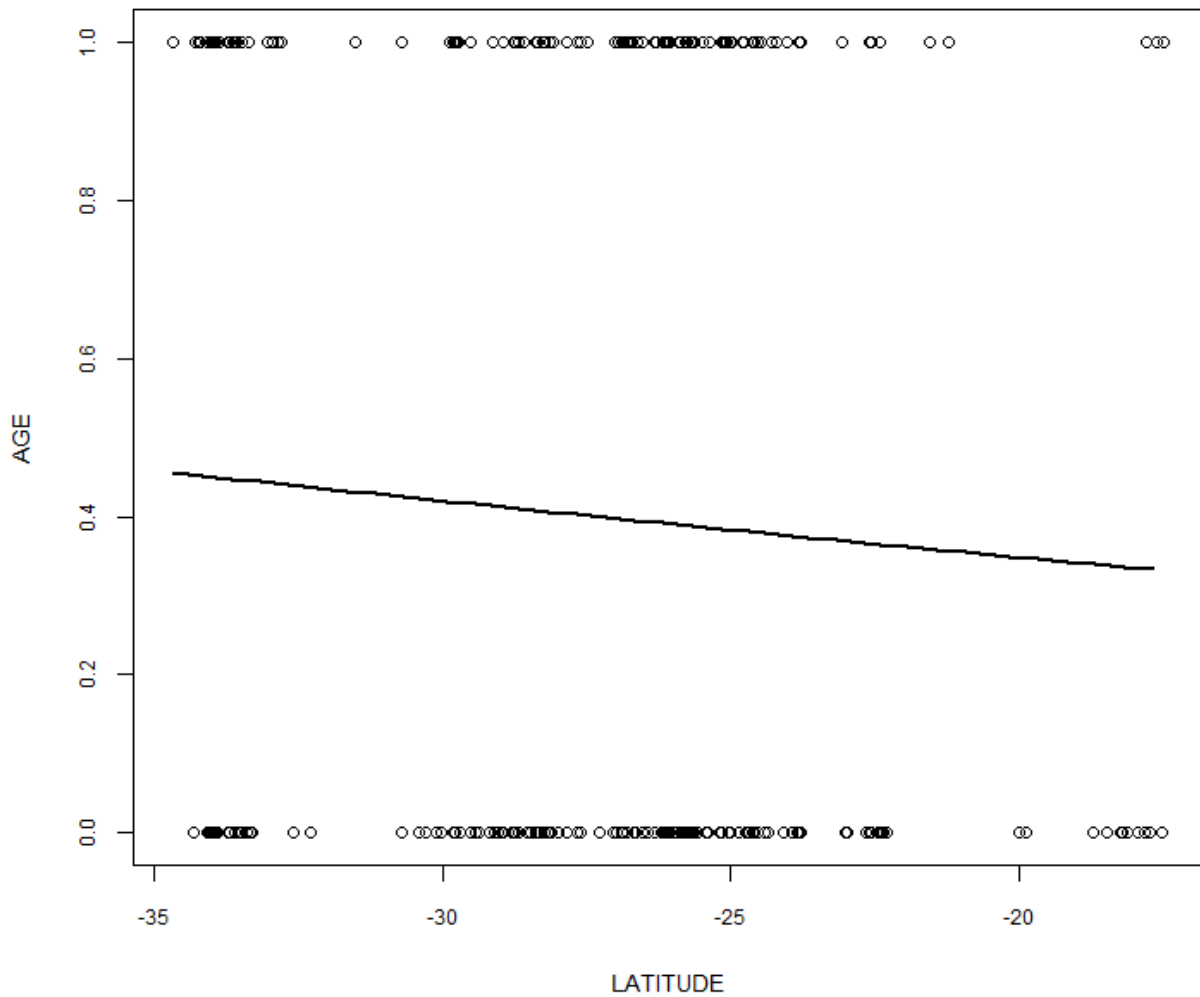
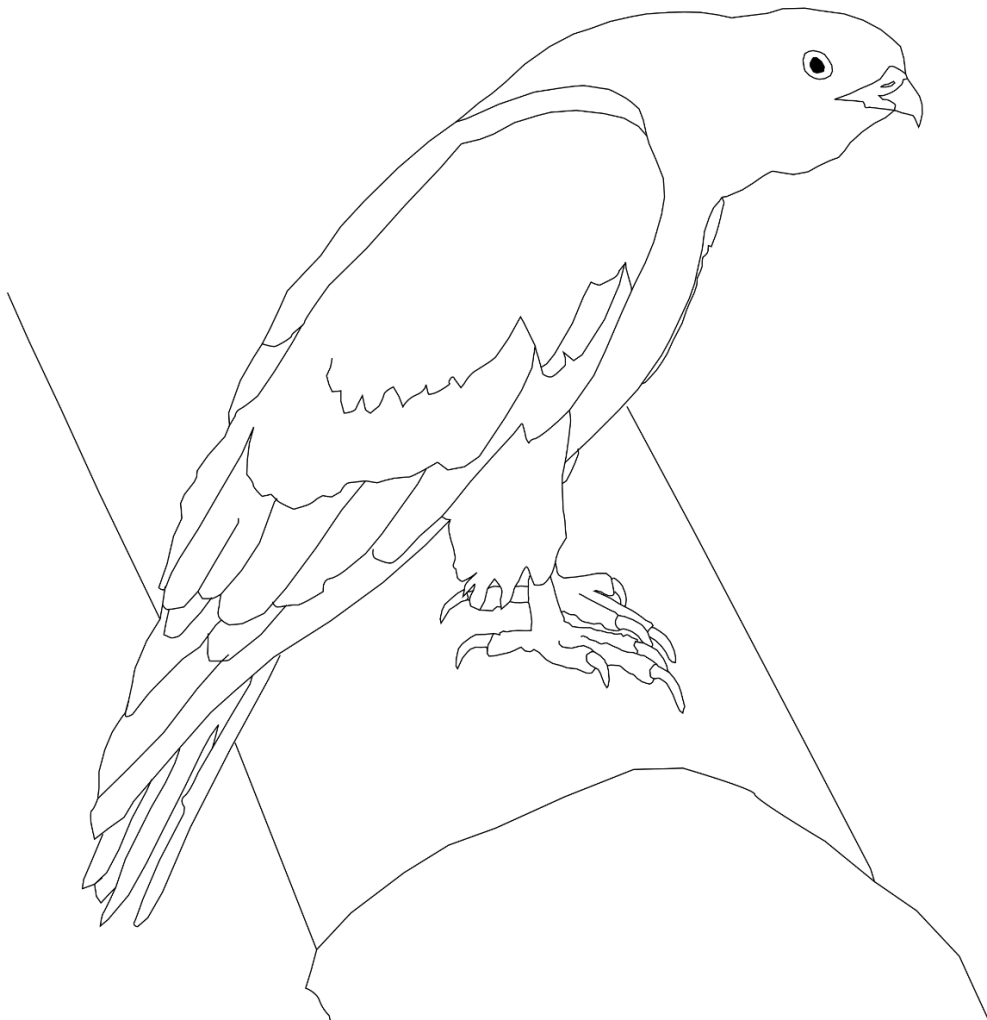


Figure S3.1: The likelihood of sub-adult European Honey-buzzard (*Pernis apivorus*) occurrence relative to latitude in southern Africa based on the model detailed in Table 3.2. Circles represent records of individuals while the line represents the predicted likelihood. 0 = adult, 1 = sub-adult.

**Temporal morph instability in  
European Honey-buzzard  
(*Pernis apivorus*)**





## *Abstract*

Plumage polymorphism, a common phenomenon in birds of prey, appears to be maintained by a variety of evolutionary processes. In this study, we assessed the colour morphs of the southern African non-breeding population of the continuously polymorphic European Honey-buzzard (*Pernis apivorus*) using photographs from several rarity-reporting and citizen-science platforms. We found significant differences across age classes with a disproportionate proportion of dark morph juveniles, as well as sexes with a greater proportion of pale morph males. The difference between age classes may indicate that juveniles exhibit temporal morph instability, but further study is needed to determine whether this is expressed in adults.

*Keywords:* colour morph, European Honey-buzzard, morph instability, *Pernis apivorus*

## *4.1 Introduction*

Plumage polymorphism occurs in 3.5% (334 species) of all bird species (Galeotti et al. 2003). Polymorphism is widespread taxonomically with at least one species that displays this plumage trait in a third of all bird families (Galeotti et al. 2003). There are three main hypotheses for the maintenance of plumage polymorphism: i) apostatic selection related to higher hunting success or lower predation risk on rarer morphs, ii) disruptive selection related to differential hunting success or thermoregulation ability for each morph depending on the habitat, or iii) sexual selection related to non-random mating of morphs (Galeotti et al. 2003, Galeotti and Rubolini 2004, Roulin and Wink 2004, Wellenreuther et al. 2014). In addition to these evolutionary explanations, there is also the possibility that there is no direct selection value for or against colour morphs.

Two bird of prey families, Strigidae and Accipitridae, have the greatest proportion of colour polymorphism of any bird families (Galeotti et al. 2003). All three of the possible evolutionary hypotheses for morph maintenance have at least some support in the Accipitridae (Galeotti et al. 2003, Galeotti and Rubolini 2004, Roulin and Wink 2004, Wellenreuther et al. 2014). Galeotti and Rubolini (2004) found that polymorphic bird of prey species were more likely to be migratory and/or live in a diversity of habitats, but found no relation between polymorphism and prey type. Based on these results, they supported the disruptive selection hypothesis for maintenance of polymorphism. Roulin and Wink (2004) examined polymorphism in two genera, *Buteo* and *Accipiter*, and contrary to Galeotti and Rubolini (2004)

found evidence that species that preyed on primarily mammals had a greater likelihood of polymorphism than species that hunted other prey, providing evidence for the apostatic selection hypothesis. Lastly, Krüger and Lindström (2001) recorded assortive mating in Common Buzzard (*Buteo buteo*), validating the sexual selection hypothesis. Based on current understanding, it seems highly likely that plumage polymorphism is driven by all three types of selection.

While plumage polymorphism has been well-studied in many raptors with discrete colour morphs (e.g. Black Sparrowhawk *Accipiter melanoleucus* (Amar et al. 2013), Tawny Owl *Strix aluco* (Brommer et al. 2005), Booted Eagle *Hieraaetus pennatus* (Bosch et al. 2019)), it has been less studied in continuously polymorphic species e.g. species with a continuum of possible morphs. This may be, in part, because 72.2% of polymorphic bird species exhibit only two morphs (Galeotti et al. 2003). Common Buzzard is the best studied of the continuously polymorphic or hyperpolymorphic raptor species (Krüger and Lindström 2001, Schreiber et al. 2001, Boerner and Krüger 2008, Chakarov et al. 2008, Boerner et al. 2013, Chakarov et al. 2013, Jonker et al. 2014, Kappers et al. 2017, 2018). Common Buzzard is commonly divided into three morphs: i) light, ii) intermediate, and iii) dark (e.g. Krüger and Lindström 2001, Boerner and Krüger 2008, Chakarov et al. 2008). Through the long-term documentation of several Common Buzzard populations, studies have documented differences in lifetime reproductive success (Krüger and Lindström 2001), annual survival (Jonker et al. 2014), aggression (Boerner and Krüger 2008), and parasite load (Chakarov et al. 2008) between the morphs. The intermediate morph has proven to be more successful over its lifetime, indicating that differences between morphs may be more complex than just plumage alone.

European Honey-buzzard (*Pernis apivorus*) is a Palaearctic migratory raptor that exhibits continuously polymorphic plumage similar to Common Buzzard (Cramp and Simmons 1979). While morphs in Common Buzzard have been well documented, there is relatively little detailing the colour morphs of the honey-buzzard, and very little is known about the colour morph ratios or temporal stability of morphs in the species. In this study, we used rarity-reporting platforms to document the colour morph ratios of the European Honey-buzzard population in southern Africa. We assessed the colour morph ratios of different age classes and sexes to examine how these ratios differed between these groups in order to better understand the temporal stability of colour morphs in honey-buzzard, and discuss the possible selection advantages of colour morphs in juveniles.

## 4.2 Methods

The European Honey-buzzard is considered a rarity in southern Africa (Howes et al. 2019). Due to this, photographs of honey-buzzard in the sub-region are regularly shared on rarity-reporting platforms and social media in the sub-region (Howes et al. 2019). Photographs of European Honey-buzzard from across the southern African sub-region were collected from four sources: i) the Zest for Birds website, ii) the Southern African Rare Bird Newsletter (SARBN), iii) the Animal Demography Unit's Virtual Museum, and iv) two Facebook groups (BirdLife South Africa and SA Rare Birds) (Howes et al. 2019). Zest for Birds is a website that records photographs of rarities in southern Africa from January 2002 to December 2010. SARBN is the email list-server used to circulate rarity information in the sub-region. SARBN records used in this study spanned July 2008 until July 2017. The Animal Demography Unit's Virtual Museum documents photographs of biodiversity from across Africa provided by citizen scientists. All photographs were downloaded and entered into a database with the date, location, photographer, and source.

Each photograph was evaluated for three variables: i) age class, ii) sex, and ii) colour morph. Three age classes were identified: i) juvenile, ii) second year, and iii) adult. We assessed four characteristics to assign each individual European Honey-buzzard to an age class: i) eye colour, ii) bill and cere colour, iii) secondary feather barring, and/or iv) primary feather pattern (Cramp and Simmons 1979, Forsman and Shirihai 1997). At least two characteristics were used to age all individuals. For further detail on assigning birds to age classes, see Chapter 3, p. 61.

Only adult European Honey-buzzards were identified to sex, as it is not possible to sex sub-adult birds using plumage characteristics (Cramp and Simmons 1979, Forsman and Shirihai 1997). Three traits were used to identify the sex of each bird: i) secondary feather barring, ii) tail feather barring, and/or iii) head colour (Cramp and Simmons 1979, Forsman and Shirihai 1997). One of these characteristics was sufficient to sex an individual. For further detail on how adult birds were sexed, see Chapter 3, p. 62.

For each photograph, four sections of the body were assessed for the proportion of melanic feathers: i) breast, ii) belly, iii) left flank, and iv) left underwing coverts (Brommer et al. 2005, Briggs et al. 2010, Dreiss et al. 2012). The percent of melanic feathers was estimated to the nearest 5% and was then assigned the following categories: 1 < 10% melanic, 2 = 10-49% melanic, 3 = 50-90% melanic, 4 > 90% melanic (Brommer et al. 2005, Briggs et al. 2010). The body part scores were averaged to get an overall score. The number of parts assessed was also recorded. Scores were assigned morphs as follows: < 2 = pale,  $\geq 2$  and < 3 = pale

intermediate,  $\geq 3$  and  $< 4$  = dark intermediate, 4 = dark (Dreiss et al. 2012). Photographed individuals from the same location and year that were also the same age class, sex, and colour morph were assessed to determine if they were different individuals. If birds were found to be the same individual based on unique markings, only the earliest photograph was included.

For colour morph analysis, a Kruskal-Wallis test was used to determine if the number of body parts assessed had an effect on the colour score of an individual honey-buzzard. Once this was assessed, the proportion of colour morphs was compared between age classes and sexes using a  $\chi^2$  test.

### *4.3 Results*

A total of 498 individual European Honey-buzzards were collected from the four rarity-reporting platforms. 67.0% of the photographed birds ( $n = 334$ ) were ascribed to a colour morph while 33.0% ( $n = 164$ ) had none of the polymorphic body parts visible. The majority of these birds (88.9%,  $n = 297$ ) were photographed in South Africa with 5.1% from Namibia ( $n = 17$ ), 3.0% from Mozambique ( $n = 17$ ), 2.1% from Zimbabwe ( $n = 7$ ), and 0.9% from Botswana ( $n = 3$ ). There was no significant difference between the colour score of European Honey-buzzards with different numbers of body parts visible ( $H(3) = 0.35$ ,  $p = 0.95$ ).

Of the identified individuals, 59.2% ( $n = 202$ ) were adults, 10.0% ( $n = 34$ ) were second years, and 30.8% ( $n = 105$ ) were juveniles. There was a significant difference in the proportion of birds of different morphs across age classes ( $\chi^2 = 83.46$ ,  $df = 6$ ,  $p < 0.01$ ) (Figure 4.1). The majority of juvenile birds were dark morphs (80.0%,  $n = 79$ ), while the majority of adult birds were dark intermediate morphs (50.1%,  $n = 103$ ). Pale morphs were very uncommon in juveniles (1.0%,  $n = 1$ ) and adults (3.5%,  $n = 7$ ), but were slightly more prevalent in second years (14.7%,  $n = 5$ ).

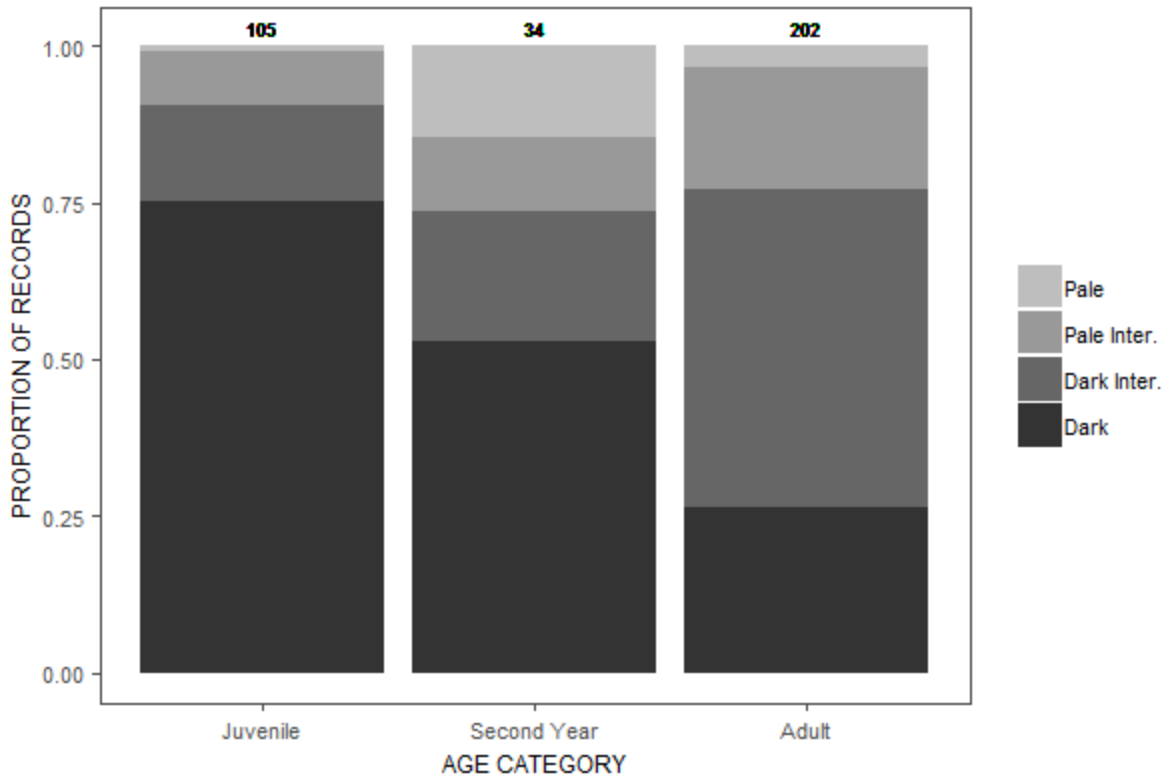


Figure 4.1: The proportion of European Honey-buzzards (*Pernis apivorus*) of four colour morphs across three age classes in southern Africa from January 2002 to July 2017.

A single juvenile European Honey-buzzard was found in the Waterberg, Limpopo province, South Africa by the Johannesburg Wildlife Veterinary Hospital in March 2016, and euthanized due to a wing injury. The individual had worn dark morph feathers, and new light intermediate feathers (Figure 4.2).

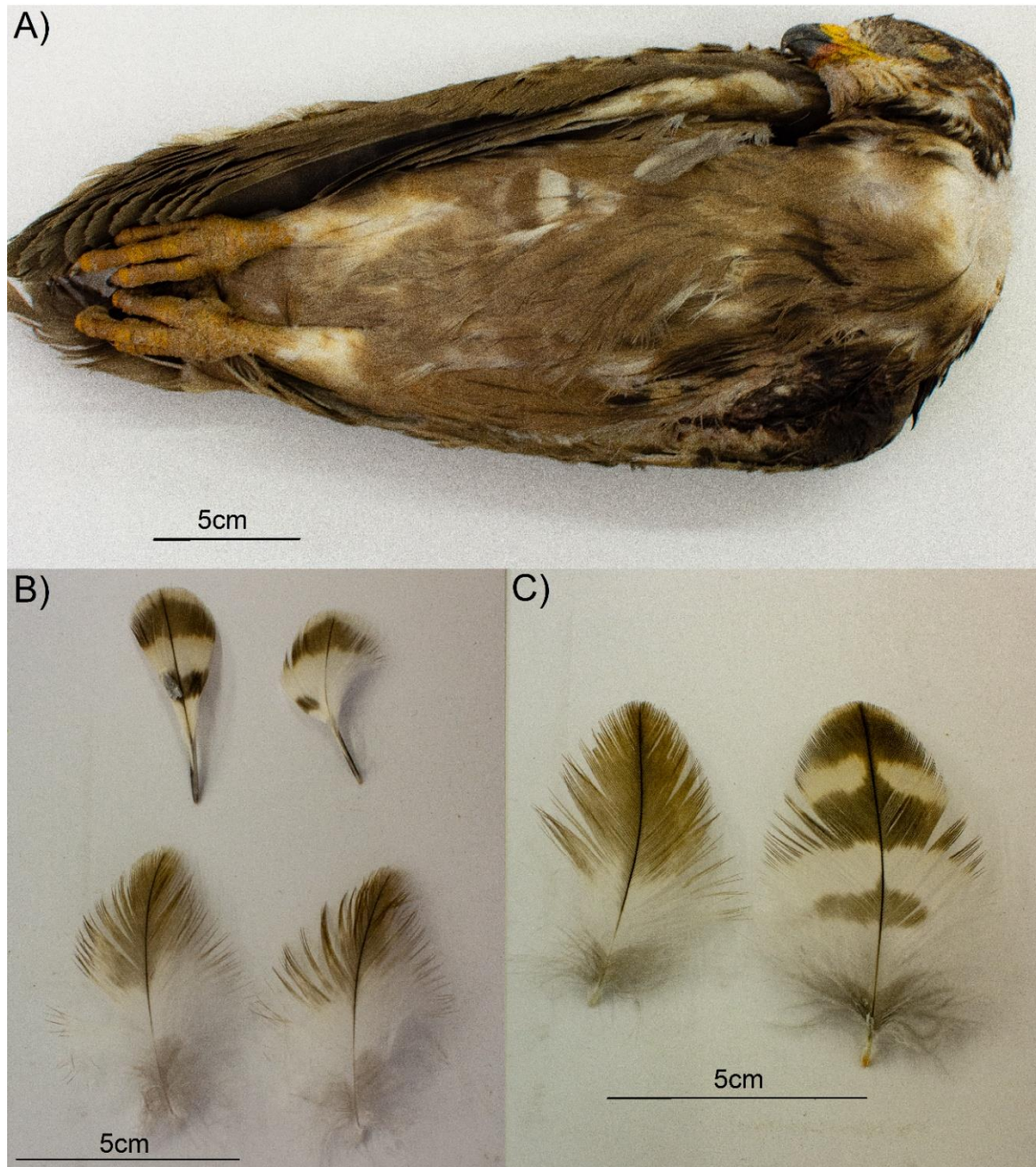


Figure 4.2: Photographs of: A) a juvenile European Honey-buzzard (*Pernis apivorus*) specimen found in March 2016 in the Waterberg, Limpopo province, South Africa, B) breast feathers (worn, dark morph feathers at bottom and new, dark intermediate morph feathers on top), and C) flank feathers (worn, dark morph feather on left and new, dark intermediate morph feather on right).

A total of 198 adult honey-buzzards designated to colour morph could also be assigned to sex. Of this sample, 7.6% were males, and 92.4% were females. There was a significant difference in the proportions of different morphs between sexes ( $\chi^2 = 17.52$ ,  $df = 3$ ,  $p < 0.01$ ) (Figure 4.3). While the majority of both male and female birds were of the dark intermediate morph, there were higher proportions of both pale (20.0%,  $n = 3$ ) and dark (33.3%,  $n = 5$ )

morphs in males than in females. Females had a greater proportion of pale intermediate morphs (20.8%, n = 38) than males.

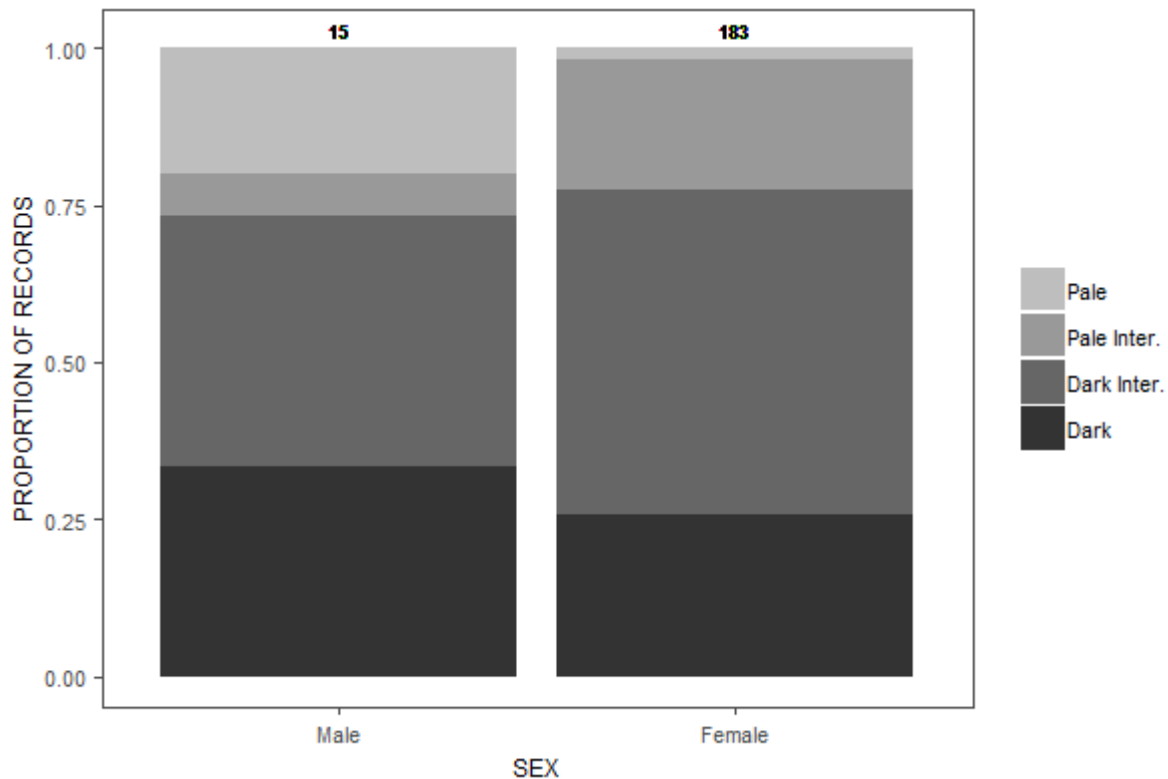


Figure 4.3: The proportion of adult European Honey-buzzards (*Pernis apivorus*) of four colour morphs across sexes in southern Africa from January 2002 to July 2017.

#### 4.4 Discussion

Colour morph ratios differed significantly between both ages and sexes of European Honey-buzzards in southern Africa. Across all ages and sexes, however, the southern African population of honey-buzzard was disproportionately of the darker morphs with over 50% melanic feathers (i.e. dark and dark intermediate). This contrasts with findings in Common Buzzard which showed that the majority of individuals were found in the intermediate range with relatively few very dark birds (Kappers et al. 2017). The small differences in colour morph ratios between the sexes showed that males were more likely to be of extreme morphs than females. However, our sample of male birds was very small due to the highly skewed sex ratio of adult birds in southern Africa (Chapter 3).

The differences between adult and juvenile European Honey-buzzard colour morph ratios were significant. The vast majority of juveniles were dark morph while the majority of adults were dark intermediate morph. The adult population also showed a greater diversity of

colour morphs than the juvenile birds. The second year birds fell in between the adult and juvenile populations in terms of colour morphs. The high proportion of dark juveniles has been previously noted in Israel during outbound migration (Forsman and Shirihai 1997). This may indicate that European Honey-buzzard does not show temporal stability in colouration as an individual matures. This hypothesis is supported by the moult of a single juvenile honey-buzzard carcass found in South Africa that had newer dark intermediate morph feathers growing in between its older dark morph feathers.

Temporal morph stability has been noted in the Black Sparrowhawk, Swainson's Hawk (*Buteo swainsonii*), and Common Buzzard (Briggs et al. 2010, Amar et al. 2013, Kappers et al. 2017). All of these species have been found through mark-recapture studies to retain their juvenile colour morph into adulthood. It should be noted, however, that both Black Sparrowhawk and Swainson's Hawk have a discrete number of morphs rather than the clinal morphs evident in Common Buzzard and European Honey-buzzard (Cramp and Simmons 1979, Briggs et al. 2010, Amar et al. 2013, Kappers et al. 2017). While this morph instability has not been recorded in raptor species, it has previously been documented in Long-tailed Jaeger (*Stercorarius longicaudus*), which has both pale and dark morph juveniles but only dark morph adults (Olsen 1989).

The high proportion of dark morph juveniles raises the question of the possible selection advantages of the dark morph for this age group. Dark morphs have shown several advantages in other species. To begin, darker feathers tend to have decreased feather wear, as has been documented in New Zealand Fantails (*Rhipidura fuliginosa*) and Barn Owls (*Tyto alba*) (Roulin 2007, Mackiven and Briskie 2014). In juvenile honey-buzzards, this may allow them to keep feathers longer and moult when they are in better body condition later in their lives. Alternately, the dark morph juvenile birds may be more suited to their typical forested habitat in Africa, where they spend a minimum of two to three years before their first northerly migration (Strandberg et al. 2012). The dark morph birds may be better able to camouflage in darker environments as has been hypothesized in Black Sparrowhawk, or may be better suited to the climates of the African continent (Galeotti et al. 2003, Tate et al. 2016). In addition, the more solid colouration of the dark morph may allow young European Honey-buzzards to better mimic more "dangerous" raptors, e.g. young hawk-eagles (*Hieraaetus* sp.) or buzzards (*Buteo* sp.) (Nijman et al. 1999, Duff 2006). This possible mimicry could allow juvenile honey-buzzards to avoid predation or conflict with other birds of prey including conspecifics.

If the dark morph plumage of juvenile European Honey-buzzards does provide individuals with selection benefits during their time in Africa, this may mean that adults of



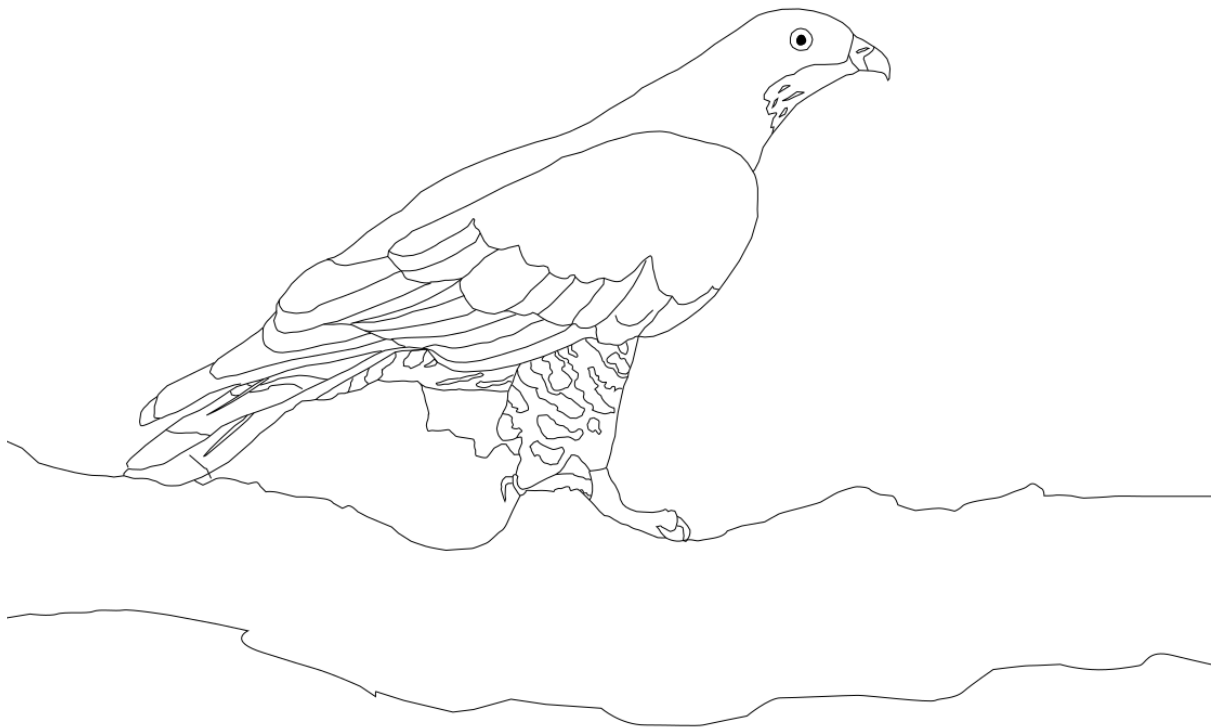
other morphs are not as fit on the non-breeding grounds. Different colour morphs are, therefore, likely to provide honey-buzzards with benefits on the breeding grounds or to be genetically linked with other traits in order to be maintained in the population. This concept has been documented in Swainson's Hawk, which showed clinal variation of colour morphs on the species' breeding grounds (Amar et al. 2019). However, there is little migratory connectivity between the breeding and non-breeding grounds of Swainson's Hawks across North America, which likely results in colour morphs mixing substantially on the non-breeding grounds (Amar et al. 2019). A thorough study of European Honey-buzzard colour morph ratios in Europe could determine if there is a selection advantage on their breeding grounds that is driving the high variation in adult morphs.

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**Forest availability and  
fragmentation drive movement  
behaviour of non-breeding  
European Honey-buzzard (*Pernis  
apivorus*) in Africa**



## *Abstract*

Decreases in suitable habitat due to loss and fragmentation on the African non-breeding grounds are believed to be a driver of declines in Palaearctic migrants. However, the direct effects of habitat loss and fragmentation on individual migrants has rarely been investigated. European Honey-buzzard (*Pernis apivorus*), a migratory forest specialist, displays the characteristics of a species that would be particularly sensitive to habitat loss and fragmentation. In this study, we assessed site fidelity, habitat selection, and home range characteristics of 32 tracked European Honey-buzzards in Africa to better understand how habitat transformation on the non-breeding grounds affects the movement behaviour (particularly habitat use and home range characteristics) of the species. Adults had greater site fidelity than juveniles indicating that young birds were exploring in order to locate suitable habitat for future non-breeding territories. Individuals of both ages were more faithful to their home range locations than their stopover sites, suggesting that birds respond to local stopover conditions rather than returning to the same sites annually. Birds of all age classes strongly selected treed habitat, as expected. For both home ranges and stopover sites, treed largest patch index and edge density had a negative effect on home range size indicating that honey-buzzards rely on large tracts of continuous forest, but can tolerate some level of fragmentation. Individuals with larger home ranges moved greater distances daily. This reveals that birds that do not have access to a large patch of forest are moving further, and likely expend more energy which may have adverse effects on their long-term survival. These analyses support the hypothesis that continuing forest loss in Africa may have a negative effect on the European Honey-buzzard population.

*Keywords:* European Honey-buzzard, fragmentation, habitat selection, home range, *Pernis apivorus*, satellite tracking

## *5.1 Introduction*

The habitat quality of migrant birds on their non-breeding grounds affects both their future survival as well as breeding success (Sherry and Holmes 1996, Norris et al. 2004, Gunnarsson et al. 2005, Grande et al. 2009). This phenomenon has been well documented, e.g. in the American Redstart (*Setophaga ruticilla*), a Neotropical migrant passerine, where individual birds that were in the least suitable habitats were found to lose significantly more body mass over the non-breeding period than those in the most suitable habitats (Sherry and Holmes

1996). The birds in poor habitat were also more likely to either die or immigrate to more suitable areas than those in better habitats. In terms of breeding success, male American Redstarts that wintered in higher-quality habitat arrived back on the breeding grounds earlier which allowed them to fledge more young (Norris et al. 2004). Females from more suitable non-breeding habitats were able to produce an additional two chicks, and to fledge their offspring almost a month earlier than females from less suitable habitats (Norris et al. 2004). While the effects of non-breeding habitat quality have been best studied in passerines, they have also been documented in other migratory bird species such as Black-tailed Godwit (*Limosa limosa*) and Egyptian Vulture (*Neophron percnopterus*) (Gunnarsson et al. 2005, Grande et al. 2009).

An important aspect of habitat quality is habitat fragmentation. Habitat fragmentation affects birds at both a community level and an individual level (Redpath 1995a, Redpath 1995b, Tellería and Santos 1995, Bueno et al. 2018). On a community level, habitat fragmentation disproportionately affects specialist, low abundance, range-restricted, and large-bodied bird species (Bueno et al. 2018). On an individual level, there is variation in how fragmentation affects behaviour and breeding success (Redpath 1995a, Redpath 1995b, Sunde and Redpath 2006, Hinam and St. Clair 2008). In Tawny Owls (*Strix aluco*), birds with a smaller area of their preferred woodland habitat had larger home ranges, and flew further each night (Redpath 1995a, Redpath 1995b, Sunde and Redpath 2006). This may indicate that the birds had to expend more energy foraging in order to feed themselves and their offspring. This trend was reversed in the Northern Saw-whet Owl (*Aegolius acadicus*), which had smaller home ranges when there was less forest cover and more fragmentation (Hinam and St. Clair 2008). However, this trend had a negative effect on the owls in fragmented habitats, which had higher stress levels and lower breeding success (Hinam and St. Clair 2008). Similarly, Black Sparrowhawk (*Accipiter melanoleucus*) pairs in the Western Cape province, South Africa, had higher breeding success in larger patches of their preferred forested habitat (Curtis 2005). The effect of fragmentation on individuals has not been well-studied in migrant birds on their non-breeding grounds.

Decreases in habitat quality on the non-breeding grounds are believed to be one of the causes of large declines in Palaearctic migrant birds (Sanderson et al. 2006, Ockendon et al. 2012). Palaearctic migrants have been declining at a greater rate than European short-distance migrant and resident species (Sanderson et al. 2006, Heldbjerg and Fox 2008, Ockendon et al. 2012, Morrison et al. 2013). Within Palaearctic migrants, Afrotropical migrants have declined at the greatest rate (Ockendon et al. 2012, Morrison et al. 2013). This may be linked with large-scale forest loss in Africa (Achard et al. 2014, Taubert et al. 2018). Over the past ten years, there has been a net deforestation rate of 1.36% per annum for dry forests, and 0.29% per annum for

humid forest (Achard et al. 2014, Taubert et al. 2018). In addition to forest loss, there is also high fragmentation, with 9.9% of African forest area comprised of fragments that are under 10,000 ha (Taubert et al. 2018). With continued deforestation at the current level, these patches will increase in number and decrease in size (Taubert et al. 2018). This is likely to cause a reduction in high-quality non-breeding habitat for many migrant bird species in Africa, particularly tropical forest migrants.

The European Honey-buzzard (*Pernis apivorus*) is a declining Palaearctic migrant (Cramp and Simmons 1979, Kostrzewa 1987, Benusan et al. 2007). On its breeding grounds in Europe, it is a forest and dietary specialist, feeding mainly on wasp larvae (Cramp and Simmons 1979, Löhmus 2005). Due to its specialist nature, it is a species that fits the profile of a fragmentation-sensitive species (Bueno et al. 2018). Currently, very little is known about the honey-buzzard's non-breeding behaviour in Africa (Strandberg et al. 2012, Vansteelant et al. 2017). Adults are generally believed to hold single territories over most of the Northern Hemisphere winter (Strandberg et al. 2012). Juveniles wander widely in Africa for at least two to three years (although often much longer) before returning for their first breeding effort (Strandberg et al. 2012, Vansteelant et al. 2017).

In this study, we assessed: i) what types of habitat are preferred by the European Honey-buzzard, and ii) how the availability of this habitat and habitat fragmentation affects the movement of this species. With regards to the first question, we hypothesise that honey-buzzards in Africa will select treed habitats (e.g. forests and woodlands) based on their forested breeding habitats (Cramp and Simmons 1979, Löhmus 2005). In terms of our second question, it seems likely that greater habitat fragmentation will result in both larger home ranges and greater daily movement in European Honey-buzzards as documented in Tawny Owls, another woodland species (Redpath 1995a, Redpath 1995b, Sunde and Redpath 2006). By better documenting the movement patterns of this declining species, this study details how habitat transformation and fragmentation modifies this specialist's daily behaviour on the non-breeding grounds. We aimed to examine habitat use and home range characteristics, particularly with regards to habitat fragmentation, of the European Honey-buzzard in order to further understand how habitat transformation may also contribute to the recently documented large-scale southwards range shift (Howes et al. 2019).

## 5.2 Methods

### 5.2.1 Origin and tracking of honey-buzzards

A total of 32 European Honey-buzzards were fitted with tracking devices (Table 5.1). Thirty of these birds (nine adults and 21 fledglings) were tagged in southern Finland (61°14'-63°12'N, 21°16'-23°31'E). Twenty-one nests in 16 territories were visited. Adults were caught at nests using a dho-ghaza (Zuberogoitia et al. 2008). Fledglings were tagged during the final stage of the brood phase. Two adult females were also tagged in South Africa (named Caroline and Shiraz). Both birds were from wildlife rehabilitation centres. Nestlings were sexed using DNA obtained from blood samples (Vansteelant et al. 2017). Adults were sexed using plumage characteristics (Forsman and Shirihai 1997, Vansteelant et al. 2017).

Birds were equipped with either solar-powered Argos-GPS platform terminal transmitters (PTTs) (Microwave Telemetry Inc.), GSM-GPS trackers (Ecotone) or UvABiTS-GPS trackers. The tags weighed 22-27 g, which is equivalent to approximately 3% of the bird's mass. Trackers were attached using the body-loop method with Teflon ribbon (Kenward 2004). The amount of tracking data from each bird varied due to settings, geographical location, weather, and tracking duration (Table 5.1).



Table 5.1: The name, sex, age, tag deployment dates, number of days tracked, and number of austral summers tracked of 32 tracked European Honey-buzzards (*Pernis apivorus*).

Device	Name	Sex	Age	Tag date	Days tracked	Austral summers
118745	Aarne	Male	Adult	24 July 2012	641	2
118746	Aida	Female	Juvenile	2 August 2012	716	2
HBFI07	Anni	Female	Juvenile	5 August 2013	1,082	3
59360	Annika	Female	Adult	5 August 2011	1,488	4
HBFI16	Caroline	Female	Adult	31 December 2017	153	1
HBFI08	Edit	Female	Juvenile	2 August 2013	686	2
59956	Ella	Female	Juvenile	13 August 2013	126	1
59963	Hans	Male	Juvenile	2 August 2012	598	2
118748	Heidi	Female	Juvenile	9 August 2013	499	2
59804	Jaana	Female	Juvenile	28 July 2011	1,386	4
621	Jari	Male	Adult	27 July 2012	1,118	2
6056	Johannes	Male	Adult	20 July 2013	1,072	2
59284	Jouko	Male	Adult	28 July 2011	1,494	5
HBFI02	Julia	Female	Juvenile	16 August 2013	151	1
59803	Kari	Male	Adult	27 July 2011	534	2
59805	Lars	Male	Juvenile	8 August 2011	1,550	4
HBFI05	Matti	Male	Juvenile	9 August 2013	658	2
HBFI06	Miika	Male	Juvenile	8 August 2013	240	1
59624	Mikko	Male	Adult	5 August 2011	1,735	5
HBFI04	Mohammed	Male	Juvenile	13 August 2013	1,082	3
59808	Päivi	Female	Adult	13 August 2013	1,759	5
59644	Piff	Female	Juvenile	6 August 2011	197	1
59957	Puff	Female	Juvenile	6 August 2011	648	2
59612	Roosa	Female	Juvenile	5 August 2011	189	1
59358	Rudolf	Male	Juvenile	2 August 2012	183	1
59955	Senta	Female	Juvenile	8 August 2012	2,077	6
59804	Shiraz	Female	Adult	6 December 2016	543	2
59808/6057	Tiina	Female	Adult	27 July 2011	1,802	5
59806	Tor	Male	Juvenile	28 July 2012	155	1
HBFI01	Ulla	Female	Juvenile	5 August 2013	127	1
59964	Valentin	Male	Juvenile	8 August 2012	1,310	5
59964	Venus	Female	Juvenile	8 August 2012	1,008	4

### 5.2.2 Home range calculation

Using ArcGIS 10.3, all tracking points were clipped to the African continent. Two types of habitat use areas were characterized: i) home ranges, and ii) stopover sites. Home ranges were defined as areas where a bird moved less than 25 km between the first and last points of a day for at least fifteen consecutive days (Limiñana et al. 2014, Vansteelant et al. 2017). Stopover sites were defined as areas where a bird moved less than 25 km between the first and last points of a day for at least three consecutive days but less than fifteen consecutive days (Vansteelant et

al. 2017). In order to calculate this, the distance between the first and last point for each day was calculated using ‘deg.dist’ from the R package ‘fossil’ (R Core Development Team 2018). Once the home ranges and stopover sites were identified, individual point shapefiles were created for each home range.

For each home range and stopover site, three metrics of home range size were calculated: i) minimum convex polygon (MCP), ii) 50% kernel, and iii) 95% kernel. All home range estimators were calculated using Geospatial Modelling Environment (GME) (Spatial Ecology LLC, 2014, vers. 0.7.4.0). MCP was calculated in order to better compare home range size with older studies of similar species, as well as to give an estimate of habitat availability. The 50% kernel was used to estimate the core of the bird’s home range, while 95% kernel was used as a conservative estimate of entire home range. For kernel density estimates in GME, least-squares cross validation was set for the bandwidth estimator for each individual bird and cell size was 20 m (Limiñana et al. 2014).

### 5.2.3 Internannual home range overlap

For all individuals with at least two seasons of data, proportion of home range and stopover site overlap was calculated for 95% kernels. The total area where two, three, four, five, and six areas overlapped over the entire tracking period was calculated. The percent overlap for both the home ranges and stopover sites for each individual was calculated as the total area where more than one site overlapped, divided by the total area used over the entire tracking period (Fieberg and Kochanny 2005, Dillon and Kelly 2008). High overlap between a birds’ home ranges indicated that the bird used the same area repeatedly across multiple seasons. The difference in proportion overlap between age classes and type of area (home range vs. stopover site) were then tested in R using a Kruskal-Wallis test.

### 5.2.4 Habitat selection analysis

In order to determine which habitats European Honey-buzzards were selecting, land cover type single pixel values were extracted to each location within each bird’s home ranges and stopover sites. The European Space Agency S2 Prototype Land Cover 20 m Map of Africa 2016 was used to assess land cover use (ESA 2018). This 20 m resolution land cover map is based on Sentinel-2A observations from December 2015 to December 2016. It includes ten generic classes: i) tree cover area, ii) shrub cover area, iii) grassland, iv) cropland, v) aquatic or

regularly flooded vegetation, vi) sparse vegetation, vii) bare areas, viii) built-up areas, ix) snow and/or ice, and x) open water. Due to low values for many of the land cover types within honey-buzzard home ranges (which can skew the results of compositional analysis), land cover classes were combined into five types: i) tree cover area, ii) shrub cover area, iii) grassland, iv) transformed (crops and built-up areas), and v) other (all other land cover types). The proportion of each land cover type was calculated for all points. All of the MCPs for each individual honey-buzzard were dissolved into two polygons: i) home ranges, and ii) stopover sites. The proportion of land cover types within the combined MCPs was calculated in GME using the ‘Intersect Polygons with Raster’ tool. The proportion of land use types utilized (based on the tracking points) was then compared to the proportion of land use types available (based on the MCPs). This was performed using ‘compana’, a compositional analysis function from the package ‘adehabitatHS’ in R. This analysis determines the ranking of habitats in terms of selection across multiple animals (Aebischer et al. 1993). Four compositional analyses were run: i) adult home ranges, ii) juvenile home ranges, iii) adult stopover sites, and iv) juvenile stopover sites.

#### 5.2.5 Home range data extraction

The area in square kilometres was calculated for all three estimates of home range and stopover site size. The longitude and latitude of the centroid of the 50% and 95% kernels were calculated. In order to look at habitat and fragmentation values within both kernels, the land cover map was clipped to each home range. Each clipped area was analysed using Fragstats (McGarigal et al. 2012). Fragstats was used to calculate largest patch index (LPI) for the entire home range, as well as each habitat type, which quantifies the percentage of the total area used made up by the largest land cover patch, as well as edge density (ED) which is the total length of all edges within the total area used divided by the total home range area. Shannon’s and Simpson’s Landscape Diversity Indices (which both give measures of habitat diversity) were also calculated. In addition to the landscape measures, the percentage of each land cover type within the area used was calculated.

#### 5.2.6 Home range modelling and model selection

The total areas of both 50% and 95% kernel home ranges and stopover sites were modelled using individual bird, temporal, and habitat variables. The areas in square kilometres of both 50% and 95% kernel home ranges and stopover sites were modelled using habitat

variables. Data were log-transformed in order to render them normal. All models were linear mixed effect models (LMMs) due to the repeat measures of individual birds. The function ‘lmer’ from the package ‘lme4’ was used for all models. Individual birds were the random variable in all models. All continuous fixed variables were scaled using the ‘scale’ function in R. This function subtracts the mean and divides that value by the standard deviation for each value within a variable, which makes variables with vastly different values more comparable. Twenty-five candidate models were calculated for the 50% and 95% kernels of home range and the 50% and 95% kernels of stopover site, including a null model (which included none of the fixed variables) and a global model (which included all of the non-correlated fixed variables). These models used a total of thirteen fixed variables (Table 5.2). Variables used in the models were partially selected based on the results of the habitat selection analysis. Treed LPI and percent treed cover were strongly correlated, and therefore, were not included together in any of the models.

In order to test model suitability, the ‘aictab’ function from the package ‘AICcmodavg’ was used to calculate AICc and  $\Delta$ AICc values. Models with  $\Delta$ AICc values of less than four were averaged using the ‘mod.avg’ function from the ‘MuMin’ package. The final averaged model was checked for normal Pearson’s residuals, as well as for variance inflation factors of less than seven.

*Table 5.2:* The fixed variables used in candidate linear mixed effect models of the home range or stopover site size of European Honey-buzzard (*Pernis apivorus*) in Africa.

Variable	Description
Sex	Male or female
Age	Adult or juvenile
Points	Number of points in the area used
Days	Number of days in the area used
Month	Starting month of the area used
Longitude	Longitude of the area used centroid
Latitude	Latitude of the area used centroid
Tree LPI	Largest patch index of treed habitat
ED	Edge density
Shan	Shannon’s Landscape Diversity Index
Simp	Simpson’s Landscape Diversity Index
%Tree	Percent treed habitat cover
%Trans	Percent transformed cover

### 5.2.7 Daily and weekly displacement analysis

The average number of daily points was calculated for each home range and stopover site. For the displacement analysis, only those with a minimum of eight tracking points per day were included. For these sites, the daily distance travelled in kilometres was calculated using the straight-line distance between all points (more than one hour apart) in temporal order for a given day. These distances were averaged to create an average daily movement distance. The daily distances were log-transformed in order to render them normal. In order to assess whether birds travelled greater daily distances in larger home ranges, two sets of candidate LMMs were created, one for home ranges and one for stopover sites. Both sets of candidate models included individual bird as a random variable. A full set of seven models (including a null model) were created using sex, age, and the log-transformed 95% kernel area for all three datasets. These models were assessed for suitability and statistical significance as detailed in the home range analyses.

### 5.3 Results

A total of 138 European Honey-buzzard home ranges in Africa were assessed (Figure 5.1a). This included 18 adult male, 18 adult female, 37 juvenile male, and 65 juvenile female home ranges. A total of 126 stopover sites were assessed (Figure 5.1b). Six of the ten adult individuals, and 20 of the 21 juvenile individuals had at least one stopover site. The stopover sites included 26 adult male, 13 adult female, 36 juvenile male, and 51 juvenile female stopover sites. Stopover sites had consistently smaller kernel areas than home ranges (Table 5.3). Juvenile birds had more home ranges and stopover sites per season than adult birds.

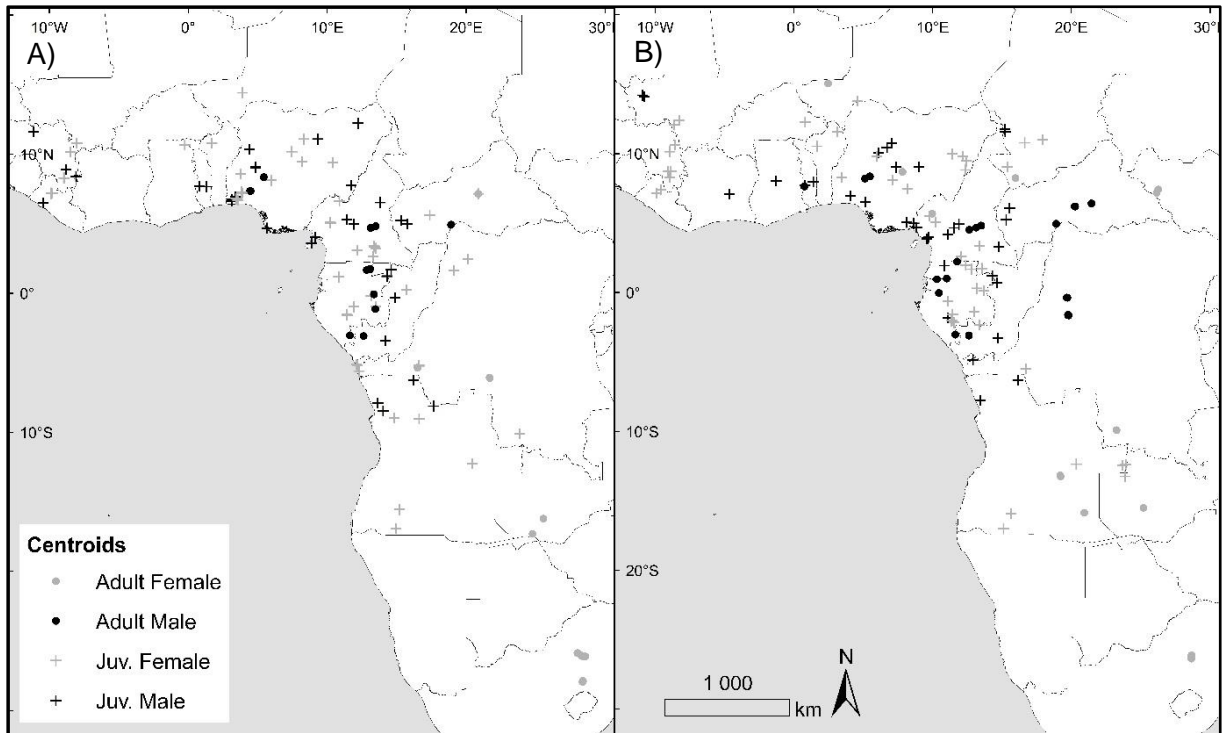


Figure 5.1: The centroids of 95% kernel: A) home ranges (n = 138), and B) stopover sites (n = 126) of 32 tracked European Honey-buzzards (*Pernis apivorus*) in Africa. Circles represent adult birds while crosses represent juveniles. Grey symbols signify female birds while black symbols signify male birds.

Table 5.3: The average number of seasons tracked and sites per individual adult (n = 9) and juvenile (n = 21) European Honey-buzzard (*Pernis apivorus*) as well as the average number of sites per season for both home ranges and stopover sites. The average number of points and days per home range or stopover site as well as the average home range or stopover site minimum convex polygon (MCP) and 50% and 95% kernel areas are also displayed.

	Home Range		Stopover Site	
	Adult	Juvenile	Adult	Juvenile
Seasons		2.34 ± 1.21		
Sites	4.31 ± 3.25		4.85 ± 3.37	
Sites per Season	1.24 ± 0.83	2.25 ± 1.43	1.07 ± 1.82	1.95 ± 1.82
Points	236.99 ± 248.02		68.56 ± 97.69	
Days	70.75 ± 66.38		6.58 ± 3.40	
MCP (km <sup>2</sup> )	105.40 ± 254.78		43.80 ± 104.87	
50% Kernel (km <sup>2</sup> )	23.12 ± 97.55		17.85 ± 54.30	
95% Kernel (km <sup>2</sup> )	119.05 ± 408.29		86.05 ± 227.87	

### 5.3.1 Interannual home range overlap

Twenty-four birds had at least two seasons of tracking data. A total of 4.2% (1 individual) had only one home range over the tracking period, and therefore, had no home range overlap. Another 20.8% (5 individuals) had more than one home range and no overlap between any of their home ranges over the tracking period. The remaining 75% (18 individuals) had overlap

between home ranges. Tracked honey-buzzards had up to six home ranges overlapping. For stopover sites, a total of 16.7% (4 individuals) had only one stopover site over the tracking period, and another 45.8% (11 individuals) had more than one stopover and no overlap. 37.5% (9 individuals) had overlap between stopover sites. No individuals had more than four stopovers overlapping.

There were statistically significant differences between the total percent overlap between age classes, and whether the area was a home range or stopover site ( $H(3) = 8.21, p = 0.04$ ). Adult home range overlap ( $22.5 \pm 10.1\%$ ) was significantly higher than adult stopover overlap ( $7.9 \pm 5.8\%$ ) and juvenile stopover overlap ( $2.7 \pm 1.6\%$ ). Juvenile home range overlap ( $10.3 \pm 3.3\%$ ) was not significantly different from adult home range, adult stopover, or juvenile stopover overlap.

### 5.3.2 Habitat selection

Adult European Honey-buzzards preferred treed habitat significantly more than shrub and transformed habitat in their home ranges (Table S5.1). They also preferred treed habitat (although not significantly) over grassland and other habitat types. In their stopover sites, adults significantly preferred treed habitat over all other types, and significantly avoided transformed habitats (Table S5.2).

Juvenile honey-buzzards significantly preferred treed habitat over all other habitat types in their home ranges and their stopover sites (Tables S5.3 and S5.4). They significantly avoided transformed habitats in their stopover sites.

### 5.3.3 Home range models

The two most appropriate LMMs for  $\log(50\%$  home range kernel area) included treed largest patch index (LPI), and edge density (Table 5.4). After model averaging, both variables had 95% confidence intervals that did not overlap zero (Table 5.5). Variance inflation values were all below seven. Both treed LPI and edge density had a negative effect on home range 50% kernel size (Figure 5.2).

Table 5.4: Linear mixed effects model selection results for log(kernel area) of European Honey-buzzard (*Pernis apivorus*) home ranges in Africa. All models include Bird as the random effect and all fixed variables are scaled. n = sample size, K = number of parameters,  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model, and  $w_i$  = model weight. Twenty-five candidate models were tested. Only the models with a  $\Delta\text{AICc} < 4.00$  are included here. Full results in the Supplementary Information (Tables S5.5 and S5.6).

Model	n	Treed LPI				Treed LPI + Edge Density			
		K	Log-likelihood	$\Delta\text{AICc}$	$w_i$	K	Log-likelihood	$\Delta\text{AICc}$	$w_i$
50% Home Range <sup>a</sup>	138	4	-125.86	0.00	0.52	5	-124.88	0.20	0.48
95% Home Range <sup>b</sup>	138	4	-131.73	0.00	0.78	5	-131.90	2.49	0.22

<sup>a</sup>AICc value of the best-fit model = 260.03; AICc value of the null model = 273.37

<sup>b</sup>AICc value of the best-fit model = 271.77; AICc value of the null model = 281.65

Table 5.5: The final, model averaged (using the models in Table 5.4) linear mixed effects models for log(kernel area) of European Honey-buzzard (*Pernis apivorus*) home ranges in Africa. The model includes Bird as the random effect and all explanatory variables are scaled. Est. = variable slope, SE = standard error, and 95% CI = 95% confidence interval.

	50% Home Range	95% Home Range
<i>Intercept</i>		
Est.	0.68	1.40
SE	0.06	0.06
95% CI	0.56 to 0.80	1.27 to 1.52
<i>Treed LPI</i>		
Est.	-0.33	-0.26
SE	0.11	0.08
95% CI	-0.55 to -0.11	-0.41 to -0.11
<i>Edge Density</i>		
Est.	-0.10	-0.03
SE	0.12	0.07
95% CI	-0.40 to -0.03	-0.31 to 0.02



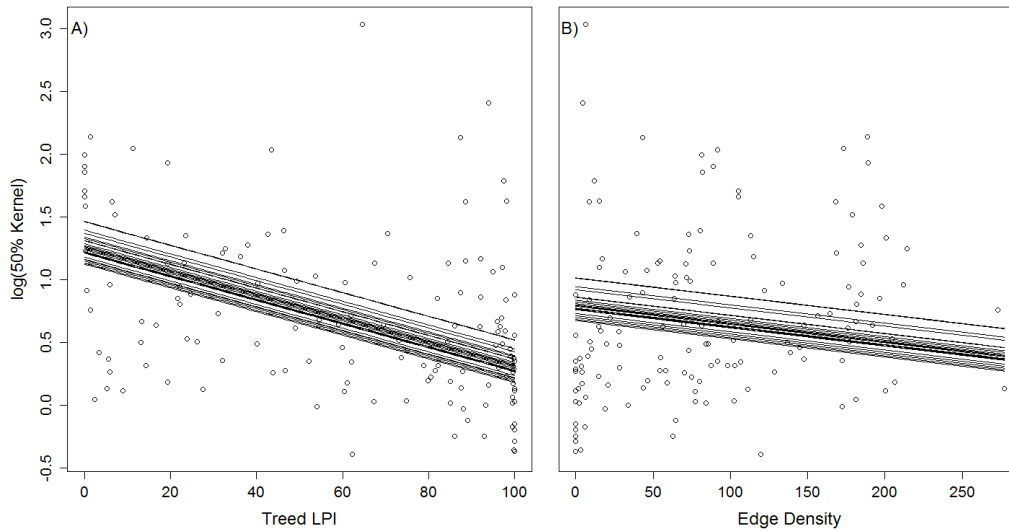


Figure 5.2: The relationship between: A) treed LPI, and B) edge density to log(50% home range kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 138 individual home ranges). Lines represent the linear mixed model (described in Table 5.5) predictions for each individual bird (n = 32). Predictions for treed LPI were calculated using the mean edge density (83.80) while predictions for edge density were calculated using the mean treed LPI (60.53%).

The two most appropriate LMMs for log(95% home range kernel area) included treed LPI, and edge density (Table 5.4). After model averaging, only treed LPI had 95% confidence intervals that did not overlap zero (Table 5.5). Both treed LPI and edge density had negative effects on 95% home range kernel area (Figure 5.3).

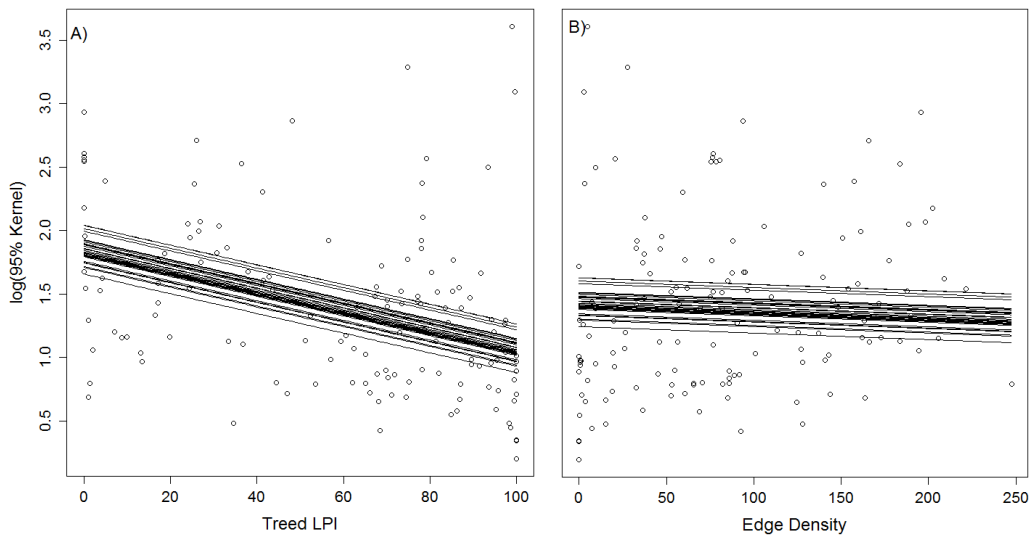


Figure 5.3: The relationship between: A) treed LPI, and B) edge density to log(95% home range kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 138 individual home ranges). Lines represent the linear mixed effects model (described in Table 5.5) predictions for each individual bird (n = 32). Predictions for treed LPI were calculated using the mean edge density (82.12) while predictions for edge density were calculated using the mean treed LPI (58.12%).

### 5.3.4 Stopover models

The two most appropriate LMMs for log(50% stopover kernel area) included treed LPI, and edge density (Table 5.6). After model averaging, only treed LPI had 95% confidence intervals that did not overlap zero (Table 5.7). Both treed LPI and edge density had negative effects on 50% stopover kernel area (Figure 5.4).

*Table 5.6:* Linear mixed effects model selection results for log(kernel area) of European Honey-buzzard (*Pernis apivorus*) stopover sites in Africa. All models include Bird as the random effect and all fixed variables are scaled. n = sample size, K = number of parameters,  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model, and  $w_i$  = model weight. Twenty-five candidate models were tested. Only the models with a  $\Delta\text{AICc} < 4.00$  are included here. Full results in the Supplementary Information (Tables S5.7 and S5.8).

Model	n	Treed LPI				Treed LPI + Edge Density			
		K	Log-likelihood	$\Delta\text{AICc}$	$w_i$	K	Log-likelihood	$\Delta\text{AICc}$	$w_i$
50% Stopover Site <sup>a</sup>	126	4	-147.11	0.00	0.61	5	-146.49	0.93	0.39
95% Stopover Site <sup>b</sup>	126	4	-151.93	0.00	0.53	5	-150.96	0.23	0.47

<sup>a</sup>AICc value of the best-fit model = 302.56; AICc value of the null model = 312.24

<sup>b</sup>AICc value of the best-fit model = 312.19; AICc value of the null model = 320.18

*Table 5.7:* The final, model averaged (using the models in Table 5.6) linear mixed effects models for log(kernel area) of European Honey-buzzard (*Pernis apivorus*) for stopover sites in Africa. The model includes Bird as the random effect and all explanatory variables are scaled. Est. = variable slope, SE = standard error, and 95% CI = 95% confidence interval.

	50% Stopover Site	95% Stopover Site
<i>Intercept</i>		
Est.	0.48	1.18
SE	0.10	0.10
95% CI	0.28 to 0.69	1.27 to 1.52
<i>Treed LPI</i>		
Est.	-0.37	-0.38
SE	0.12	0.14
95% CI	-0.61 to -0.13	-0.65 to -0.11
<i>Edge Density</i>		
Est.	-0.03	-0.12
SE	0.07	0.16
95% CI	-0.48 to 0.01	-0.51 to -0.01

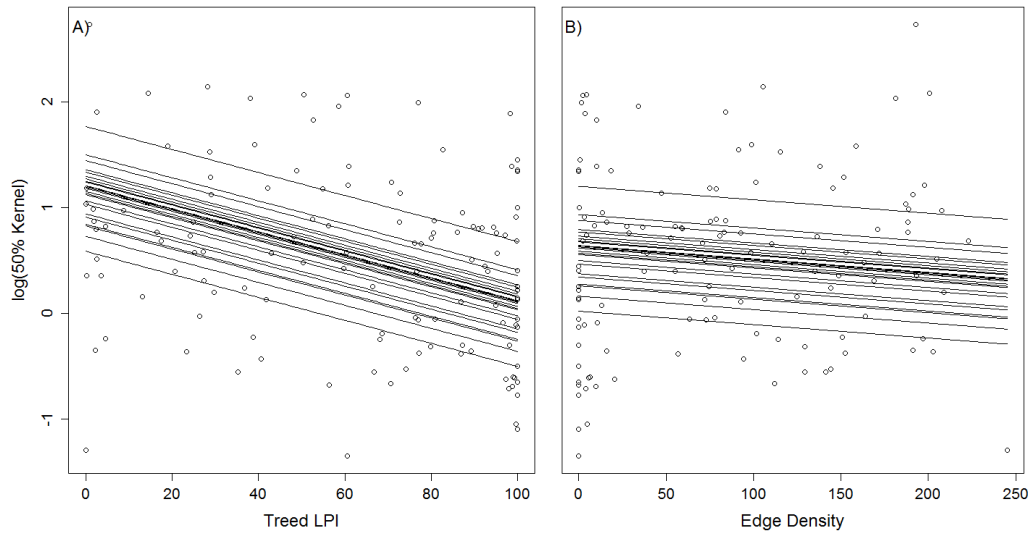


Figure 5.4: The relationship between: A) treed LPI, and B) edge density to log(50% stopover kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 128 individual stopover sites). Lines represent the linear mixed effects model (described in Table 5.7) predictions for each individual bird (n = 26). Predictions for treed LPI were calculated using the mean edge density (81.42) while predictions for edge density were calculated using the mean treed LPI (61.50%).

The two most appropriate LMMs for log(95% stopover kernel area) included treed LPI, and edge density (Table 5.6). After model averaging, both variables had 95% confidence intervals that did not overlap zero (Table 5.7). Both treed LPI and edge density had negative effect on 95% stopover kernel area (Figure 5.5).

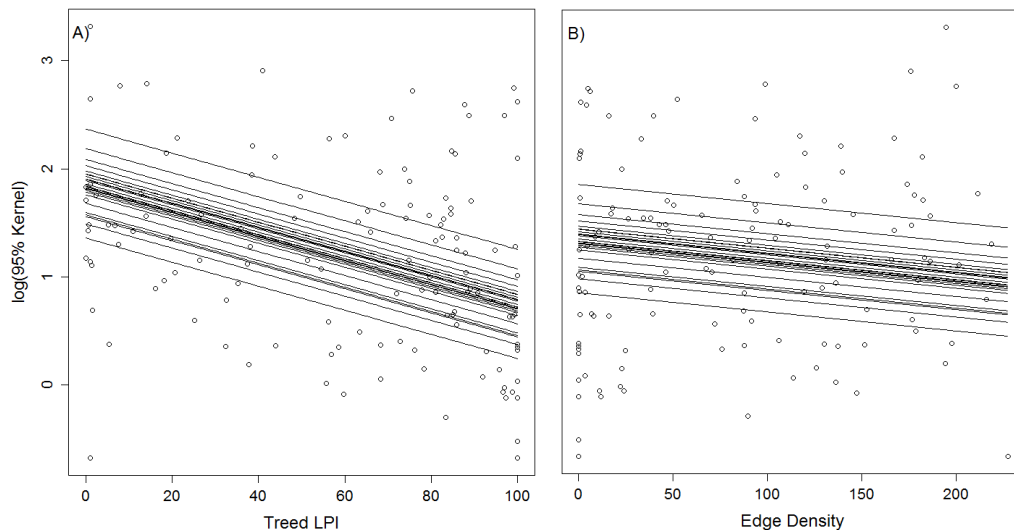


Figure 5.5: The relationship between: A) treed LPI, and B) edge density to log(95% stopover kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 128 individual stopover sites). Lines represent the linear mixed effects model (described in Table 5.7) predictions for each individual bird (n = 26). Predictions for treed LPI were calculated using the mean edge density (82.63) while predictions for edge density were calculated using the mean tree LPI (59.16%).

### 5.3.5 Daily distance models

A total of 25 home ranges of thirteen individual European Honey-buzzards (2 adult males, 5 juvenile males, and 6 juvenile females) had sufficient data to examine daily displacement distances travelled. The average daily distance travelled by birds in their home range was  $3.56 \pm 1.90$  km. Forty-three stopover sites of 20 individuals (3 adult males, 2 adult females, 7 juvenile males, and 8 juvenile females) had sufficient data to assess the daily distances travelled. In stopover sites, birds travelled an average of  $5.49 \pm 4.51$  km.

The linear mixed effects models for  $\log(\text{average daily distance})$  in honey-buzzard home ranges showed extremely low variance between birds ( $< 0.00001$ ), and therefore, a linear model was used without random effects. The number of points per home range were not included due to the lack of significance in the home range size models. The three most appropriate models included sex, age, and  $\log(95\% \text{ home range kernel area})$  (Table S5.9). After model averaging of the three best fit models, only  $\log(95\% \text{ home range kernel area})$  had 95% confidence intervals that did not overlap zero (Table 5.8). Ninety-five percent home range kernel area had a positive effect on average daily distances (Figure 5.6).

*Table 5.8:* The final model averaged linear model (including the top three models in Table S5.9) for  $\log(\text{average daily distance})$  within home ranges of European Honey-buzzard (*Pernis apivorus*) in Africa ( $n = 30$ ). The model includes Bird as the random effect. Estimate = variable slope, SE = standard error, and 95% CI = 95% confidence interval.

Variable	Estimate	SE	95% CI
Intercept	0.51	0.03	0.45 to 0.56
Sex (Male)	< 0.01	< 0.01	-0.26 to 0.06
Age (Juv)	< 0.01	< 0.01	-0.07 to 0.30
Log(95% Kernel Area)	0.15	0.03	0.09 to 0.20

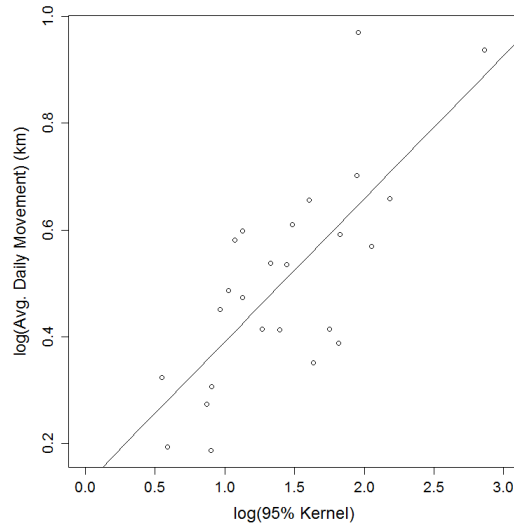


Figure 5.6: The relationship between log(95% home range kernel area) and log(average daily distance) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 13). The line represents the linear model described in Table 5.8.

The most appropriate LMMs for log(average daily distance) in stopover sites included only log(95% stopover kernel area) (Table S5.10). The single variable had 95% confidence intervals that did not overlap zero (Table 5.9). Log(95% stopover kernel area) had a positive effect on log(average daily distance) (Figure 5.7).

Table 5.9: The final linear mixed effects model for log(average daily distance) within stopover sites of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 20). The model includes Bird as the random effect and all explanatory variables are scaled. Estimate = variable slope, SE = standard error, and 95% CI = 95% confidence interval.

Variable	Estimate	SE	95% CI
Intercept	0.60	0.03	0.56 to 0.65
Log(95% Kernel Area)	0.31	0.02	0.26 to 0.35

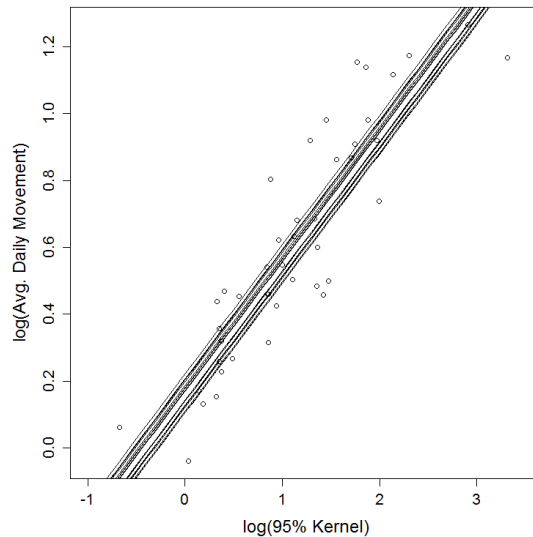


Figure 5.7: The relationship between  $\log(95\%$  stopover kernel area) and  $\log(\text{average daily distance})$  of European Honey-buzzard (*Pernis apivorus*) in Africa ( $n = 43$ ). Lines represent the linear mixed effects model (described in Table 5.9) predictions for each individual bird ( $n = 20$ ).

#### 5.4 Discussion

This study validates that adult European Honey-buzzards, on their non-breeding grounds, have higher site fidelity (at least for home ranges) than juvenile birds, as has been found in previous studies of both European and Oriental Honey-buzzards (*Pernis ptilorhynchus*), and other Palearctic migrant bird species (Salewski et al. 2000, Shiu et al. 2006, Strandberg et al. 2012, Blackburn and Cresswell 2016). The lower site fidelity, and therefore greater wandering, of juvenile honey-buzzards supports the hypothesis that young birds are driving the range shift of this species southwards (Howes et al. 2019). This is in line with the population resilience portion of the *serial residency hypothesis* in Cresswell (2014) that posits that juvenile birds will use the early non-breeding period of their life to locate suitable habitat to return to as adults. This allows for population-level resilience in the face of global change. Juvenile European Honey-buzzards spend a minimum of two to three years in Africa which provides them with the opportunity to find the appropriate habitat for their continued survival (Strandberg et al. 2012, Vansteelant et al. 2017).

Both adult and juvenile honey-buzzards had much lower site fidelity (7.9 and 2.7% respectively) for stopover sites than for home range areas (22.5 and 10.3% respectively). While this is a novel finding for the European Honey-buzzard, this has been documented in other large migratory species including the Egyptian Vulture, and Black Stork (*Ciconia nigra*) (Chevallier et al. 2011, Lopez-Lopez et al. 2014). One possible explanation for the low fidelity for stopover sites is that environmental conditions vary between years which could: i) change migratory

routes due to wind direction and speed, or ii) change the stopover sites themselves due to rainfall or temperature changes which may in turn change food or habitat availability. It is highly likely that climate and land cover changes in these stopover sites will result in Palaearctic migrants locating new areas during each migration. This is particularly true for birds stopping in the Sahel region, a regular stopover area for Palaearctic migrants in sub-Saharan Africa (including European Honey-buzzard), which is rapidly losing the woodland and savanna habitats that migrants depend on (Bayly et al. 2012, Adams et al. 2014, Norevik et al. 2016).

Besides site fidelity, there were no significant differences between the areas selected for home ranges and stopover sites. Forested habitats were selected above all other habitats by both adult and juvenile birds. Once again, this corresponds with previous work on this species suggesting that habitat loss could be a driver of the recently documented southwards shift in European Honey-buzzard (Strandberg et al. 2012, Howes et al. 2019). This is further supported by the large-scale loss of forest across much of sub-Saharan Africa, with the exception of South Africa which has experienced a net-forest gain due to increased forestry and urban afforestation (Allan et al. 1997, Hockey and Midgley 2009, Achard et al. 2014, Taubert et al. 2018). Many raptor species in South Africa, e.g. Crowned Eagle (*Stephanoaetus cornatus*), and Black and Rufous-breasted (*Accipiter rufiventris*) Sparrowhawks, have been able to adapt to these transformed forest landscapes, although there is evidence that they may not be as successful in terms of breeding in these habitats (Allan et al. 1997, Curtis 2005, Hockey and Midgley 2009, Swatridge et al. 2014). European Honey-buzzards tracked in South Africa also appear to be using forested environments made up of predominantly alien vegetation, perhaps due to the lack of suitable natural forest habitat, or in response to prey availability (Howes, Byholm, and Symes unpubl. data). The use of these novel man-made forest habitats is particularly interesting in terms of the southwards shift in the honey-buzzards range, and the increase in these alien forests is likely contributing to the increase in numbers in southern Africa (Howes et al. 2019).

Fragmentation does appear to have an effect on the movements of European Honey-buzzard as indicated by the home range and stopover site models. The best predictor of core and total home range and stopover site size was largest patch index (LPI) of treed habitat. Birds with larger home ranges had a smaller LPI of treed habitat. Birds with a smaller LPI of treed habitat may require larger home ranges with many smaller forest patches in order to piece together a suitably large amount of forest for their survival. Moving between smaller forest patches over a larger area may require a greater amount of energy than staying in a single large patch, and may also put the bird at higher risk of predation when exposed between patches. Birds may also be at greater risk of intraspecific competition due to conspecifics moving into seemingly vacant

patches. The fact that birds that had larger home ranges moved greater daily distances supports the idea that these birds may be spending more energy on a daily basis. Greater daily distances travelled in fragmented habitats have been documented in other species (i.e. Tawny and Northern Saw-whet Owls) during their breeding season (Redpath 1995a, Hinam and St. Clair 2008). Greater energy expenditure could put individual honey-buzzards at a survival disadvantage during migration and breeding success. It has been demonstrated in numerous species that poorer habitat quality on the non-breeding grounds leads to decreased survival and reduced breeding success (Sherry and Holmes 1996, Norris et al. 2004, Gunnarsson et al. 2005, Grande et al. 2009). In the case of juvenile honey-buzzards, the survival effect may be critical.

While European Honey-buzzards did appear to require large forest patches as indicated by LPI, edge density also had a negative relationship with home range size which means that birds with more fragmented habitats had smaller home ranges. This may indicate that honey-buzzards are not as sensitive to fragmentation, as long as they have a suitable forest patch that is not occupied by other honey-buzzards, a superior competitor of another species, or a dangerous predator. These birds may even be using edge habitats for improved foraging visibility. This suggests that this species may be more resilient to land cover change and habitat fragmentation than expected. The use of urban afforested habitats by European Honey-buzzards in southern Africa further indicates that the species is more adaptable than its specialist nature would suggest. It should, however, also be noted that small patches with fewer resources may leave honey-buzzards more vulnerable to exclusion by other territorial raptor species, and may in turn lead to higher risk of predation or higher competition (Byholm et al. 2012).

This study supports the hypothesis that the European Honey-buzzard's southwards shift may be driven by forest loss (Howes et al. 2019). This species appears to depend on suitably large tracts of forest, and vastly prefers treed habitats to all others. The European Honey-buzzard is unusual among Afrotropical Palaearctic migrants as it heavily utilizes treed habitats rather than shrub habitats as is common in migrants (Leisler 1992, Cresswell et al. 2009). Many of the tracked honey-buzzards also spent the non-breeding season in Central Africa, an area with a low diversity of migrants, likely linked to the large amount of forest in the region (Barbet-Massin et al. 2009). This specific niche may have allowed the European Honey-buzzard to reduce competition from other migrant species as well as to remain in habitat that is relatively similar to its preferred breeding habitat. The continuing loss of honey-buzzard habitat on the African continent may be putting this species at risk of poorer breeding success due to diminished resources, higher competition, and a greater chance of mortality during both migration and the non-breeding season (Achard et al. 2014, Taubert et al. 2018). However, juvenile birds do move



extensively and allow the species continued adaptation to habitat loss by locating remaining patches of forested habitat, and in the case of southern Africa, expanding urban woodlands.

## 5.5 References

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## 5.6 Supplementary Information

*Table S5.1:* The simplified ranking matrix for eleven adult European Honey-buzzards (*Pernis apivorus*) based on comparing the proportions of tracking points in each habitat type to the proportion of habitat type within the birds' home range MCPs. + indicates the land cover is selected for while - indicates that the land cover is selected against. A triple sign indicates significant differences at  $p < 0.05$ .

	Treed	Shrub	Grassland	Transformed	Other	Ranking
Treed	0	+++	+	+++	+	1
Shrub	---	0	-	+	-	4
Grassland	-	+	0	+	+	2
Transformed	---	-	-	0	-	5
Other	-	+	-	+	0	3

*Table S5.2:* The simplified ranking matrix for six adult European Honey-buzzards (*Pernis apivorus*) based on comparing the proportions of tracking points in each habitat type to the proportion of habitat type within the birds' stopover MCPs. + indicates the land cover is selected for while - indicates that the land cover is selected against. A triple sign indicates significant differences at  $p < 0.05$ .

	Treed	Shrub	Grassland	Transformed	Other	Ranking
Treed	0	+++	+++	+++	+++	1
Shrub	---	0	-	+++	-	4
Grassland	---	+	0	+++	-	3
Transformed	---	---	---	0	---	5
Other	---	+	+	+++	0	2

*Table S5.3:* The simplified ranking matrix for 22 juvenile European Honey-buzzards (*Pernis apivorus*) based on comparing the proportions of tracking points in each habitat type to the proportion of habitat type within the birds' home range MCPs. + indicates the land cover is selected for while - indicates that the land cover is selected against. A triple sign indicates significant differences at  $p < 0.05$ .

	Treed	Shrub	Grassland	Transformed	Other	Ranking
Treed	0	+++	+++	+++	+++	1
Shrub	---	0	+	+	+	2
Grassland	---	-	0	+	+	3
Transformed	---	-	-	0	+	4
Other	---	-	-	-	0	5

Table S5.4: The simplified ranking matrix for 20 juvenile European Honey-buzzards (*Pernis apivorus*) based on comparing the proportions of tracking points in each habitat type to the proportion of habitat type within the birds' stopover MCPs. + indicates the land cover is selected for while - indicates that the land cover is selected against. A triple sign indicates significant differences at  $p < 0.05$ .

	Treed	Shrub	Grassland	Transformed	Other	Ranking
Treed	0	+++	+++	+++	+++	1
Shrub	---	0	+	+++	+++	2
Grassland	---	-	0	+++	+	3
Transformed	---	---	---	0	---	5
Other	---	---	-	+++	0	4

Table S5.5: Linear mixed effects model selection results for log(50% home range kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 138) for all 25 candidate models. All models include Bird as the random effect and all fixed variables are scaled. K = number of parameters, and  $\Delta AICc$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model.

Model	K	Log-likelihood	$\Delta AICc^a$
<b>Treed LPI</b>	<b>4</b>	<b>-125.86</b>	<b>0.00</b>
<b>Treed LPI + Edge Density</b>	<b>5</b>	<b>-124.88</b>	<b>0.20</b>
Treed LPI + Edge Density + % Developed	6	-126.09	4.80
Treed LPI + % Developed	5	-127.52	5.46
% Treed	4	-129.29	6.86
% Developed	4	-131.03	10.33
Edge Density + % Treed	5	-130.54	11.51
% Developed + % Treed	5	-130.66	11.74
Sex	4	-132.03	12.34
Null	3	-133.60	13.35
Edge Density	4	-132.65	13.58
Edge Density + % Developed	5	-131.89	14.21
Age + Sex	5	-132.78	15.99
Edge Density + % Developed + % Treed	6	-131.77	16.15
Age	4	-134.50	17.28
Latitude	4	-134.73	17.73
Longitude	4	-135.03	18.33
Points	4	-135.48	19.23
Days	4	-135.49	19.26
Longitude + Latitude	5	-136.10	22.63
Points + Days	5	-137.37	25.18
Month	13	-134.91	38.73
Latitude + Month	14	-136.22	43.83
Treed LPI Global	22	-134.52	61.82
% Treed Global	22	-139.11	71.00

<sup>a</sup>AICc value of the best-fit model = 260.03; AICc value of the null model = 273.37

Table S5.6: Linear mixed effects model selection results for log(95% home range kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 138) for all 25 candidate models. All models include Bird as the random effect and all fixed variables are scaled. K = number of parameters, and  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model.

Model	K	Log-likelihood	$\Delta\text{AICc}^a$
<b>Treed LPI</b>	<b>4</b>	<b>-131.73</b>	<b>0.00</b>
<b>Treed LPI + Edge Density</b>	<b>5</b>	<b>-131.90</b>	<b>2.49</b>
% Treed	4	-134.38	5.30
Treed LPI + % Developed	5	-133.31	5.31
% Developed	4	-135.61	7.75
Treed LPI + Edge Density + % Developed	6	-133.45	7.77
Null	3	-137.73	9.88
Edge Density + % Treed	5	-135.61	9.91
% Developed + % Treed	5	-135.68	10.04
Sex	4	-136.98	10.50
Edge Density	4	-137.84	12.21
Edge Density + % Developed	5	-136.95	12.59
Age	4	-138.53	13.58
Latitude	4	-138.62	13.78
Age + Sex	5	-137.57	13.82
Edge Density + % Developed + % Treed	6	-136.79	14.46
Longitude	4	-139.12	14.78
Points	4	-139.33	15.20
Days	4	-139.68	15.90
Longitude + Latitude	5	-139.99	18.66
Points + Days	5	-141.22	21.12
Month	13	-139.26	35.69
Latitude + Month	14	-140.26	40.16
Treed LPI Global	22	-142.06	65.14
% Treed Global	22	-144.58	70.20

<sup>a</sup>AICc value of the best-fit model = 271.77; AICc value of the null model = 281.65

Table S5.7: Linear mixed effects model selection results for log(50% stopover kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 126) for all 25 candidate models. All models include Bird as the random effect and all fixed variables are scaled. K = number of parameters, and  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model.

Model	K	Log-likelihood	$\Delta\text{AICc}^a$
<b>Treed LPI</b>	<b>4</b>	<b>-147.11</b>	<b>0.00</b>
<b>Treed LPI + Edge Density</b>	<b>5</b>	<b>-146.49</b>	<b>0.93</b>
Treed LPI + % Developed	5	-148.46	4.86
Treed LPI + Edge Density + % Developed	6	-147.76	5.68
Null	3	-153.02	9.68
% Treed	4	-152.35	10.47
% Developed	4	-152.99	11.76
Edge Density	4	-153.03	11.83
Age	4	-153.42	12.62
Longitude	4	-153.67	13.11
Sex	4	-153.75	13.28
Points	4	-154.15	14.08
Days	4	-154.45	14.67
Edge Density + % Treed	5	-153.39	14.74
Latitude	4	-154.61	15.00
% Developed + % Treed	5	-153.54	15.04
Edge Density + % Developed	5	-153.84	15.62
Age + Sex	5	-154.12	16.18
Longitude + Latitude	5	-154.12	17.63
Points + Days	5	-155.19	18.34
Edge Density + % Developed + % Treed	6	-154.47	19.10
Month	14	-150.19	29.65
Latitude + Month	15	-151.11	34.08
Treed LPI Global	23	-149.68	53.74
% Treed Global	23	-156.22	66.81

<sup>a</sup>AICc value of the best-fit model = 302.56; AICc value of the null model = 312.24



Table S5.8: Linear mixed effects model selection results for log(95% stopover kernel area) of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 126) for all 25 candidate models. All models include Bird as the random effect and all fixed variables are scaled. K = number of parameters, and  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model.

Model	K	Log-likelihood	$\Delta\text{AICc}^a$
<b>Treed LPI</b>	<b>4</b>	<b>-151.93</b>	<b>0.00</b>
<b>Treed LPI + Edge Density</b>	<b>5</b>	<b>-150.96</b>	<b>0.23</b>
Treed LPI + % Developed	5	-153.35	5.01
Treed LPI + Edge Density + % Developed	6	-152.40	5.31
% Treed	4	-155.43	7.01
Null	3	-156.99	7.99
% Developed	4	-156.16	8.47
Edge Density + % Treed	5	-156.18	10.67
Age	4	-157.34	10.81
Edge Density	4	-157.46	11.06
% Developed + % Treed	5	-156.51	11.33
Sex	4	-157.60	11.34
Longitude	4	-157.80	11.75
Points	4	-158.03	12.21
Days	4	-158.12	12.38
Edge Density + % Developed	5	-157.44	13.19
Latitude	4	-158.62	13.38
Age + Sex	5	-157.96	14.23
Edge Density + % Developed + % Treed	6	-157.31	15.13
Points + Days	5	-158.60	15.52
Longitude + Latitude	5	-158.82	15.95
Month	14	-154.05	27.70
Latitude + Month	15	-155.24	32.66
Treed LPI Global	23	-153.56	51.75
% Treed Global	23	-158.71	62.05

<sup>a</sup>AICc value of the best-fit model = 312.19; AICc value of the null model = 320.18

Table S5.9: Linear model selection results for log(daily distance) within home ranges of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 25) for all eight candidate models. All fixed variables are scaled. K = number of parameters, and  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model. Model covariates: Sex = sex; Age = age class; HR = log(95% kernel area)

Model	K	Log-likelihood	$\Delta\text{AICc}^a$
<b>HR</b>	<b>4</b>	<b>16.02</b>	<b>0.00</b>
<b>Age + HR</b>	<b>5</b>	<b>16.16</b>	<b>2.57</b>
<b>Sex + HR</b>	<b>5</b>	<b>16.08</b>	<b>2.74</b>
Global	6	16.17	5.72
Null	3	5.84	17.77
Age	4	6.73	18.58
Sex	4	6.68	18.69
Sex + Age	5	7.01	20.88

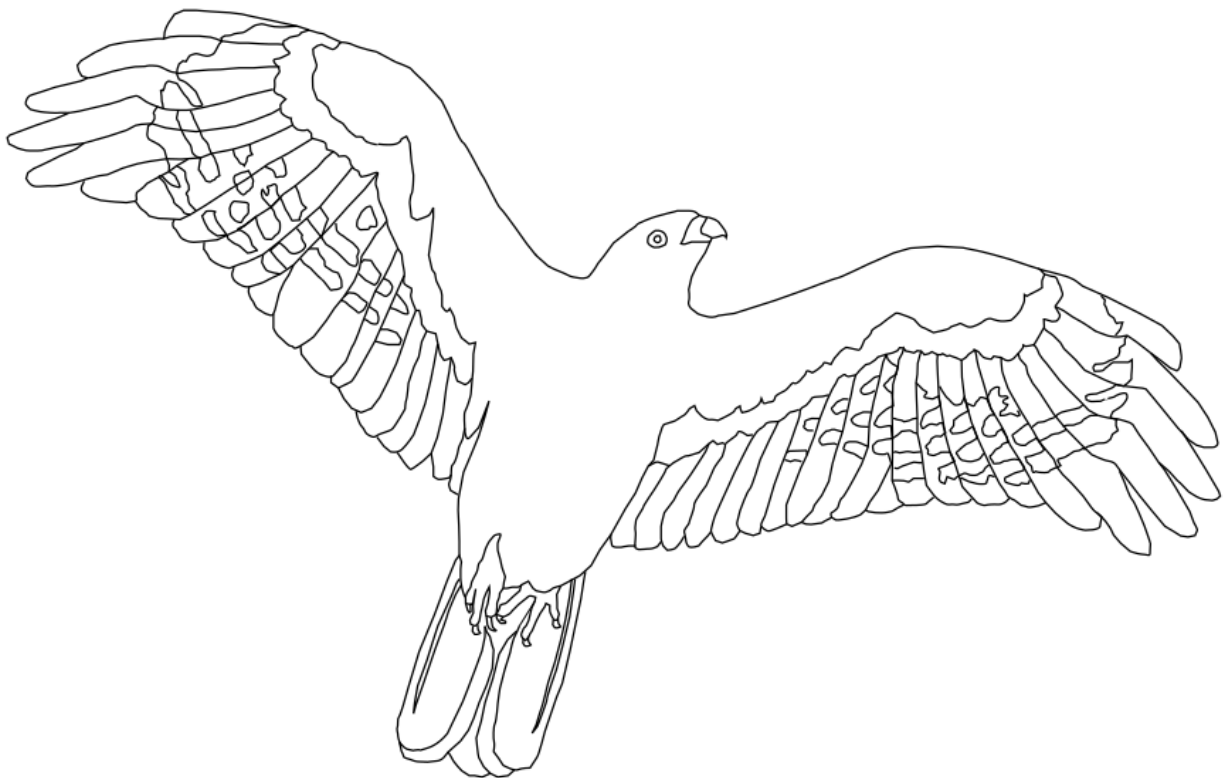
<sup>a</sup>AICc value of the best-fit model = -24.90; AICc value of the null model = 5.84

*Table S5.10:* Linear mixed effects model selection results for log(daily distance) within stopover sites of European Honey-buzzard (*Pernis apivorus*) in Africa (n = 126) for all eight candidate models. All models include Bird as the random effect and all fixed variables are scaled. K = number of parameters, and  $\Delta\text{AICc}$  = the difference in AICc (Akaike's Information Criterion corrected for small sample size) relative to the best model. Model covariates: Sex = sex; Age = age class; HR = log(95% kernel area)

Model	K	Log-likelihood	$\Delta\text{AICc}^a$
<b>HR</b>	<b>4</b>	<b>15.26</b>	<b>0.00</b>
Age + HR	5	13.55	6.00
Sex + HR	5	13.37	6.35
Global	6	11.67	12.48
Null	3	-15.03	58.16
Age	4	-15.28	61.09
Sex	4	-16.11	62.76
Sex + Age	5	-16.38	65.85

<sup>a</sup>AICc value of the best-fit model = -21.48; AICc value of the null model = 36.68

**Evidence of primary moult  
during the extended migration  
of a Palaearctic raptor using  
stable isotope analyses**



## *Abstract*

The spatiotemporal patterns of moult vary widely between bird species depending on their life history characteristics. Due to the availability of new biogeochemical analyses, there has been increased attention to the moult strategies of individual species. The European Honey-buzzard (*Pernis apivorus*) is a Palaearctic migrant raptor with an annual descendant primary moult, although the exact timing and location of their primary moult is poorly known. We used photographs, tracking data, and detailed stable isotope analysis to assess honey-buzzard primary moult to better determine the migratory connectivity of this species. Photographs revealed that the outer five primaries (P6 - P10) were often moulted in southern Africa between December and March. This aligns with the period that tracked birds were found in South Africa. The stable isotope data were highly variable with one juvenile bird growing all of its feathers in Europe, and two adults moulting two and three primaries, respectively, in Europe. The other four individuals appear to have moulted all of their primary feathers at sites across Africa, perhaps indicating that they were young birds who had yet to migrate to Europe to breed, or breeding birds that had failed to moult any feathers in Europe. Based on previous knowledge, along with the photographs and stable isotope analysis, it seems likely that adult honey-buzzards moult up to three primaries in Europe (P1-P3), the middle two to three primaries on migration in Africa (P3-P5), and the final outer five primaries on their African non-breeding grounds (P6-P10). However, primary moult during migration may be unique to South African individuals due to their exceptionally long migration. This study provides valuable evidence for future sampling protocols to examine migratory connectivity of European Honey-buzzard and other Palaearctic migrants.

*Key words:* European Honey-buzzard, moult, *Pernis apivorus*, primary moult, stable isotope analysis

## *6.1 Introduction*

Migratory birds must perform three energy-intensive processes during the course of a year: i) breeding, ii) moulting, and iii) migrating (Svensson and Nilsson 1997, Inger and Bearhop 2008, Bridge 2011, Cherel et al. 2016). Moulting of flight feathers can be particularly taxing on large, soaring bird species, such as seabirds and raptors (Edelstam 1984, Cherel et al. 2000, Bridge 2011). Many moulting strategies have evolved in these large species, and

therefore, spatiotemporal patterns of moult vary widely between species (Edelstam 1984, Herremans 2000, Clark 2004, Atkinson et al. 2005, Newton 2009, Bridge 2011). Generally small and medium raptors, such as Northern Goshawk (*Accipiter gentilis*) and *Milvus* kites, moult all their primaries annually, beginning with the innermost primary (P1) and ending with the outermost primary (P10) (Edelstam 1984). In migratory species, this process often begins during the breeding season, and is paused during migration, before being resumed on the non-breeding grounds (Edelstam 1984). Larger species may moult in either multiple waves, losing more than one feather at once, or over a course of two or more years (Edelstam 1984).

In recent years, there has been increased interest in moult due to the use of feathers in biogeochemical analysis (Inger and Bearhop 2008, Ramos et al. 2008). Feather analyses are used for studying trophic level changes (Hobson et al. 1994, Knoff et al. 2002), assessing heavy metal contamination (Fasola et al. 1998, Kim and Koo 2008), and understanding species' migratory connectivity (Van Wilgenburg and Hobson 2011, Nelson et al. 2015, Reudink et al. 2015). This has renewed interest in when and where birds moult their feathers.

Stable isotope analysis has proven to be a useful tool for understanding moult in migratory species (Atkinson et al. 2005, Ramos et al. 2008, González-Solís et al. 2011). Stable light isotopes ( $\delta^2\text{H}$ ,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{18}\text{O}$ ) are often used to determine inputs into food webs, as well as trophic levels (Hobson et al. 1994, Hedd and Montevicchi 2006). Depending on the geographic area, these inputs are different; therefore, the stable isotope signatures are also unique (Ehleringer et al. 1999, Hobson 1999, Bowen et al. 2005). Animals fractionate these isotopes, and assimilate them into their tissues through their diet (Gannes et al. 1997, Bearhop et al. 2003). Depending on the tissue, the temporal scale of isotopic integration differs significantly (Bearhop et al. 2003). In the case of feathers, the isotopic values often reflect the location of feather growth (Hobson and Clark 1992, Bowen et al. 2005, Hobson et al. 2012a). This, combined with predictable seasonal moult, means that feathers can be used to examine migratory movements over time (Atkinson et al. 2005, Ramos et al. 2008, González-Solís et al. 2011, Nelson et al. 2015, Reudink et al. 2015).

For migratory birds, the isoscapes (spatially explicit predictions of isotope ratios) of their breeding and non-breeding locations, which may be thousands of kilometres apart, are often very different (Ramos et al. 2008, González-Solís et al. 2011). These differences may be associated with different habitats or diet shifts (Vogel et al. 1990). Therefore, feather isotope values of breeding and non-breeding periods may differ significantly. For example,  $\delta^2\text{H}$  values of precipitation Europe are generally lower than those in Africa (Bowen et al. 2005, Hobson et al. 2012b). This can be used to determine if the feathers of Palaearctic migrant birds were

grown in Europe or Africa (Bowen et al. 2005, Hobson et al. 2012b). The location of feather growth, particularly in Africa, can then be further narrowed down using  $\delta^{13}\text{C}$  values, which are higher in  $\text{C}_4$  plants (such as those found in tropical grasslands and savannas) than  $\text{C}_3$  plants (such as those found in forests) (Bowen et al. 2005, Reichlin et al. 2013). This allows for the potential assignment of both breeding and non-breeding locations of Palaearctic migratory birds which can then be used to assess migratory connectivity and moult strategies (Ramos et al. 2008, González-Solís et al. 2011).

The European Honey-buzzard (*Pernis apivorus*) is a long-distance migrant, moving between its breeding grounds in Europe, and its non-breeding grounds in Africa (Cramp and Simmons 1979, Hake et al. 2003, Vansteelant et al. 2017). This species spends relatively little time (approximately 115 to 120 days) on the European breeding grounds (Cramp and Simmons 1979). Honey-buzzards breed in mature, damp woodland, where the majority of their diet is made up of Hymenoptera insects (Itämiés and Mikkola 1972, Kostrzewa 1996, Gamauf et al. 2013). Most honey-buzzards winter in the humid forests of central and West Africa with a minority spending their winters in East and southern Africa (Cramp and Simmons 1979, Strandberg et al. 2012, Howes et al. 2019). Adult European Honey-buzzards perform a full descendant primary moult annually (Cramp and Simmons 1979). They begin their primary moult (up to four primaries) while breeding in Europe, and are believed to suspend moult during their migration (Cramp and Simmons 1979, Forsman 2016). The rest of primaries are inferred to be moulted in Africa on their non-breeding grounds with the full moult completed by March (Cramp and Simmons 1979, Forsman 2016). The juvenile moult is poorly known in European Honey-buzzards, but young birds are known to moult from their juvenile to their adult plumage between one and two years after fledging (second calendar year) (Cramp and Simmons 1979, Forsman 1984). This would likely include a full primary moult (Cramp and Simmons 1979).

In this paper, we assessed the spatiotemporal patterns of primary moult in migrating European Honey-buzzards using three stable light isotopes ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ,  $\delta^2\text{H}$ ). We evaluated photographs of the southern African population of European Honey-buzzard in order to determine which feathers were commonly moulted during the non-breeding season. We then conducted detailed stable isotope analyses of primary feathers from seven South African honey-buzzard specimens. These analyses, along with tracking data of southern African honey-buzzards, allowed us to better understand the timing and location of moult in a long-distance migrant, which may allow for better determination of the migratory connectivity of this species in the future.

## 6.2 Methods

### 6.2.1 Photograph collection and analysis

European Honey-buzzard is considered a rarity in southern African, and therefore, photographs of the species are regularly shared on regional birdwatching platforms (Howes et al. 2019). Photos of European Honey-buzzards in southern Africa were collected from: i) the Zest for Birds website, ii) the Southern African Rare Bird Newsletter (SARBN), iii) the Animal Demography Unit's Virtual Museum, and iv) two Facebook Groups (BirdLife South Africa and SA Rare Birds). Zest for Birds is a website documenting rare birds in southern Africa from January 2002 to December 2010. SARBN is a rarity reporting email list-server for southern Africa. Photographs from July 2008 to July 2017 were collected from SARBN. The Animal Demography Unit's Virtual Museum is a citizen science database based at the University of Cape Town with photographs of southern African fauna. All photographs were downloaded and databased with the date, location, photographer, and source. Birds were aged from the photographs (Forsman and Shirihai 1997, Chapter 3).

Honey-buzzards in flight were evaluated for the absence of primary feathers. If an individual was missing a primary, the number of the primary was recorded. These data were then assessed to determine which age categories were moulting in southern Africa, as well as which primaries were missing during which month.

### 6.2.2 Tracking data collection and analysis

To better understand the spatiotemporal components of moult, tracking data from four adult female European Honey-buzzards that spent the non-breeding season in South Africa were analysed. These data were included in order to assess the timing of migration events, and when birds were where. The understanding of the timing of annual movements of honey-buzzards was then linked back to stable isotope signatures. Of the four tracked honey-buzzard females, one bird was caught in southern Finland at the nest using a dho-ghaza (Zuberogoitia et al. 2008), while the other three were from wildlife rehabilitation centres in South Africa. Birds were equipped with either solar-powered Argos-GPS platform terminal transmitters (PTTs) (Microwave Telemetry Inc.), or GSM-GPS trackers (Ecotone). The tags weighed 22-27 g, which is equivalent to approximately 3% of the bird's mass at the time of tagging. Trackers were attached using the body-loop method with Teflon ribbon (Kenward 2004). The

amount of tracking data from each bird varied due to settings, geographical location, and weather.

One year per honey-buzzard was included in analysis (with the exception of one individual which was tracked for six months). A full year included a breeding season, a northward and a southward migration, and a non-breeding season. Four dates were assessed for each bird's track: i) the arrival on the breeding grounds, ii) the departure from the breeding grounds, iii) the arrival in South Africa, and iv) the departure from South Africa. For each of the four birds, 95% kernel home range estimators were calculated for: i) the breeding area, and ii) the non-breeding area. For kernel density estimates in Geospatial Modelling Environment (Spatial Ecology LLC, 2014, vers. 0.7.4.0), least-squares cross validation was set for the bandwidth estimator and cell size was 20 m (Limiñana et al. 2015).

### 6.2.3 Feather collection

A total of seven European Honey-buzzard carcasses were collected from wildlife rehabilitation facilities in Gauteng province, South Africa, from 2017 and 2018 (Table 6.1). The ten primaries from the right wing of the honey-buzzards were removed and labelled. Primary moult in European Honey-buzzard has been recorded as descendant, meaning that the innermost primary is moulted first and outermost primary is moulted last (Cramp and Simmons 1979). Therefore, the innermost primary (closest to the bird's body) was labelled primary 1 (P1) and the outermost was labelled primary 10 (P10). The length of the rachis covered with barbs was measured on each feather. All primaries were photographed, and scored for moult using the South African Ringing Scheme (SAFRING) moult scoring system (Snow 1967, de Beer et al. 2001).

*Table 6.1:* The European Honey-buzzard (*Pernis apivorus*) specimens sampled for stable isotope analysis.

Bird ID	Age	Sex	Location	Date Collected
Uju	Adult	Male	Bryanston, Gauteng, South Africa	17 April 2017
Asali	Adult	Female	Ruimsig, Gauteng, South Africa	23 April 2017
Bird 1	Adult	Female	Gauteng, South Africa	December 2016
Bird 3	Adult	Female	Riebeeckstad, Free State, South Africa	February 2018
Bird 4	Adult	Female	Gauteng, South Africa	February 2018
Bird 5	Adult	Female	Gauteng, South Africa	April 2018
Bird 2	Juvenile	Unknown	Waterberg, Limpopo, South Africa	3 March 2017



#### 6.2.4 Isotope analysis

All feathers were washed in 2:1 chloroform:methanol solution, and dried for at least 24 hours (Parrite and Kelly 2009). After washing, feathers were measured and marked at locations 1 (0.6cm from the tip of the feather), 5 (the centre of the barb-covered rachis), and 9 (0.6cm from the bottom of the barb-covered rachis) (Figure 6.1).

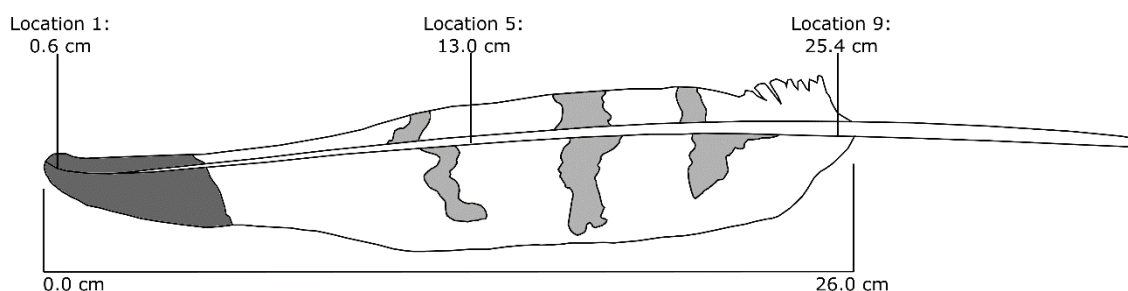


Figure 6.1: The sixth primary (P6) of an adult female European Honey-buzzard (*Pernis apivorus*) with the total length of the barb-covered rachis, and the three stable isotope sampling locations (1, 5, and 9).

Samples for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analysis (0.40-0.50 mg) were cut from the feathers, and placed in a pre-tared tin cup. Two samples of each of two working standards (Merck high purity  $\text{CaCO}_3$  and Urea) were placed every 25 samples. The samples were then combusted at  $1020^\circ\text{C}$  in an Elemental Analyser (Flash EA, 1112 Series, Thermo Electron Corporation, Bremen, Germany). The  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios were measured using Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer (CFIRMS) (Thermo Electron Corporation) plumbed in-line with the elemental analyser via a ConFlo IV gas controller (Thermo Fisher Scientific, Bremen, Germany). The measured  $\delta^{15}\text{N}$  and the actual  $\delta^{15}\text{N}$  of the standards were used to create a linear regression to correct the measured  $\delta^{15}\text{N}$  of the feather samples. The same analysis was performed with  $\delta^{13}\text{C}$  values. The  $^{13}\text{C}/^{12}\text{C}$  isotope ratios are conveyed relative to Vienna Pee Dee Belemnite (VPDB) and the  $^{15}\text{N}/^{14}\text{N}$  ratios are expressed relative to Air.

Samples for non-exchangeable  $\delta^2\text{H}$  analysis (0.20-0.30 mg) were cut from the feathers, and placed in a pre-tared silver cup. Two samples of each of two keratin working stands (KHS  $\delta^2\text{H} = -54.1 \pm 0.6 \text{ ‰}$  and CBS  $\delta^2\text{H} = +197.0 \pm 1.8 \text{ ‰}$ ) were placed every 25 samples (Soto et al. 2017, Wassenaar and Hobson 2010). The ratio of  $^2\text{H}/^1\text{H}$  were measured using a high temperature TC/EA elemental analyser (Thermo Fisher Scientific, Bremen Germany) with pyrolysis at  $1450^\circ\text{C}$  coupled to the CFIRMS. The measured  $\delta^2\text{H}$  and the actual  $\delta^2\text{H}$  of the standards were used to create a linear regression to correct the measured  $\delta^2\text{H}$  of the feather

samples. The  $^2\text{H}/^1\text{H}$  ratios are expressed relative to Vienna Standard Mean Ocean Water (VSMOW). The average and standard deviation of the three sampling locations on each feather were calculated for  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and  $\delta^2\text{H}$ . These values were plotted by primary for each individual.

### 6.3 Results

#### 6.3.1 Moulting in photographs

A total of 169 photographs of European Honey-buzzard in southern Africa had all primaries visible on at least one wing. Of these photos, 95 were adults, 11 were second years, 61 were juveniles, and 2 were of unknown age. A total of 34.7% ( $n = 33$ ) of adults were moulting at least one primary, 36.4% ( $n = 4$ ) of second years were moulting at least one primary, and 1.6% ( $n = 4$ ) of juveniles were moulting at least one primary. One adult was missing two primaries.

In adults, the most commonly missing primaries were P7 and P9 in South Africa, both of which were recorded as missing eight times. P2, P4, and P5 were never recorded as missing. Later in the non-breeding season, birds were more commonly moulting outer primaries (e.g. P9 and P10) (Figure 6.2). By April, no birds were recorded moulting any primary feathers.

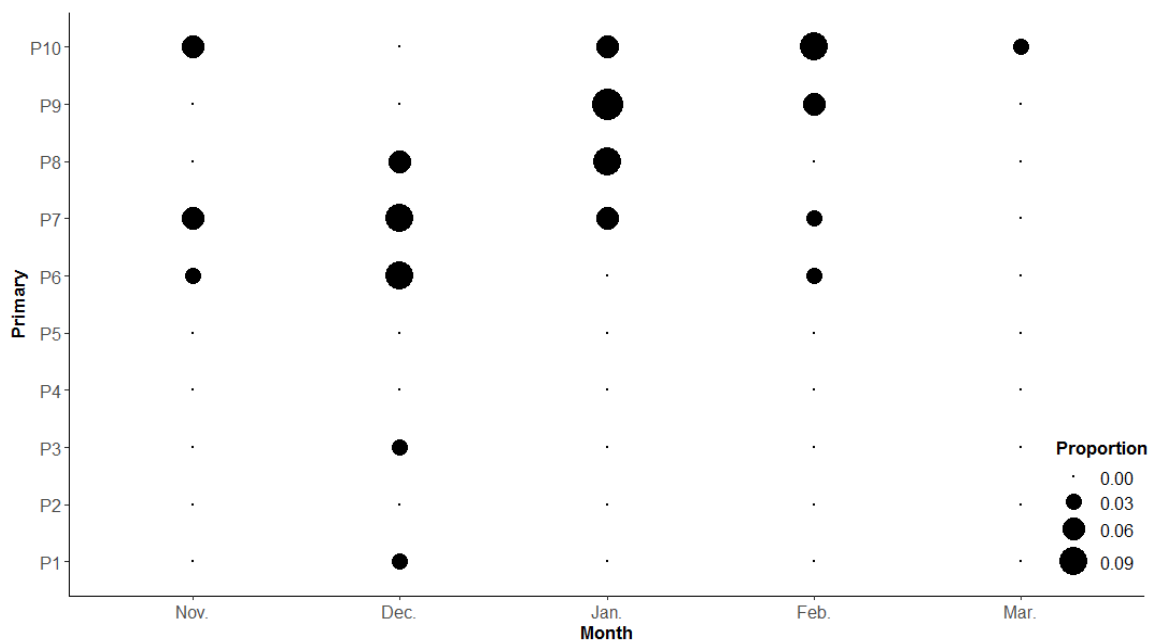


Figure 6.2: The missing primaries of photographed European Honey-buzzard (*Pernis apivorus*) in southern Africa ( $n = 34$ ) by austral summer months. The size of the circles indicates the proportion of the total number of missing primaries.

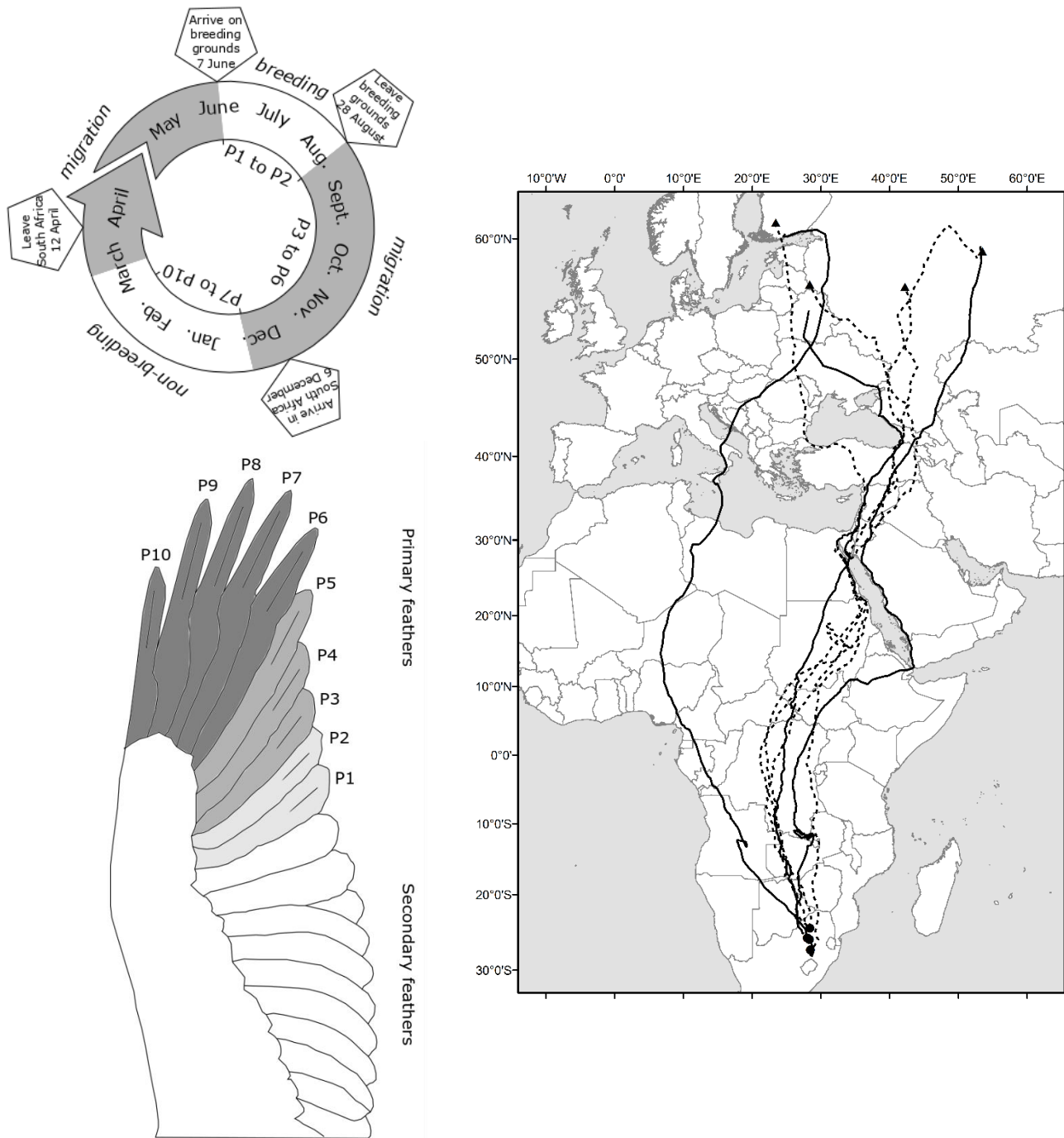


Figure 6.3: The hypothesized primary moult groups of European Honey-buzzard based on previous European documentation along with the photos from southern Africa. The primaries in the lightest grey (P1-P2) are likely moulted on the European breeding grounds, the primaries in the medium grey (P3-P5) are likely moulted on migration, and the primaries in the darkest grey (P6-P10) are likely moulted in southern Africa. The circular calendar represents where the four tracked southern African birds travelled throughout the year and gives an indication of which primaries would likely be moulted during which period. Lastly, the map shows the areas where the four tracked honey-buzzards moved in a single year. Black circles represent the centroid of each birds' non-breeding home range. Black triangles represent the centroid of each birds breeding home range. Solid black lines indicate the birds' southward migration while dashed black lines indicated their northern migration.

### 6.3.2 Spatiotemporal movement patterns

The four tracked European Honey-buzzards arrived on their European breeding grounds on a median date of 8 June, and remained there until a median date of 29 August ( $82 \pm 4.0$  days at their breeding territory) (Figure 6.3). Their migration south continued until they arrived in South Africa on a median date of 8 December ( $99.3 \pm 4.7$  days on southerly migration). They remained in South Africa until a median date of 14 April ( $134.3 \pm 3.5$  days in South Africa). The honey-buzzards' northerly migration took an average of  $57.8 \pm 5.0$  days. Three of the birds migrated to Russia while one migrated to Finland.

### 6.3.3 Moulting in specimens

Three of the adult European Honey-buzzard specimens (Uju, Asali, and Bird 5) had all new feathers with no apparent moult (Table 6.2). All three were collected in the month of April. Bird 1, Bird 3, and Bird 4 were all actively growing at least one primary and up to three primaries, while all other feathers were new. They were collected in February and December. Bird 2, a juvenile, had all worn primaries.

*Table 6.2:* The moult scores (based on the SAFRING Bird Ringing Manual) of the ten primaries of seven European Honey-buzzard (*Pernis apivorus*) collected in South Africa from 2016-2018. The codes are as follows: i) 0 = old feather remaining, ii) 1 = feather missing or new feather in pin, iii) 4 = new feather between 2/3 and fully grown with waxy sheath, iv) 5 = new feather fully developed with no waxy sheath (de Beer et al. 2001, Snow 1967).

Bird <sup>a</sup>	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Bird 1	5	5	5	5	5	5	5	5	5	4
Bird 3	5	5	5	5	5	5	5	5	4	4
Bird 4	5	5	5	5	5	5	5	4	1	4
Bird 5	5	5	5	5	5	5	5	5	5	5
Uju	5	5	5	5	5	5	5	5	5	5
Asali	5	5	5	5	5	5	5	5	5	5
Bird 2	0	0	0	0	0	0	0	0	0	0

<sup>a</sup> Individuals are presented in the order of the month they were collected with the exception of Bird 2, a juvenile bird.

#### 6.3.4 Primary feather isotopes

For  $\delta^{15}\text{N}$ , the male honey-buzzard (Uju) showed little variation across the primaries (Figure 6.4). Of the female birds, three individuals showed a shift in  $\delta^{15}\text{N}$ , Asali, Bird 1, and Bird 5. Asali showed a shift on P4. Bird 1 showed the largest shift on P2. Bird 5 showed a smaller increase at P9. Bird 3 and Bird 4 had little variation across their primaries with Bird 3 having a consistently high  $\delta^{15}\text{N}$ . The juvenile European Honey-buzzard (Bird 2) showed very little variation across all primaries.

For  $\delta^{13}\text{C}$ , the adult male European Honey-buzzard (Uju) showed a shift at P6 (Figure 6.4). Of the adult female individuals, all but Bird 4 showed shifts in carbon. Asali shifted  $\delta^{13}\text{C}$  values at P4. Bird 1 and Bird 3 showed a smaller  $\delta^{13}\text{C}$  shift at P7. Bird 5 had the latest  $\delta^{13}\text{C}$  shift at P9. Bird 4 had a high  $\delta^{13}\text{C}$  value for all primaries. The juvenile honey-buzzard (Bird 2) had low  $\delta^{13}\text{C}$  values across all primaries.

For  $\delta^2\text{H}$ , the male honey-buzzard (Uju) had consistently high  $\delta^2\text{H}$  values across primaries (Figure 6.4). Two female European Honey-buzzards, Asali and Bird 1, had shifts in their  $\delta^2\text{H}$  values. The  $\delta^2\text{H}$  values shifted at P4 in Asali's primaries. In the primaries of Bird 1, the  $\delta^2\text{H}$  values shifted at P3. The  $\delta^2\text{H}$  values of Bird, 3, 4, and 5 were consistently high across all their primaries. The  $\delta^2\text{H}$  values of the juvenile bird's (Bird 2) primaries were all low.

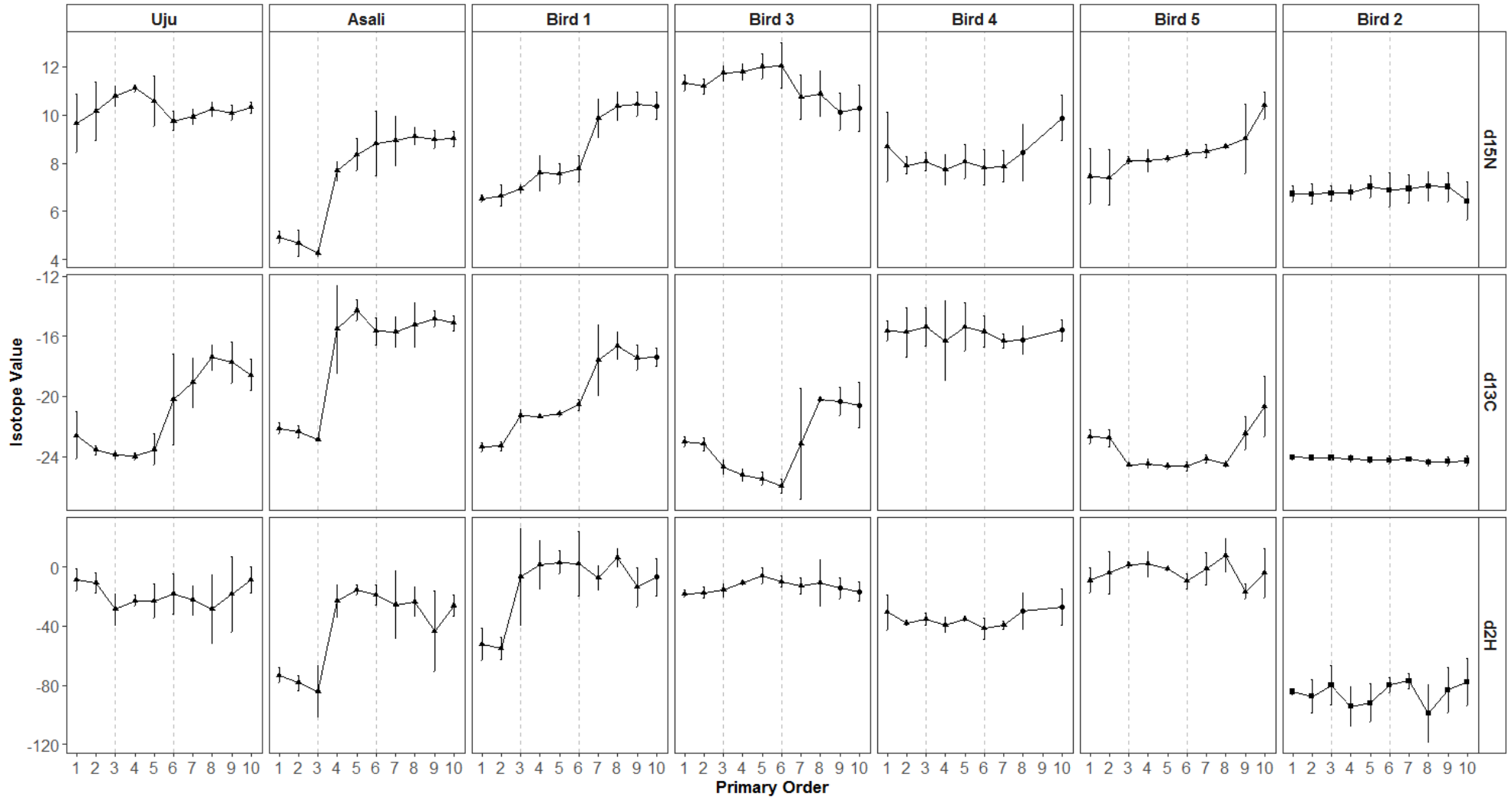


Figure 6.4: The  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and  $\delta^2\text{H}$  of three sampling locations on each of ten primaries from an adult male European Honey-buzzard (*Pernis apivorus*) (Uju), five adult female honey-buzzards (Asali, Bird 1, Bird 3, Bird 4, and Bird 5), and one juvenile honey-buzzard (Bird 2). All birds were collected in South Africa. Shapes indicate moult score: square = 0, circle = 4, and triangle = 5. Error bars represent the standard deviation of the three sampling locations of each primary. Grey dashed lines indicate primary 3 (P3) and primary 6 (P6)

#### 6.4 Discussion

Based on previous evidence from the European breeding grounds and our photographic evidence from southern Africa, it seems likely that adult European Honey-buzzards moult their first two primaries in Europe (P1 and P2) while breeding during the Northern Hemisphere summer (June-August), and their last five primaries in southern Africa (P6-P10) during the Northern Hemisphere winter (December-March) (Cramp and Simmons 1979, Forsman 2016). This leaves three middle primaries (P3-P5) that are moulted elsewhere, perhaps at stopover sites during migration.

The relatively large proportion of feathers moulted on migration is unusual among birds of prey. Most species will pause flight feather moult during migration because of the increased nutrient demand as well as the impairment of flight ability due to missing feathers (Edelstam 1984, Gorney and Yom-Tov 1994, Newton 2009). Both of these factors could result in a slower, and therefore, longer and more dangerous migration for a bird (Newton 2009). However, this is less likely to be an important factor for individuals on their southwards, post-breeding migration, when there is less urgency to arrive timeously on the non-breeding grounds in comparison with the northwards migration to reach their breeding territories. This allows for more stopovers to refuel. The slower southward migration pattern was demonstrated by the four female honey-buzzards tracked to and from South Africa, which took an average of almost 100 days to migrate to South Africa but approximately 60 days to migrate back to Europe. The extra 40 days on the southward migration likely included many stopovers for refuelling, which may allow the birds to moult and migrate at the same time. This is supported by the isotope values of the primaries of some of the birds tested (particularly Bird 1), which had high  $\delta^2\text{H}$  values (indicating feathers of African origin) and varying  $\delta^{13}\text{C}$  values (indicating that the birds had likely moved between  $\text{C}_3$  and  $\text{C}_4$  dominated habitats, e.g. forests and savanna/grassland) (Hobbie and Werner 2004, Bowen et al. 2005, Hobson et al. 2012b, Reichlin et al. 2013). This indicates that feathers are being grown from resources obtained on stopover sites. The southern African honey-buzzards may be moulting during their migration due to their longer migration relative to West or East African individuals. Hake et al. (2003) found that adult European Honey-buzzards migrating to West Africa took an average of 42 days, less than half of the time it took birds to migrate to South Africa. Southern African honey-buzzards spend about 43% of their year on migration (an average of 157.1 days), and therefore, need to begin moult on their migration in order to complete a full primary moult annually.

#### 6.4.1 Stable isotopes and primary moult patterns

There was high variation in the isotope values of European Honey-buzzard primaries, indicating both different age classes and diverse moult timing. To begin, Bird 2, a juvenile honey-buzzard, had consistently low values for  $\delta^2\text{H}$  as well as low  $\delta^{13}\text{C}$  values (indicative of a  $\text{C}_3$  tree-dominated environment) (Hobbie and Werner 2004, Bowen et al. 2005, Hobson et al. 2012b). These isotope values suggest that all of its feathers were grown in Europe, consistent with the hypothesis that all of its primaries were produced while it was still on its nest. Besides Bird 2's full set of feathers, only five other primaries tested had similar European signatures, the first three primaries (P1-P3) of Asali, and the first two primaries (P1-P2) of Bird 1.

All other adult birds (four individuals) had consistently high  $\delta^2\text{H}$  values, which indicate that all of their primaries were grown in Africa (Bowen et al. 2005, Hobson et al. 2012b). There are two likely explanations for individual honey-buzzards growing all their feathers on the Africa continent: i) these birds represent young adult birds that have yet to migrate north for their first breeding season, or ii) these birds are breeding adults who did not have the time and/or resources to moult on the breeding grounds. With regards to the first hypothesis, European Honey-buzzards are known to spend at least two years in Africa before returning to breed for the first time (Strandberg et al. 2012, Vansteelant et al. 2017). These individuals travel widely across the continent for these years, exploring potential non-breeding territories (Strandberg et al. 2012, Vansteelant et al. 2017, Chapter 5). The similar  $\delta^2\text{H}$  with varying  $\delta^{13}\text{C}$  of the primaries of most of the birds (Uju, Bird 3, and Bird 5) could reflect this movement. This hypothesis is further supported by the relatively high proportion of sub-adult honey-buzzards found in southern Africa, elevating the chance of sampling a high proportion of young birds (Chapter 3).

A single bird (Bird 4) appeared to have grown all of its feathers in an African savanna or grassland environment (based on high  $\delta^{13}\text{C}$  values indicating a  $\text{C}_4$ -dominated habitat), more than likely South Africa in this case, as the bird was still in active moult when it died. This is particularly interesting as there have been very few records of European Honey-buzzards in southern Africa during the austral winter (June-August), all of them sub-adult birds (Howes et al. 2019). This provides evidence that this particular bird may, in fact, be a young bird which has yet to return to Europe.

In terms of the second hypothesis, European Honey-buzzards are known to skip all moult on the breeding grounds in some cases (Forsman 1984). These birds may not have had adequate nutrition to breed and moult over the same period. They may also be leaving the



breeding grounds in relatively poor condition, hence the large number of apparent stopovers in the isotopic signatures. This failure to moult on the breeding grounds, once again, may be particularly common in European Honey-buzzards migrating to southern Africa due to their long migration further south, which may result in birds beginning breeding in a more energetically-depleted state.

Despite some broad-scale patterns, there is also high variability between European Honey-buzzards with regards to how many primaries are moulted in different regions. The sudden shifts in  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$  values between primaries suggest a movement into a new area. Only one adult bird, Bird 4, did not show any shifts in any of the feather isotope values, signifying that all of its primaries were grown in a single region, an African  $\text{C}_4$ -dominated area, likely South Africa. Bird 5 showed only a single small shift in  $\delta^{13}\text{C}$  in the last two primaries (P9 and P10) with the first eight primaries likely grown in an African  $\text{C}_3$ -dominated area (Central Africa) and the final two grown in a more  $\text{C}_4$ -dominated area (southern Africa). As mentioned earlier, Asali seems to have grown the first three primaries in Europe while the rest were produced in southern Africa (or another  $\text{C}_4$ -dominated area in Africa). Similarly, Bird 1 grew two primaries in Europe, followed by four primaries (P3-P6) in an African  $\text{C}_3$ -dominated area, and four primaries in a more  $\text{C}_4$ -dominated area such as southern Africa. Lastly, both Uju and Bird 3 moulted all of their primary feathers in Africa with the first five and six primaries respectively grown in Central Africa, and the final four and three respectively grown in southern Africa with a single middle primary demonstrating mixed resources from both regions (P6 and P7 respectively). Based on all of these adult individuals, between zero and two primaries were grown in Europe, between zero and nine primaries were grown in Central Africa, and between two and ten were grown in southern Africa. This high variation in which primaries were grown where indicates how important differences between individuals can be in isotope studies.

It should also be mentioned that while these differences in isotopic values may reflect change in location, there is also the confounding effect of a possible change in diet (Knoff et al. 2002, Rubenstein and Hobson 2004). This is particularly true for  $\delta^{15}\text{N}$  values, which often reflect the trophic level of a bird's diet (Hobson and Clark 1992, Knoff et al. 2002). Some of the individuals (Asali and Bird 1) showed changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at the same moulted feather, which could potentially reflect a change in diet. However, these birds also showed a change in their  $\delta^2\text{H}$  values, an element that is more strongly linked to location than diet, at the same time, indicating that it is likely that the individuals moved, and that the changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values may also signify this movement (Bowen et al. 2005).

#### 6.4.2 Capital vs. income contributions

The primary feather analysis revealed that the isotopes of all three elements generally shifted at the same point in the birds' moult. The best example of this would be the shift between third and fourth primaries (P3 and P4) of Asali, where  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and  $\delta^2\text{H}$  values all changed at the same point. This indicates that all of the isotopes used to grow the fourth primary were from the same new environment in comparison with the third primary. A singular shift may indicate that the primary feathers were grown with income contributions, meaning that whatever the individual consumed went directly into feather growth (Fox et al. 2009). On the other hand, some birds showed shifts where the isotopes of all three elements are not aligned. For example, the shift between Bird 1's second and third primaries (P2 and P3) showed shifts in  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$ , but not  $\delta^{15}\text{N}$ , perhaps indicating that the bird had sufficient capital nitrogen resources from stored protein reserves to grow a feather, but used income resources for the required carbon and hydrogen. The differences between income and capital growth of feathers may be due to differing body condition of individuals when they begin migration (Klaassen et al. 2001). Those that have early or completely failed breeding attempts, allowing for greater foraging on the breeding grounds, may have sufficient fat and protein reserves to grow some of their primaries using capital resources while others, perhaps successful breeders, may need to use income resources. To better differentiate between these strategies, a more complete understanding of both the movement and diet of these individuals would be needed to determine where exactly birds are procuring resources (Fox et al. 2009).

#### 6.4.3 Future use of stable isotopes of European Honey-buzzard feathers

The results of this study emphasize the variability of individual European Honey-buzzards in their moult and spatiotemporal movement patterns. While the majority of the birds were identified as adults by their plumage, the isotope signatures of their primaries indicated that these birds are unlikely to have left the continent, and may be relatively young birds (although in adult plumage), or adults who have moulted all their feathers in Africa (Strandberg et al. 2012). Therefore, these individuals do not provide meaningful information on migratory connectivity on a larger scale. The variability between each of the birds assessed likely depends on a host of variables including age, sex, movement patterns, breeding success, and diet (Hobson and Clark 1992).

For the two adult birds that had feathers with European signatures, the first two primaries (P1 and P2) seem the most likely candidates for sampling to determine their European breeding grounds. Based on the tracking data presented in this study, this likely indicates that they were moulted between May and August. Of the two birds, Asali had much lower  $\delta^2\text{H}$  values than Bird 1 for these primaries, perhaps indicating that Asali had a more north-eastern breeding ground than Bird 1 (Bowen et al. 2005). However, more data on diet-tissue fractionation in this species is needed in order to assign locations. In addition, there is strong evidence that there is high variability in fractionation between individuals, making it difficult to draw meaningful conclusions from the isotopic differences of these two individuals (Hobson and Clark 1992, Bearhop et al. 2002). For determining the non-breeding grounds of individuals, the outer three primaries (P8-P10) are the best sampling locations. For all birds, these primaries had African grassland or savanna signatures, likely indicating that they were grown in South Africa in this particular case, although the Sahel savanna region is another possible region for growth (Hobson et al. 2012b).

The middle primaries (P3-P7) were highly variable in their signatures in terms of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , but had consistently African  $\delta^2\text{H}$  values (Bowen et al. 2005, Hobson et al. 2012b). These feathers can likely provide information on stopover sites, at least for South African birds which endure a particularly long migration. In order to better identify stopovers (and non-breeding areas), it is important to include  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in the analysis as the  $\delta^2\text{H}$  variability on the African continent is relatively low, and therefore, less useful in assigning potential non-breeding areas (Hobson et al. 2012b). In addition to having high variation between feathers, some of the middle primaries also had high variation within the feathers (e.g. P7 of Bird 3). This may indicate that there is a combination of capital and income resources used for growing the feathers from multiple regions in Africa which may make it challenging to assign an accurate geographic origin. This further documents the difficulties associated with interpreting stable isotope data and the need for large sample sizes in migratory connectivity studies.

Lastly, this study further emphasizes the consequences of European Honey-buzzards migrating to southern Africa, a far more distant non-breeding area than West or Central Africa. The continuation of moult through migration indicates a mistiming of energetic events for the species. By moulting during migration, individuals are likely to be at greater risk of mortality during an already dangerous period. This along with the other risks of a longer migration could have population-level effects if more honey-buzzards spend their non-breeding season in southern Africa.

## 6.5 References

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# **Conclusion**



## 7.1 Introduction

Over the past 200 years, profound changes in habitat and climate have played a large role in determining how bird species are currently distributed (Jetz et al. 2007, Sekercioglu et al. 2007, Powers and Jetz 2019). Some raptor species have proven highly successful at adapting to urban or cultivated anthropogenic landscapes while others have been far less successful, relying on large tracts of untransformed land (Machange et al. 2005, Thiollay 2007, Hockey and Midgley 2009, Amar et al. 2014, McPherson et al. 2016). Large raptors (e.g. eagles and vultures) appear to be particularly sensitive to habitat changes, disappearing from human-transformed landscapes (Curtis 2005, Thiollay 2007, Hofmeyer et al. 2014). An example of one such species is the Martial Eagle (*Polemaeetus bellicosus*), which is absent from cultivated land, and has a strong preference for land with indigenous game animals over land with domestic stock (Machange et al. 2005). The southern African endemic Black Harrier (*Circus maurus*) shows a similar trend, breeding almost exclusively in native renosterveld patches of at least 100 ha (Curtis 2005).

In contrast, other raptors in Africa have been able to adapt to, or tolerate human landscapes. Urban and plantation landscapes appear to be particularly important for these range-expanding species in South Africa (Hockey and Midgley 2009, Amar et al. 2014, McPherson et al. 2016). The three best-studied raptors that have adapted to human landscapes in southern Africa, the African Crowned Eagle (*Stephanoaetus coronatus*), Rufous-breasted Sparrowhawk (*Accipiter rufiventris*), and Black Sparrowhawk (*A. melanoleucus*), are all forest-adapted species that were originally found in the native Afromontane and coastal forest habitats of the country (Hockey and Midgley 2009, Amar et al. 2014, McPherson et al. 2016). Each of these species now extensively use urban and plantation matrices, and have, therefore, adapted their breeding behaviour and diet to succeed in their new environments (Hockey and Midgley 2009, Amar et al. 2014, McPherson et al. 2016). By understanding these raptors, as well as other adapting and range changing species, we can better assess how species survive and adapt in the face of intense global change.

## 7.2 What are the drivers of European Honey-buzzard range change?

In the case of the European Honey-buzzard (*Pernis apivorus*), the drivers of the perceived increase in southern Africa were initially unclear. I started with three possible explanations for the growth of honey-buzzard records in southern Africa: i) an increase in the



source breeding population, ii) an increase in the birdwatching effort and skill in southern Africa resulting in an improved detection rate of the species, and iii) a southwards shift in the non-breeding population from more northern non-breeding populations (Figure 7.1). In this thesis, I have investigated two of the three hypotheses. The change in breeding population hypothesis was not explored as it seemed highly unlikely based on previously published work on the species' breeding grounds (Kjellén and Roos 2000, Agostini et al. 2007, Verhelst et al. 2011, Galushin 2012, Martín et al. 2016). Based on the tracking data of South African female honey-buzzards (Chapter 6), the southern African population is likely of Eastern European and Russian origin. A review of European Honey-buzzard status in European Russia showed no increase in the species population in the region (Galushin 2012). The Russian population data are further supported by migration counts, which have documented either declining or stable numbers of European Honey-buzzard across Europe including Batumi, Georgia, a migratory bottleneck through which many of the eastern population birds (including tracked South African birds) migrate (Kjellén and Roos 2000, Agostini et al. 2007, Verhelst et al. 2011, Martín et al. 2016).

Both the increased birdwatching effort hypothesis and the change in non-breeding range hypothesis were investigated in Chapter 2 of this thesis. Birdwatching effort alone does not account for the growth in honey-buzzard records in the sub-region. There is good evidence that the trends documented in the South African Bird Atlas data are generally accurate, despite changes in effort and method over time (Robertson et al. 1995, Amar et al. 2016, Howes et al. 2019). It should, however, be noted that while these trends are generally accurate, it is still important to take observer effort into account in future studies to ensure that the initially apparent trends in the data are correct.

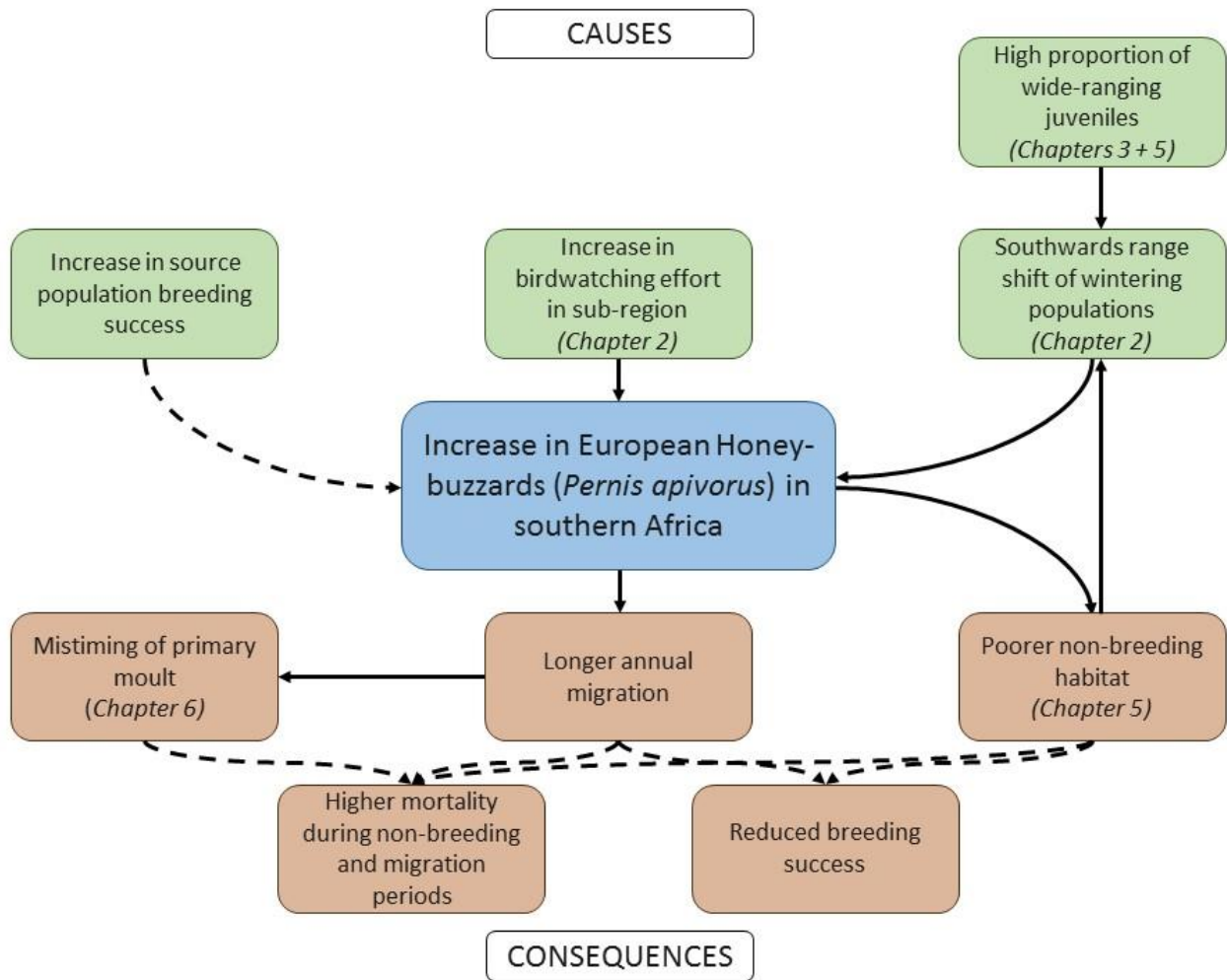


Figure 7.1: A summary of the findings of this thesis with the possible causes of the increase in European Honey-buzzards (*Pernis apivorus*) in southern Africa in green boxes and the possible consequences of the increase in red boxes. Relevant chapter numbers are in italics in the boxes. Solid arrows signify links that have been investigated in this study while dashed arrows indicate links for future research directions.

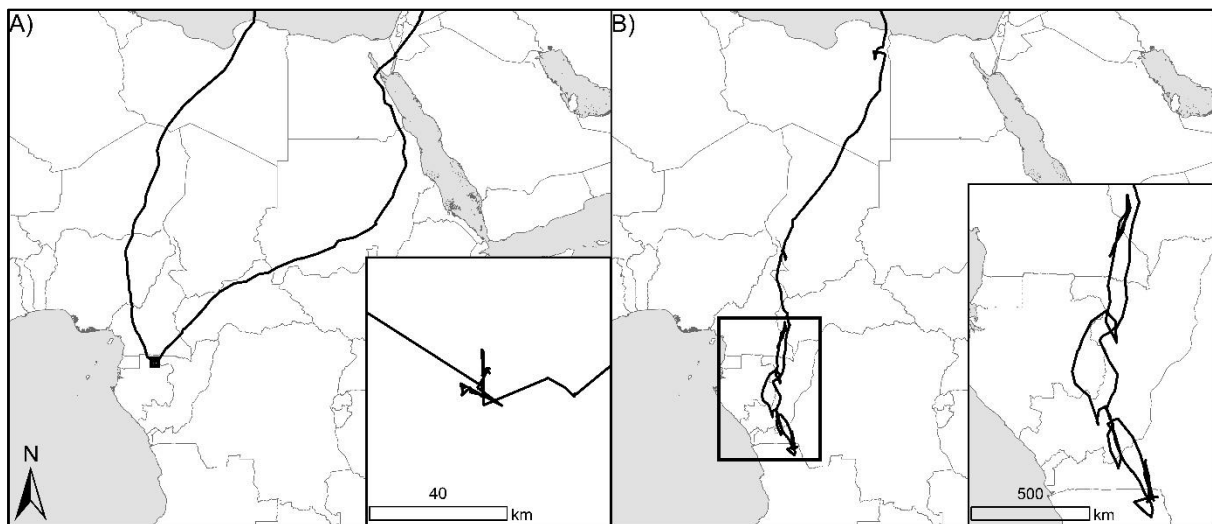
The final conclusion of Chapter 2 was that habitat loss further north on the African continent has forced European Honey-buzzards to spend their non-breeding season further south. Chapter 2 presented evidence of a large-scale relationship between available forest area in East Africa and the number of honey-buzzard records in both Tanzania and southern Africa. East African forest loss was associated with a greater number of honey-buzzards in southern Africa. Over the period of honey-buzzard record increases in southern Africa, East Africa lost a substantial portion of its forest (about 10%). Forest loss has now pushed non-breeding European Honey-buzzards further south on the African continent in search of suitable habitat, resulting in a non-breeding range shift in this migrant species.

On a finer scale, the importance of contiguous and unfragmented forest habitat for European Honey-buzzard on their non-breeding grounds was verified in Chapter 5. Both adult and juvenile European Honey-buzzards with a large patch of forested habitat were able to survive in smaller home ranges than those in more fragmented areas. This, in turn, allowed birds to reduce their daily distance travelled which: i) lessens their risk of predation due to decreased exposure to predators (Yoder et al. 2004), and ii) decreases their daily energy expenditure which may allow them to gain mass more easily, and in turn, give them a greater chance of survival on their northwards migration. These data confirm that reduction and fragmentation of forested habitats in Africa results in changes in the behaviour of European Honey-buzzard, and further supports the hypothesis that forest loss is driving a range shift in this species.

While this thesis has primarily focused on land cover change as the driver of the southwards range shift of European Honey-buzzard in Africa, climate change may also be contributing to the documented range change. The response of Palaearctic migrants to climate change on the non-breeding grounds has been varied, as are the predictions for range shifts under future climate scenarios (Barbet-Massin et al. 2009, Doswald et al. 2009, Ambrosini et al. 2011, Potvin et al. 2016). Species such as Osprey (*Pandion haliaetus*) and Caspian Tern (*Hydroprogne caspia*) have shown southward range shifts in Africa while Barn Swallows (*Hirundo rustica*) have shown the opposite trend (Ambrosini et al. 2011, Potvin et al. 2016). In the case of the honey-buzzard, the rate at which the species has expanded in southern Africa seems to be more rapid than has been previously documented in climate change studies, with the bulk of the increase over the past decade. However, the effect of climate change on the non-breeding range of this species should certainly be assessed in the future.

The southwards range shift in European Honey-buzzard was likely advanced by juvenile and sub-adult individuals, which exhibit lower site fidelity than adult birds (Chapter 5). As in other large soaring migratory birds, juvenile honey-buzzards moved widely across the African continent for a minimum of two years (Figure 7.2). Adults remained faithful to one or two known locations over the entire non-breeding season. The wide-ranging movements of juvenile European Honey-buzzards make them the most likely instigators of range change as detailed by *serial residency hypothesis* (Cresswell 2014). By remaining faithful to a single site as adults, the birds are likely relying on staying in their suitable site in order to reduce mortality risk by venturing into areas of unknown suitability, which may also carry a higher risk of predation (Switzer 1993, Cresswell 2014). Juvenile birds put themselves at higher risk by moving greater distances, and therefore, face higher mortality than adults (Cresswell 2014).

However, in the longer term, juvenile honey-buzzards that wander are more likely to find suitable non-breeding habitat to return to annually, enhancing their chance of long-term survival (Cresswell 2014). During these movements, sub-adult European Honey-buzzards are more than likely exploring the habitats in southern Africa to assess their suitability (as supported by a high proportion of juvenile birds presented in Chapter 3) and are, therefore, more likely to establish a territory in the sub-region. Young birds are even more likely to explore further south in Africa if they cannot find suitable areas further north due to habitat loss and fragmentation. These extensive juvenile movements in long-lived species such as European Honey-buzzard are thought to improve overall population resilience (Cresswell 2014). During their wanderings, at least a few juvenile birds discover suitable habitat which allows for species-level adaptation to changes in land cover and climate.



*Figure 7.2:* The hourly African tracking data of: A) an adult male (Jouko) and B) a juvenile male (Mohammed) European Honey-buzzard (*Pernis apivorus*) between August 2013 and August 2014 with insets of their non-breeding movements. Note that the adult male had a direct trip without stopovers to a single non-breeding location while the juvenile male wandered extensively with many stopovers and home ranges over the same period. The juvenile bird did not migrate to Europe to breed for at least four years.

While habitat changes further north in the European Honey-buzzard's African range are critical, it seems unlikely that the population would be expanding if there was not suitable habitat for the species in southern Africa. In southern Africa, European Honey-buzzards appear to be relying on both natural woodlands and forests, as well as man-made forests and well-wooded urban areas, particularly in the grassland biome of central South Africa. Southern Africa has relatively little natural forest in comparison with regions further north in Africa (Hansen et al. 2013). The majority of southern Africa's forested area is made up of plantations

of *Eucalyptus* and pines, as well as some ‘forested’ urban habitats (Hansen et al. 2013). Honey-buzzards in the sub-region are often found in non-native *Eucalyptus* trees (Figure 7.3). The amount of available urban and *Eucalyptus* forest is increasing in southern Africa; in fact, both South Africa and Swaziland have had net afforestation over the past two decades due to this trend (Allan et al. 1997, Neke and Du Plessis 2007, Hockey and Midgley 2009, Hansen et al. 2013, Symes et al. 2017). In light of this habitat change, it seems likely that European Honey-buzzards are adapting to, and utilizing the same habitats as many of the resident raptor species such as Black Sparrowhawk and Crowned Eagle. However, as will be discussed further, it is not clear whether this habitat is equally suitable to more natural habitats.



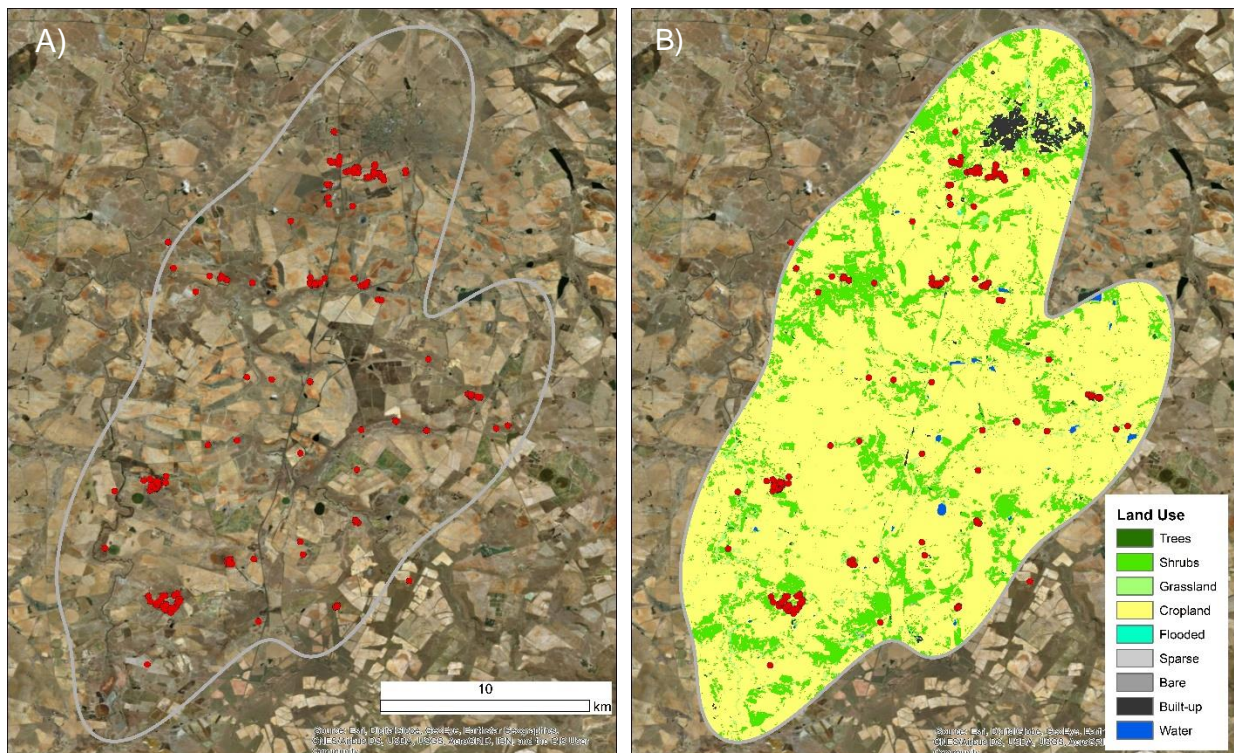
Figure 7.3: Four photographs of typical European Honey-buzzard (*Pernis apivorus*) non-breeding habitat utilized by a tracked adult female (Päivi) in Reitz, Free State province, South Africa. Photo C by Craig Symes.

### 7.3 What are the consequences of European Honey-buzzard range change?

The southern Africa European Honey-buzzard population allows for an assessment of the consequences of a shifting non-breeding range. Two outcomes of the range shift stood out in this study: i) individuals in southern Africa may have poorer non-breeding habitat, and ii) individuals in southern Africa have a longer annual migration (Figure 7.1). In addition to the

immediate effects, both of these findings may have consequences for the population in the long-term.

The quality of non-breeding habitats of European Honey-buzzards in southern Africa differs from that of the Afrotropics. The South African European Honey-buzzards had the smallest proportion of treed or forested habitat of any of the adult individuals tracked in this study (Figure 7.4). As detailed in Chapter 5, the South African population also tended to have larger home ranges, and therefore, moved greater distances on a daily basis than birds in less fragmented habitats further north in Africa. As mentioned above, European Honey-buzzards in southern Africa appear to be dependent on *Eucalyptus* patches and urban forests. These habitats are both more fragmented and less structurally complex than natural forest (Carlson 1986, Wethered and Lawes 2003, 2005). Despite the low diversity of bird species in these habitats, they support numerous potential competitors or predators of European Honey-buzzard, including Black Sparrowhawk, Rufous-chested Sparrowhawk, and Crowned Eagle (Hockey and Midgley 2009, Amar et al. 2014, McPherson et al. 2016).



*Figure 7.4:* The 95% kernel home range (404.33 km<sup>2</sup>) and tracking points of an adult female European Honey-buzzard (*Pernis apivorus*) (Päivi) in Reitz, South Africa from 19 February to 19 April 2016 with: a) an ESRI satellite image, and b) the European Space Agency land use map with nine habitat categories. The home range was made up of 0.31% treed habitat, 1.10% built-up habitat, 2.38% grassland habitat, 17.89% shrub habitat, and 77.97% cropland.

Perhaps the single most obvious consequence of honey-buzzards spending the non-breeding season further south is the significantly longer migration. Hake et al. (2003) documented that adult European Honey-buzzards from Sweden took an average of 42 days on their southward migration to arrive at their non-breeding grounds in West Africa. The juveniles of the same population took slightly longer at 64 days (Hake et al. 2003). The South African adult female birds (n = 4) tracked in this study spent an average of 99 days on their southward migration, 2.35 times longer than adult West African birds. Migration is the period of highest mortality in the life of migrant birds (Owen and Black 1989, Strandberg et al. 2010, Klaassen et al. 2014, Lok et al. 2014, Oppel et al. 2015). By extending their migration, southern African honey-buzzards are likely to be at a higher risk of mortality on an annual basis. This may be exacerbated by the need to expend more energy while on migration, as well as having less time on the non-breeding grounds to forage and gain the necessary fat reserves. In addition to the higher risk of mortality, the longer migration of southern African honey-buzzards may also put the species at risk of lower breeding success due to late arrival, or poor body condition on arrival.

The stable isotope analysis in Chapter 6 indicated that European Honey-buzzards in South Africa moulted their middle primaries (P4-P6) during migration. Based on my isotope results, these feathers are likely grown from income resources from stopover sites during migration. This likely links to the longer migration to South Africa which forces honey-buzzards to continue moulting as they move south in order to complete a full moult before the following breeding season. Overall, the longer migration and change in non-breeding habitat from natural forest to *Eucalyptus* patches, may add up to an overall higher mortality and reduction in breeding success for European Honey-buzzards migrating to southern Africa.

For many Palaearctic migrant species including European Honey-buzzard, the link between non-breeding site habitat quality and location, and breeding success, is still poorly understood. Questions about the links between non-breeding and breeding locations in honey-buzzard could be further answered using tracking data on a larger scale. Tracking data from adult honey-buzzards breeding at monitored nests could allow for the linking of type and location of non-breeding habitat, as well as non-breeding behaviour, to arrival data on the breeding grounds and nesting success across sequential years. This could be particularly effective if data from multiple populations in Europe were combined. Understanding how the non-breeding season affects breeding success in honey-buzzard would allow for a more holistic interpretation of the costs and benefits of a longer migration.

#### 7.4 What are the potential benefits of European Honey-buzzard range change?

While the aforementioned factors may increase risk for the European Honey-buzzards migrating to southern Africa, this range change still indicates remarkable adaptation in a specialist species. This flexibility may boost the species' long-term survival prospects under global change scenarios. Honey-buzzards have successfully adapted to a novel and expanding vegetation type in southern Africa. In this new habitat, the birds may be experiencing lower intraspecific competition due to the relatively low abundance of the species in the sub-region. The range shift of European Honey-buzzard to southern Africa indicates that migrant and specialist species, as a whole, may be more able to adjust to Africa's rapidly changing environment than would be expected.

In addition to adapting to new habitats, the European Honey-buzzards in southern Africa may also be shifting their diets to survive in the relatively sterile *Eucalyptus* islands available in the sub-region. While the majority of honey-buzzard diet is usually made up of Hymenoptera larvae, the species is known to take nestlings from birds as large as the Common Wood Pigeon (*Columba palumbus*) in Europe (Itämiies and Mikkola 1972, Gamauf 1999). These nestlings may be located by honey buzzards by observing the nestlings' parents go to and from the nests with food items. The honey-buzzard can then locate the nest, and prey upon nestlings. In the cropland-*Eucalyptus* matrices of southern Africa, where many honey-buzzards are found, there are likely to be up to four species of breeding dove: Rock Dove (*Columba livia*), Laughing Dove (*Spilopelia senegalensis*), Red-eyed Dove (*Streptopelia semitorquata*), and Cape Turtle Dove (*Streptopelia capicola*). The abundance of grain (especially maize) available in the croplands heavily supplements the population of these doves (van Niekerk and van Ginkel 2009). It seems highly likely that the European Honey-buzzards in these environments are preying heavily upon these doves and their nestlings. This is supported by a slightly higher  $\delta^{15}\text{N}$  value (e.g. an average of  $6.95 \pm 0.32$  for  $\delta^{15}\text{N}$  of two European-grown feathers and  $10.66 \pm 0.36$  for  $\delta^{15}\text{N}$  of four South African-grown feathers of Bird 1) in the feathers of southern African honey-buzzards, indicating that they are eating foods higher up the food chain like birds rather than insects (Chapter 6). In addition, honey-buzzards taken to wildlife rehabilitation centres in South Africa regularly test positive for *Trichomonas gallinae*, a parasite most commonly carried by pigeons and doves (Stabler 1954, pers. comm. N. Wright). The parasite is often transferred to birds of prey when the predator feeds on infected individuals, although can also be transmitted via an infected water source (Stabler 1954). This potential diet switch further indicates the ability of the specialist European Honey-buzzard to



adapt to new situations, and signifies that the species may be more adaptable than would be hypothesized. In future, further research on honey-buzzard diet across the African continent would allow for a better understanding of the resources used by the species, and how resource use differs from the breeding grounds as well as between different non-breeding areas.

### *7.5 Future applications of citizen science data in the study of Palaearctic migrants*

European Honey-buzzard demonstrates how quickly migrant species may be able to react to global change. The majority of the documented southwards range shift of honey-buzzard occurred over the past ten years (2009-2019), a relatively short period. This may indicate that migrant species are able to rapidly shift their range on the non-breeding grounds. During the non-breeding period, migrants are not tied to a breeding site which makes them more able to wander widely, and potentially, locate new non-breeding locations under global change. Migrants have high dispersal capability as indicated by their ability to migrate thousands of kilometres, which may allow them to explore a wide range of non-breeding areas.

This study demonstrates that it is critical to understand the non-breeding season of Palaearctic migrant birds in order to aid their conservation. Vickery et al. (2014) states that threats to Palaearctic migrants on the non-breeding grounds have only been assessed in a quarter of all species. This is despite the fact that many Palaearctic bird species, including honey-buzzard, spend more of their life in Africa than in Europe, and that non-breeding habitat has a strong effect on both their survival and breeding success (Holmes 2007, Åkesson et al. 2012, Schmalijohann et al. 2012, Kristensen et al. 2013, Stach et al. 2013, Rushing et al. 2016, Briedis et al. 2016a, Briedis et al. 2016b, Norevik et al. 2017). By understanding which non-breeding habitats are critical for Palaearctic migrants, better conservation initiatives can be implemented in these areas, hopefully helping to ensure these species' continued survival.

In order to identify important migrant areas in Africa, data need to be collected across the continent. Currently, the documentation of African avifauna, including migrants, is underway in the form of numerous bird atlas projects. At the moment, there are at least five atlas projects collecting data on bird distribution in three different African regions. The Southern African Bird Atlas Project covers the southern African sub-region, and is the most developed of the African atlas projects with over twelve million records collected over the past decade in its database. In East Africa, there are two atlases, Kenya and Tanzania. The Kenya Bird Map project now includes over 250,000 bird records. The newest of the African atlas projects, the Nigerian Bird Atlas Project, is beginning to cover West Africa and has collected over 100,000

records in about three years. All of these atlas initiatives are growing, resulting in more data available to ornithologists. In addition to the atlas projects, the African Raptor Database has collected over 200,000 raptor records across the entirety of the continent. As documented in this study, these atlas projects and citizen science data can provide important information about population trends, important habitats and regions, and range changes for Palaearctic migrants. It is, therefore, critical to support, develop, and grow these data collection projects.

With the extensive alterations on the African continent due to climate and land cover change, the importance of different regions to Palaearctic migrants is likely to change, as has been documented in several modelling studies (Barbet-Massin et al. 2009, Doswald et al. 2009). South Africa, in the extreme south of the African continent, is an excellent place to examine some of these changes. Currently, European Honey-buzzard is not the only migrant that has grown more common in the sub-region; Olive-tree Warbler (*Hippolais olivetorus*) is another example. There are also many migratory species that appear to be declining in southern Africa, at least on a local scale, such as Spotted Flycatcher (*Muscicapa striata*), Red-backed Shrike (*Lanius collurio*), and Willow Warbler (*Phylloscopus trochilus*) (Tarboton, unpubl. data). An assessment and review of the population and distribution trends of all terrestrial migrants in southern Africa using citizen science data from the Southern African Bird Atlas Project would provide information on which species have been the ‘winners’ and ‘losers’ over the last thirty years. Matching these African trends with European trends may indicate which traits benefit and/or hinder migrant species’ long-term survival. Over a longer period, as the African atlas datasets in Kenya and Nigeria grow, data from these two key regions for Palaearctic migrants can also be used to document trends of migrant birds in Africa.

The African Raptor Database may be able to provide data at a continental level on the non-breeding ranges of migrant raptors over the long-term. Using these data, perhaps along with older museum specimen collection data, range shifts in other migrant raptors could be assessed, as has been done with ring recoveries in some passerine migrants. This would allow for an assessment of the habitat and climatic drivers of movements in migrant raptor species over time. Raptors, especially juveniles, are highly able to move large distances, making them particularly capable of shifting their non-breeding ranges rapidly in response to global change as has been documented in this study. Some species may be more adaptable on the non-breeding grounds due their diet or habitat preferences, which may make them more able to survive in the face of global change.

## *7.6 Final conclusions*

Currently, the global environment is experiencing change at an unprecedented rate. Range expansions and contractions are inevitable for many species under these human-driven modifications. The specialist European Honey-buzzard is just one of these species, but it presents a unique case study for how both migrant and specialist species are adapting and surviving in the face of large-scale anthropogenic change. Honey-buzzards in southern Africa have adapted to novel, human-created habitats, demonstrating that some specialist species may be more accommodating of changes to their world than one would expect. The flexibility of juvenile honey-buzzards is key to the species' survival, allowing for rapid range changes in response to habitat and food availability. Adaptable juveniles are likely important for the survival of many long-lived migrant birds, and more research on their movements is critical for further understanding of Palearctic migrant birds and their recent declines.

Despite the fact that the European Honey-buzzards are surviving in southern Africa, my research also indicates that there are consequences of their range shift. These consequences could have a longer term and larger scale impact on the overall population of the species (Figure 7.1). It is, therefore, critical for the conservation of European Honey-buzzards and other Palearctic migrants to understand both the breeding and non-breeding biology of these birds, as well as how their two worlds interact. With a good grasp on the European breeding biology of most Palearctic species, it is now essential to better research the African non-breeding biology of these international wanderers to ensure their continued survival.

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