Ecology of the Verreaux's eagle *Aquila verreauxii* in natural and agriculturally transformed habitats in South Africa

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Thesis abstract

Agricultural transformation generally has a negative impact on biodiversity. Owing to landscape fragmentation and reduced prey availability, predators that inhabit transformed areas are usually forced to increase hunting effort or diversify their diet and this can have negative consequences for fitness or demographic parameters. Agricultural landscapes are therefore rarely considered important in the conservation of top predators. The Verreaux's eagle *Aquila verreauxii* has experienced loss of natural habitat due to agricultural transformation through much of its range. Despite the conspicuous nature and widespread distribution of Verreaux's eagles in sub-Saharan Africa, there is a paucity of information on the mechanism behind the recently observed population declines of this species, which have resulted in the recent re-classification as "Vulnerable" (from "Least Concern") in South Africa. This thesis aims to explore how land transformation influences changes in several key ecological components and demographic parameters, namely breeding performance, diet and movement ecology.

In this thesis, I study two geographically adjacent populations of Verreaux's eagles; one located in a natural area (Cederberg) and one in an agriculturally transformed area (Sandveld), in the Western Cape Province, South Africa, from 2011–2014. I investigate the breeding performance of the two populations. In contrast to what was anticipated I found that breeding productivity was 2.7 times greater in the agricultural than in the natural area. Population modelling suggested that in isolation the Cederberg population is unlikely to be self-sustaining, whereas the eagles breeding in the Sandveld region are likely to be acting as a source population. However, I did not have any information about juvenile or adult survival in either area. Contrasting survival rates could distort these results and are in need of further research.

Verreaux's eagles are generally regarded as dietary specialists. I therefore investigated the diet composition of eagles in the two study areas as a proxy to better understand prey availability and to look for evidence of behavioural flexibility to different availability of prey resources. The relationship between diet breadth and

breeding performance was explored locally and regionally using data from previous studies. Eagles in the Sandveld were found to have a more diverse diet than eagles in the Cederberg, which rely on their traditional prey, rock hyrax *Procavia capensis*. Theory on specialist predators assumes that diet diversification will cause reduced breeding performance. In particular, individuals within a species with more diverse diets due to reduced availability of primary prey species can display reduced breeding performance. In direct contrast to this, eagles with broad diet did not exhibit trends for reduced breeding performance, both locally and across southern Africa.

The movements of five adult Verreaux's eagles were investigated using high-resolution GPS trackers. Thereby providing detailed information on ranging behaviour of this species, including home range estimates and spatiotemporal parameters of trips away from the nest site. Although no differences between the two study areas were found in trip parameters/effort, there was some evidence for a difference in the timing of peak activity, which may have been caused by topographical differences driving contrasting lift availability between the study areas. Additionally, a habitat selection analysis within the Sandveld suggested a preference for partially transformed areas, which is likely to be related to prey availability.

Lastly, data from the high-resolution GPS tags were used to identify different flight behaviours and evaluate the availability of lift in the topographically contrasting study areas. This chapter identified topographical and meteorological correlates of orographic and thermal soaring so that the spatial distribution of lift driving soaring flights could be predicted across the study areas. This research indicated the relatively flat Sandveld region might actually be a more favourable energy landscape by providing an environment with greater predicted lift availability compared to the Cederberg Mountains.

Following the findings of this study, I conclude that agricultural land use areas can actually contribute positively to the conservation of Verreaux's eagle. Although this species is typically thought of as a mountain specialist, the findings here demonstrate that the agricultural Sandveld region can sustain a productive population, provided that there is some suitable breeding habitat (i.e. rocky outcrops with cliffs). The productivity of this population is contributed to by the provision of a diverse prey base, an environment conducive to good nesting success and a landscape favourable for low-energy flying. The current level of agricultural transformation in the Sandveld does not appear to cause fitness constraints. However, further expansion or intensification of the agricultural footprint is likely to incur negative effects and it will also be important to maintain heterogeneous habitat.

Further research should be aimed at assessing the ecology and life history traits of Verreaux’s eagle in other agricultural environments that have transformed more than the Sandveld. This would help to find the ecological threshold for transformation that I predict from the findings of this thesis. Beyond a threshold point, further agricultural transformation will probably be detrimental to Verreaux’s eagle and other biodiversity. These results highlight the potential conservation value of some agricultural areas and the need for effort to be made to integrate agriculture and conservation worldwide.

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I’ll keep on climbing mountains
With you by my side
Because you were my inspiration
And now you are my guide

Chapter 1

Introduction

Land use change and biodiversity

The global human population reached 7.3 billion in mid-2015, a near three-fold increase since 1950 (United Nations, 2015). Population growth is putting an increasing demand on the environment for resources (Schneider et al. 2011). World food demand is expected to double between 2000 and 2050 (Tilman et al. 2002) necessitating either increased yield from existing farmland or further conversion of natural land for food production, particularly in the developing world (Balmford et al. 2005). Land cover assessments suggest that *c.* 40 % of the land surface has already been converted for agricultural purposes (Ramankutty and Foley 1999, Asner et al. 2004, Foley et al. 2005). This conversion of natural land into farmland is thought to be responsible for the greatest losses of global biodiversity (Newbold et al. 2015). Agricultural transformation and intensification threatens biodiversity by causing the loss of habitats (Tscharntke et al. 2005), reduction in food availability (Benton et al. 2002, Rodríguez et al. 2006), increased risk of predation (Bayne and Hobson 1997, Vander Haegen et al. 2002, Sergio et al. 2009) or direct mortality (Arroyo et al. 2002). Currently around one quarter of mammal species and one seventh of bird species are considered to be threatened by extinction (IUCN 2014) and for many species their endangerment level is closely linked to conversion of natural land for agriculture within their distribution (Scharlemann et al. 2005). For birds, farming (both the initial conversion of land into farmland and its intensification thereafter) is currently the single biggest danger to threatened and near-threatened species globally (Green et al. 2005).

A well documented example of the negative effects of agriculture on avifauna was the collapse of farmland bird populations in western Europe during the last quarter of the 20th century, a period characterised by agricultural expansion and intensification (Fuller et al. 1995, Donald et al. 2001, 2006; Stoate et al. 2001). There was an estimated 40 % decline in populations of farmland birds between 1970–2000, mostly species with masses less than 0.5 kg (Gregory et al. 2001). In one study increased cereal yield alone explained over 30 % of the population declines and range contractions (Donald et al. 2001). Examples of similar decreases in bird populations or diversity associated with agricultural intensification can be found worldwide: North

America (Brennan and Kuvlesky 2005, Flynn et al. 2009), South America (Philpott et al. 2008, Goijman et al. 2015), Australia (Saunders 1989, Olsen 2008), Asia (Amano and Yamaura 2007, Wood et al. 2010) and Africa (Mangnall and Crowe 2003, Child et al. 2009).

In response to these negative effects of agriculture, the concepts of ‘land sharing’ and ‘land sparing’ have been proposed to balance food production yields with conservation of biodiversity. Land sharing implements biodiversity friendly farming practices to promote species persistence in the environment, at the cost of reduced crop yield and larger area footprint than land sparing. Land sparing uses intensive farming methods, including chemical inputs, to produce high crop yields from smaller land footprints and this essentially allows other areas to be set aside for conservation (Balmford et al. 2005, Green et al. 2005). Although there is some debate over the best practise (Kremen 2015), the land sparing strategy is thought to sustain higher populations of most species than land sharing (Phalan et al. 2011). However, there is not a simple linear relationship between increasing crop yield and decreasing area footprint (Kremen 2015) and the success of this method is dependent on adequate protection of the remaining natural areas.

In 2010 the Convention on Biological Diversity declared a revised Strategic Plan to conserve biodiversity globally. The vision of this plan is to “Live in Harmony with Nature”, with the foremost goal of “by 2050, biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people” (CBD, 2016). Within the programme of work for these targets, agricultural biodiversity features as a priority. Amongst the Aichi Biodiversity Targets (named after the host region for the meeting in Japan) is the objective to halve the rate of loss of all natural habitats by 2020, and where feasible bring it close to zero, as well as significantly reducing fragmentation and degradation. Furthermore, the targets aim to see all that all areas used for agriculture, aquaculture and forestry are managed sustainably (CBD, 2016). The implementation of these targets at a global level will contribute significantly to halting the loss of biodiversity. However, the effectiveness of the Strategic Plan and the Aichi Targets will be dependant on participation at all levels and the provision of adequate financial support to developing countries, particularly those which are most environmentally vulnerable (CBD, 2006). Furthermore, an adequate baseline from which to measure the implementation of targets and the environmental changes that occur will be required (Perrings et al. 2011).

Responses to land use change

A species response to land use change is largely determined by the specific changes in resource availability, the intensity of the change and the degree to which individuals within the species can adapt (Butler et al. 2007, 2010). Within a threshold of transformation, human-altered landscapes can provide previously scarce food or nesting resources and can contribute positively to conservation by promoting habitat diversity (Tscharntke et al. 2005, Koks et al. 2007, Balbontín et al. 2008, Cardador et al. 2011). For example, the blue crane *Anthropoides paradiseus,* an endemic southern African grassland specialist, experienced declines in the eastern parts of its range where transformation and fragmentation of natural grasslands have occurred. However, in the Western Cape, South Africa, agricultural development has transformed Fynbos and Renosterveld vegetation into ‘artificial grassland’ resulting in a range expansion and this region now supports nearly half of this species’ national population (McCann et al. 2007). Similarly, in France a population of little bustards *Tetrax tetrax* increased after the conversion of steppe habitat into arable land (Wolff et al. 2001).

Among avian groups, raptors are particularly sensitive to habitat change due to their high trophic level and narrow ecological niches (Newton 1979). As a result raptors are often considered to be good ‘indicator species’ for the health of an ecosystem or for identifying important biologically diverse areas (Machange et al. 2005, Sergio et al. 2005, 2006; Jenkins et al. 2012. But see Cabeza et al. 2007, Rodríguez-Estrella et al. 2008). Raptors can be useful as early warning signals of ecologically negative effects of anthropogenic pressures (Balbontín et al. 2003, Ferrer et al. 2003). Furthermore, large raptors have frequently been identified as ‘umbrella species’, whereby conservation management plans aimed at adequately preserving habitat for large, mobile species automatically conserves resources for multiple other less demanding species in an ecosystem (Sergio et al. 2006). Human modification of land has caused reduction in prey density or distribution (Butet and Leroux 2001, Butet et al. 2010) and loss of nesting sites (Butler et al. 2010), which can result in reduced breeding productivity, range contractions and/or population declines of raptors. For instance, the abundance or distribution of lesser kestrel *Falco naumanni* (Tella et al. 2004), Montagu's harrier *Circus pygarus* (Butet and Leroux 2001), hen harrier *Circus cyaneus* (Amar and Redpath 2005) and Bonelli's eagle *Hieraaetus fasciatus* (Sanchez-Zapata et al. 2002) have been negatively correlated with agricultural land use.

The degree to which an individual can adapt to environmental change may be associated with their specialist to generalist characteristics, whereby more specialised individual might cope less well than generalists to environmental change, therefore often incurring greater population decreases (Mangnall and Crowe 2003, Reif et al. 2008). In contrast species that are made up of more generalists individuals can favour the loss of natural habitat in some instances (Carrara et al. 2015). Within the raptor guild and even between individuals of a species there is variation in generalist to specialist traits, which have been described along a gradient of adaptability (Arroyo and Garcia 2006). As a result there is some dispute over the usefulness of all raptors as indicator species (Cabeza et al. 2007, Rodríguez-Estrella et al. 2008). However in broad terms, generalist individuals or species are characterized by catholic dietary or habitat requirements and are therefore often able to exploit the availability of new resources. Indeed, some raptors appear to readily adapt to human-modified habitats, presumably due to the increased availability of food resources or suitable breeding habitat (Rodríguez-Estrella et al. 2008). For example, deforestation and cultivation of areas of the Iberian Peninsula may have benefited black-shouldered kites *Elanus caeruleus* by providing suitable open habitats and prey abundances within low-intensity agricultural systems, and this may have facilitated their range expansion into this area in the 1960s (Balbontín et al. 2008). Another prominent example is that of the marsh harriers *Circus aeruginosus*, where its occupancy is positively correlated with man-made wetlands used for nesting and the availability of irrigated herbaceous crops, which are likely to offer high densities of small mammal prey (Cardador et al. 2011).

Raptor declines and ecological importance

Raptors are experiencing population declines and range contractions globally (Leptich 1986, Butet and Leroux 2001, Thiollay 2006, Burfield 2008, Ogada and Keesing 2010). Among raptors, *c.* 20 % of the order Acciptriformes are considered to be globally threatened (IUCN 2014) and this has been attributed to a range of human induced factors. Intentional (due to human-wildlife conflicts) and unintentional (due to ingestion of poisoned carrion or environmental contamination) poisoning have been responsible for raptor deaths and population decreases (Whitfield et al. 2004, Ogada et al. 2012). Large eagles have been routinely persecuted for their apparent predation on livestock or game (Brown 1991, Davies 1999, Pedrini and Sergio 2001, Whitfield et al. 2004, Sarasola and Maceda 2006). In Africa, widespread raptor population decreases have been documented since the 1970s (Sorley and Anderson 1994, Virani 1999, Herremans and Herremans-Tonnoeyr 2000, Thiollay 2006, 2007a, b; Ogada and Keesing 2010, Anadón et al. 2010, Virani et al. 2011, Ogada and Buij 2011, Ogada et al. 2012). In particular, African raptor population declines associated with human-modified environments have been identified by comparing raptor assemblages inside protected areas with those in cultivated areas and over time (Brandl et al. 1985, Herremans and Herremans-Tonnoeyr 2000, Thiollay 2006, 2007b; Buij et al. 2013). Declines outside of protected areas in the latter part of the 1900s were recorded for large vulture species (up to 98 %) and eagles (86−93 %) in West Africa (Thiollay 2006). There are multiple potential reasons for this, all of which are linked to issues associated with a rapidly growing human population; habitat loss, overhunting, disturbance and poisoning (Thiollay 2007b, Buij et al. 2013).

The population decline and loss of apex predators impacts the structure and functioning of ecosystems (Terborgh et al. 2001, Ripple et al. 2014). Trophic cascades due to decreases in numbers of top predators can cause large changes at lower trophic levels with overall detrimental effects on an ecosystem (Estes et al. 2011). For example, the removal of sea otters *Enhydra lutris* has been identified as the cause of increases in abundance of herbivorous sea urchins *Strogylocentrotus sp.*, which ultimately resulted in overgrazing of macrophyte communities with profound negative effects on the stability of the near shore marine community (Estes and Palmisano 1974). Furthermore, due to interconnectivity of food webs, indirect effects of changes in sea otter abundance reach as far as other apex predators such as the bald eagle *Haliaeetus leucocephalus* (Anthony et al. 2008). Raptors are important top predators that influence prey populations by top-down trophic effects (Reid et al. 1995, Harvey et al. 2012). Within agricultural landscapes raptors can be responsible for limiting populations of rodent and avian pest species (Brown et al. 1988, Davies 1994, Abramsky et al. 2002). Their indirect impact on prey populations also creates important landscape level dynamics by altering prey behaviour through reducing foraging activity or increasing vigilance (Brown et al. 1988, Kotler et al. 1999, Abramsky et al. 2002, Druce et al. 2006, Cresswell and Whitfield 2008). Therefore, the loss of raptors in agricultural systems has the potential to incur ecosystem costs via increased populations of pest species (Lees et al. 2013).

Understanding how species use their habitat can help predict how land use change will influence their demographics. Land use change has been linked to changes in animal movement and habitat selection in a wide range of birds and mammals (Amar and Redpath 2005, Whittingham et al. 2005, Rajaratnam et al. 2007, Camacho et al. 2014, Lande et al. 2014, Oleksy et al. 2015). Raptors typically have large home ranges which can change seasonally and in different stages of life history (Moss et al. 2014, Pérez-García et al. 2013, Newton 1979). Therefore, tracking studies have helped to improve understanding of raptor movements in relation to land use change and other anthropogenic threats by providing robust evidence to inform management strategies and mitigate development associated risks (Donazar et al. 1993, Ferrer and Harte 1997, Marzluff et al. 1997, Cardador and Manosa 2011, Watson et al. 2014, Reid et al. 2015).

GPS technology and remote sensing: Development and usefulness

Since the pioneering use of VHF (Very High Frequency) telemetry in the 1960s by the Craighead brothers to track grizzly bears *Ursus arctos horribilis* and elk *Cervus* *canadensis* in the Yellowstone National Park (Craighead 1982, Craighead et al. 1995) the size, weight, lifespan, spatiotemporal resolution and methods of data retrieval in tracking animals have improved (Kays et al. 2015). Early VHF tracking equipment in feasibility studies weighed as much as 10 kg (Milner 1971). This rapidly declined and today VHF tags are available weighing as little as 0.3g (Guilford et al. 2011). However, telemetry equipment relies on researcher effort to triangulate and locate animals regularly in order to collect data and can therefore only be applied to animals with relatively small and accessible home ranges (Seegar et al. 1996).

Although species-specific considerations need to be applied, ethical guidelines require tags to be no more than 3−5 % of the body weight of the subject (Kenward 2001, Casper 2009). In the development of tracking technology trade-offs between device size and capabilities have been made. For example, geolocators can determine an organisms' location indirectly by recording ambient light levels and can weigh as little as 0.6g allowing small passerines to be tracked (Bridge et al. 2013). However, spatial accuracy (*c.* 200 km) and temporal resolution (up to two location per day) are limited and tracked animals must be recaptured to obtain the data (Rodrigues et al. 2009, Catry et al. 2011, Bridge et al. 2013). The development of satellite tracking and download provided improvements on data collection, but the size of devices currently precludes tracking of small passerines. ARGOS satellites are used to estimate locations from the Doppler shift of a signal transmitted from animal-borne PTTs (Platform Terminal Transmitters) and transmit data back to researchers remotely (Sokolov 2011). However, the accuracy of location estimates are variable (150 m−2 km, Seegar et al., 1996) and this method is both financially costly and energetically expensive on batteries so eludes the transmission of large volumes of data.

The US Department of Defence began the development of Global Positioning System (GPS) technology in 1973, initially only for military use. With civilian use later permitted, this technology revolutionized animal tracking by improving the spatial accuracy of locations while allowing automated transmission of data via satellites (Tomkiewicz et al. 2010). Since the inception of GPS animal tracking, the size and lifespan of tags have improved alongside advances in the spatial precision and temporal resolution of data collected (Wikelski et al. 2007, Tomkiewicz et al. 2010, Bridge et al. 2011, Sokolov 2011, Kays et al. 2015). The introduction of small solar panels began to combat the limitations usually conceded between tag duration, data resolution and battery-life (Bouten et al. 2013). Following the collection of high-resolution data, improvements in data retrieval have been made, including download via cell phone networks (GSM) and remotely placed base stations, which download the data through UHF (Ultra High Frequency) (Bridge et al. 2011). Although trade-offs between different tag features (e.g. weight, frequency of fixes, accuracy, costs, fix retrieval) still need to be made when planning studies, the ecological questions that we can answer extend far beyond typical questions of home range size and migration routes. Animal-borne tracking tags can now collect spatially accurate (*c.* 1 m error), temporally high-resolution (up to 3 sec, with varying schedules) data for extended periods of time, with potential to collect entire lifespan tracks for some species (Bouten et al. 2013, Kays et al. 2015).

Equally, there has been a rapid development in remote sensing of the environment, including topographical, meteorological and land cover data. This has allowed the influence of the immediate environment on animal movement and life history to be explored (Kays et al. 2015). By analysing animal derived locations alongside remotely sensed environmental data, we can learn about habitat preferences, resource use (Marzluff et al. 1997, Watson et al. 2014), the impacts of habitat fragmentation and land use change (Graham et al. 2009, Colchero et al. 2011, Camacho et al. 2014) and the influences of weather variables (Vansteelant et al. 2014) on animal movement. This provides a better understanding of what characterizes suitable habitat for conservation planning and could be important in detecting anthropogenically-driven changes (Kays et al. 2015, Reid et al. 2015).

Study species: The Verreaux's eagle

The Verreaux's eagle *Aquila verreauxii* is a large accipitrid raptor typically associated with mountainous or rocky habitat in sub-Saharan Africa. This monogamous, non-colonial and sexually dimorphic eagle usually nests on cliffs, although instances of breeding on trees and manmade structures such as electricity infrastructure are not uncommon (Steyn 1982, Jenkins et al. 2013). Females can be *c.* 1kg heavier than males (Simmons 2005). With a wingspan of 181−219 cm (Ferguson-Lees and Christie 2001), this species is the largest of the *Aquila* eagles through most of its range, rivalled only by the Golden eagle *Aquila chrysaetos* in the northern regions of its range (Davies 1994). One life history trait of Verreaux's eagle which differs from other *Aquila* species is that it routinely rears only one young per breeding attempt. Despite regularly laying two eggs, obligate siblicide occurs if both eggs hatch, with few reliable accounts of successful raising of two young (Gargett 1990, Anderson 2002).

Verreaux's eagles are frequently considered to be specialist predators of hyrax (*Procavia* and *Heterohyrax* spp.), which comprise 88−98 % of their diet in most studies (Gargett 1977, Tarboton and Allan 1984, Davies 1994). However, some variation has been noted across different biomes of South Africa where hyrax contribution ranges from 49−89 % of the prey items collected below nests (Boshoff et al. 1991) and at one nest, located at the Walter Sisulu National Botanical Gardens in a suburban area of Johannesburg, hyrax contributed 22 % of the diet (Symes and Kruger 2012). Despite this variation, the core distribution of Verreaux's eagle closely follows hyrax distribution, extending through much of the mountainous areas of southern and east Africa as far north as Ethiopia and Eritrea, thereafter they maintain a patchy distribution from Sudan to the Arabian Peninsula (Figure 1). Verreaux's eagles occur at lower density in parts of Lesotho, Swaziland and the former Transkei section of the Eastern Cape compared to the rest of their southern African range (Davies and Allan 1997, Ferguson-Lees and Christie 2001).

Figure 1. Global distribution of the Verreaux's eagle *Aquila verreauxii* (source: www.birdlife.org).

A long-term study of a Verreaux’s eagle population in the Matopos Hills, Zimbabwe began in 1964 (Gargett 1990). This included the first detailed study of breeding performance, diet and various aspects of eagle behaviour. Estimates of the breeding density, inter-nest distances and breeding productivity indicated that this was a productive, high-density population. However, even from this early study it was evident that Verreaux’s eagles are susceptible to increasing human pressures revealed by comparison of breeding productivity between the protected area and “communal lands”. Communal lands are densely occupied areas where land use includes small livestock grazing and cultivation of small-scale plots; furthermore small game and hyraxes are routinely hunted (Gargett 1990). In these areas, the proportion of pairs attempting to breed each year was reduced by as much as 74 % compared with inside the protected area. Nesting density was also considerably lower in the communal lands than the protected area, and this difference was not explained simply by availability of nest sites (Gargett 1990).

Globally, the Verreaux’s eagle is listed as a Species of Least Concern given its extensive range (BirdLife International 2014). However, within South Africa the species was elevated in 2015 from the “Least Concern” category to “Vulnerable” (Taylor 2015) due to localised decreases in range and abundance recorded by the Southern African Bird Atlas Projects (Loftie-Eaton 2014). High site-fidelity leaves this species more vulnerable to local habitat deterioration and fluctuations in conditions or resource availability compared to mobile species due to their year-round reliance on their home range to sustain them (Ewers and Didham 2006). Both agricultural land use and urbanization have caused the depletion of traditional prey resources in some parts of the species' distribution, thereby potentially increasing the energetic demands of hunting forays and the exposure to other sources of human-caused risks and possibly reducing breeding productivity (Gargett 1990, Albertson 2008, Symes and Kruger 2012). Mortalities (collisions or electrocutions) via power lines (Lehman, 2001; pers. obs.), direct persecution in livestock farming areas (shooting and poisoning) (Davies et al., 2015; M. Drouilly pers. comm.), drowning in reservoirs (Anderson 2000) and the increasing abundance of wind turbines (Reid et al. 2015, Smallie 2015) all pose threats to Verreaux's eagle populations. Persecution incidents are largely unrecorded and are likely to occur at a much higher rate than are reported (Whitfield et al. 2004, Sarasola and Maceda 2006, Fairbrass et al. 2016). Attempts to curtail persecution have been initiated by the formation of local raptor conservancies and conservation campaigns (Anderson 2000). Short-term and localized previous conservation efforts for the species have also included supplementary feeding (Symes and Kruger 2012). Nevertheless, an improved understanding of this species' habitat requirements and responses to land use change are required to better understand potential risk factors.

Study area: The Cederberg Mountains and the Sandveld

The study area encompasses the central area of the Cederberg Mountains and the Sandveld region, which stretches from the West Coast inland, in the Western Cape of South Africa (Figure 2). Both areas are located within the Cape Floristic Region (CFR), which is recognized as a biodiversity hotspot of global significance due to the species richness, high endemism of plants and animals and vulnerability of the ecosystem (Picker and Samways 1996, Myers et al. 2000, Cowling and Pressey 2003, Cowling et al. 2003). Concerns over the conservation status of the CFR date back to the early 1900s, when the presence of non-native plants and introduced species, agricultural land use, plantations, overharvesting and exploitation of natural resources and irregular fire damage were first highlighted as factors motivating the conservation of this region (Wicht 1943). During the study period, land use and topography of the Cederberg and the Sandveld show distinct contrasts.

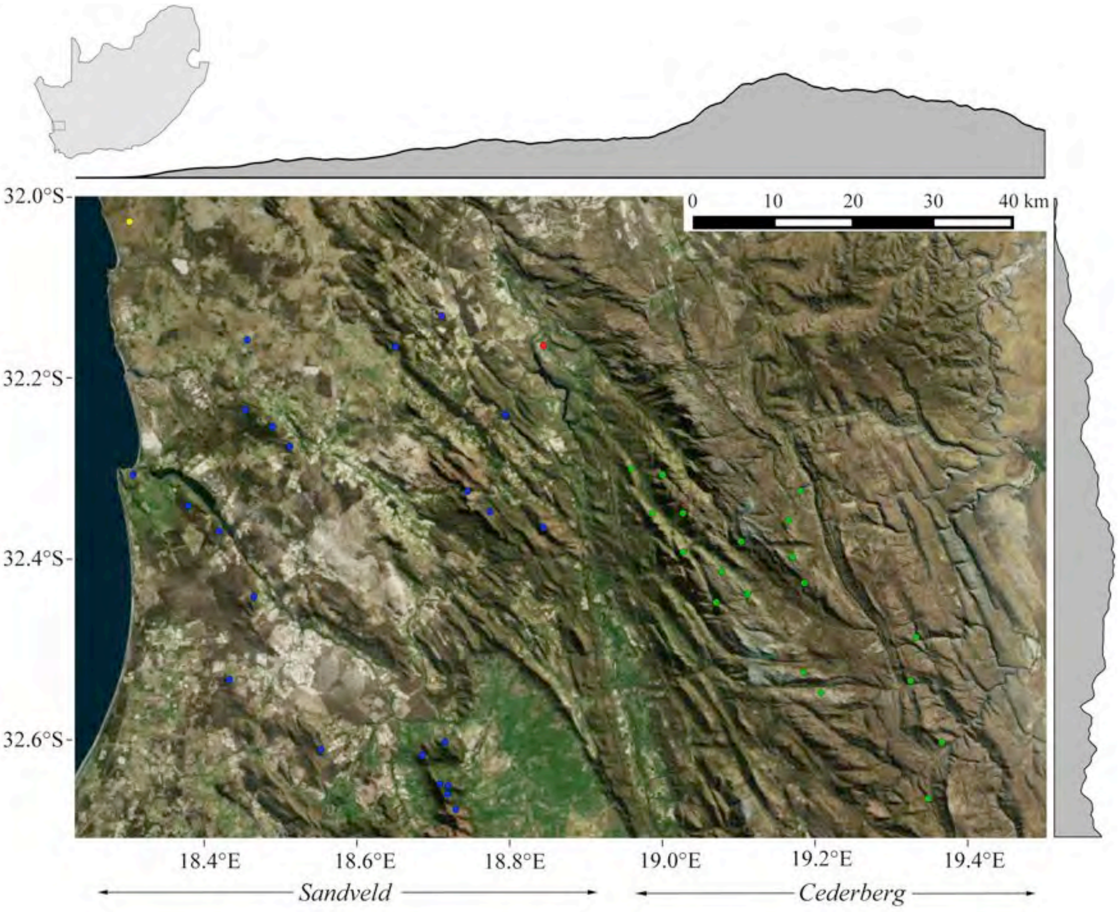

Figure 2. Map of study areas in the Western Cape, South Africa. Blue indicates core study nests in the Sandveld area and green indicates core study nests in the Cederberg area. Yellow dot is Lambert's Bay (32.0350S, 18.3320E) and red dot is Clanwilliam (32.1760S, 18.8880E), all meteorological data used in analyses in this thesis are derived from South African Weather Services stations at these locations. Grey altitude profiles show mean altitude change through the region.

Forming the northern extent of the Cape Fold Mountains, the Cederberg falls largely under the management of CapeNature, the statutory conservation body in the Western Cape, and within this protected area no recent land use change has occurred and there is limited human presence (Maree and Vromans 2010). Two main reserves, the Cederberg Wilderness Area (71 000 ha) and Matjiesrivier Nature Reserve (12 000 ha), form an integral part of the total 312 000 ha conservation area which is contributed to by conservancies of local land owners and private nature reserves (Maree and Vromans 2010). The elevation of the mountainous topography ranges from 150 m to 2027 m (SAEON 2014) and the vegetation cover is predominately mountain Fynbos with Karoo succulent vegetation occurring in the eastern region. The Cederberg experiences a mean annual rainfall of 706 ±174 mm (2004–2014 Algeria weather station 32.374S, 19.058E) (CapeNature 2015), of which peak rainfall occurs from May to August (Saul et al. 2011) during the austral winter and coincides with the breeding season of the eagles.

The Sandveld holds one of the most westerly breeding populations of Verreaux’s eagles. In contrast to the Cederberg, the topography of the Sandveld is generally much flatter and most eagles in this region nest on isolated cliffs and rocky outcrops. Altitude ranges from sea level up to *c.* 1000 m and the average total annual rainfall is *c.* 300 mm (1990–2008 Graafwater weather station 32.155S, 18.603E, Franke et al., 2011). The Sandveld features at least 12 vegetation types, of which nine are ‘critically endangered’, ‘endangered’ or ‘vulnerable’ (Maree and Vromans 2010). However, there is little formal conservation and there has been extensive agricultural development in the region following the installation of electricity infrastructure in the 1980s allowing for large-scale centre-pivot irrigation in an otherwise agriculturally unsuitable area (Heydenrych 1993). The Sandveld is now amongst the most important areas for potato production in South Africa. Approximately 6600 ha are under production annually and due to crop rotations and fallow periods, approximately 15 times more than the area required annually has been ploughed (Franke et al. 2011). This agricultural transformation has caused loss of endemic Renosterveld and Fynbos vegetation and associated biodiversity (Low et al. 2004). The rate at which natural biodiversity is being destroyed in this area is of serious concern (Rouget et al. 2003). Additional concerns include leaching of agro-chemicals and increased pressure on groundwater resources (Münch and Conrad 2007, Franke et al. 2011).

Research aims

Considering the various effects that agricultural transformation can have on biodiversity, as described above, and the expectation for continued increase in agricultural output worldwide, it is important to better understand the mechanisms behind species responses to land use change so that we can predict future scenarios and effectively manage biodiversity in a rapidly changing environment.

Despite the conspicuous nature and widespread distribution of Verreaux’s eagles in sub-Saharan Africa, there is a paucity of information on the mechanism behind the recently observed population declines of this species in southern Africa (Loftie-Eaton 2014, Taylor 2015). The main aim of this thesis is to explore for causal links between land transformation and life history traits, namely breeding productivity, diet and movement ecology to explore how land use change might influence presumed specialists such as the Verreaux’s eagle.

Thesis overview

This thesis is presented as a series of stand-alone chapters formatted to facilitate publication (Chapters 2−5). As such, there is some inevitable repetition of information in the introduction and methods sections of these chapters. Redundancies and inconsistencies may occur between chapters. For example the use of the term “high-resolution” in reference to the temporal frequency of GPS data differs between Chapter 4 and Chapter 5, however, each are clarified in the methods section of respective chapters.

Chapter 2 reports data on breeding performance from 2011−2014 in the two study areas with the aim of identifying differences in productivity between areas. Our hypothesis here was that agricultural transformation in the Sandveld may have reduced productivity in this area, and if so we predict that breeding performance would be lower in the Sandveld compared with the Cederberg. Links between breeding productivity and climatic variables were explored and the reproductive output was compared with previous studies on this species to identify relatively more or less productive populations. Area-specific productivity estimates were then used to model population growth within the two regions.

Chapter 3 investigates the diet composition of Verreaux’s eagles in the two study areas as a proxy to better understand prey availability and to look for evidence of diversion away from specialist traits in response to agricultural transformation. The relationship between diet composition, habitat diversity and agricultural land transformation in the home range (which was based on estimates of home range size provided in Chapter 4) are investigated. The relationship between diet breadth and breeding performance is explored locally and regionally using data from previous studies.

Chapter 4 uses GPS technology to provide detailed information on ranging behaviour of Verreaux’s eagles in the two contrasting study areas, including home range estimates, habitat selection and temporal and spatial parameters of trips made away from the nest site. These analyses of movement ecology were performed to look for evidence for greater foraging effort by eagles in either area. The principle aim of the habitat selection analyses was to identify if eagles in the Sandveld showed a preference for the use of remaining natural areas.

Chapter 5 uses high-resolution GPS data to identify behavioural states of eagles (i.e. perched, thermal soaring, orographic soaring and gliding). The topographic and meteorological correlates of the soaring flight behaviours were identified and used to predict the availability of lift in territories in the topographically contrasting study areas. Lift is an important source of potential energy for large soaring birds and the availability of lift can effect energy requirements and therefore contribute to determining the suitability of an area for large raptors, irrespective of land use features.

Chapter 6 synthesises the findings of this study, puts them into a wider context and evaluates their relevance to conservation. In doing so, conclusions are drawn on the effects of land use change and the importance of conservation in agricultural areas for avian predators such as the Verreaux’s eagles.

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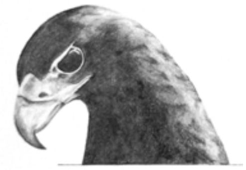
Chapter 2



The influence of agricultural transformation on the breeding performance of a top predator: Verreaux's eagles in contrasting land use areas

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Abstract

Breeding productivity frequently shows variation across a species' range or locally between different habitat types. Agricultural transformation generally has negative effects on biodiversity and often results in reduced prey abundance or increased foraging effort in top predators, and consequently often reduces breeding productivity. Major factors affecting reproductive performance also include climatic variables, breeding density and the timing of breeding. In this study we explore the influence of agricultural transformation on a raptor that is generally viewed as a predatory specialist, Verreaux's eagle (*Aquila verreauxii*). We examine productivity in two geographically adjacent populations of eagles, one in a natural area (the Cederberg Mountains) and the other in an agriculturally transformed area (the Sandveld region), in the Western Cape Province, South Africa, from 2011–2014. Counter-intuitively, we found the breeding productivity was 2.7 times higher in the agricultural than in the natural area. In particular, the proportion of pairs that attempted to breed (breeding rate) was higher in the Sandveld (0.94 ±0.07 attempts/pair/year) than the Cederberg (0.48 ±0.14 attempts/pair/year). Nesting success was also higher in the Sandveld (0.80 ±0.05 fledged young/attempt/year) than the Cederberg (0.57 ±0.13 fledged young/attempt/year) and the probability of nesting successfully was also related to the lay date (with success decreasing with later laying) and the total cumulative rainfall up to 28 days after hatching (with success decreasing with increasing rainfall). Using the area-specific breeding rates to produce a population model, we found that in isolation the Cederberg population is unlikely to be self-sustaining, whereas the eagles breeding in the agriculturally developed Sandveld region are likely to be an important source population. Our results, contrary to our expectations, suggest that the Verreaux's eagle may be more adaptable to agricultural transformation than previously thought, with breeding performance in this example of a highly transformed habitat remaining sufficiently productive to maintain the population.

Introduction

Transformation of land for agriculture is a key driver of biodiversity loss (Haines-Young 2009). However, the effects of agriculture on biodiversity depend largely on the intensity of land use (Reidsma et al. 2006) and the ability of a species to adapt to changes in resource availability (Butet et al. 2010). A well-documented example of the negative effects of agriculture on biodiversity has been the collapse of farmland bird populations in Europe during the late 20th century, a period characterized by agricultural intensification (Fuller et al. 1995, Donald et al. 2001). However, some species apparently benefit from cultivated landscapes and this is often associated with the provision of food or breeding resources in areas where they were previously scarce or unavailable (Wolff et al. 2001, Moreno-Mateos et al. 2009, Cardador et al. 2011).

Raptors are considered to be good indicators of ecosystem health due to their position as apex predators and sensitivity to a changing environment (Sergio et al. 2006). Agricultural transformation can degrade or destroy preferred habitats and deplete prey resources (Donazar et al. 1993, Amar and Redpath 2005, Jenkins et al. 2012), resulting in decreased breeding productivity (Arroyo et al. 2002), reduced offspring condition (Almasi et al. 2015) or delayed egg-laying (Costantini et al. 2014). Breeding performance can be further impacted by climatic variables. In a study of Mauritius Kestrels (*Falco punctatus*), agricultural transformation exacerbated the negative impacts of high rainfall on nesting success by reducing the availability of native prey species around nest sites (Cartwright et al. 2014). However, for some raptorial species there is evidence that agricultural land use can in fact increase breeding performance, which may be linked to increases in prey availability or the abundance of suitable nesting areas (Coates et al. 2014). Cultivation of oilseed rape has been positively correlated with vole abundance and breeding productivity of common buzzards (*Buteo buteo*) (Panek and Hušek 2014). In marsh harriers (*Circus aeruginosus*) increases in breeding productivity, egg size (Sternalski et al. 2013) and nest-site occupancy (Cardador et al. 2011) have been correlated with increased agricultural land use.

The Verreaux's eagle (*Aquila verreauxii*) is a long-lived raptor which reproduces slowly, producing a maximum of one young per year (Gargett 1990). Verreaux's eagles are generally considered as a specialist predator, with a single prey type (hyraxes: *Procavia* and *Heterohyrax* spp.) comprising 88–98 % of their diet in most studies (Gargett 1977, Tarboton and Allan 1984, Davies 1994), although this varies between biomes (Boshoff et al. 1991). Breeding productivity has been monitored in several regions of the Verreaux's eagle's southern African range (Tarboton and Allan 1984, Allan 1988, Gargett 1990, Davies 1994), however, factors affecting productivity have rarely been investigated (but see Gargett 1990, Gargett et al. 1995). Gargett *et al.* (1995) found an inverse relationship between Verreaux's eagle reproductive performance and the volume of rainfall in the preceding summer. However, results might have been distorted by interference from egg-collectors and this pattern broke down following severe drought. It was speculated that low rainfall reduces vegetation cover thereby increasing hyrax vulnerability and accessibility to eagles, while prolonged drought may cause prey population crashes (Gargett et al. 1995).

In light of declines in the population of Verreaux's eagles indicated by the Southern African Bird Atlas Projects (Loftie-Eaton 2014) and the recent up-listing of the conservation status to 'vulnerable' in southern Africa (Taylor 2015), this study aims to evaluate the productivity of two adjacent populations (*c.* 20 km) nesting in contrasting habitats in the Western Cape, South Africa. The first population is located in a predominately natural habitat, the Cederberg Mountains. The second population breeds in the nearby Sandveld, which has been heavily transformed for agriculture, and consequently may have compromised breeding productivity. Both of these areas fall into the relatively moist Fynbos biome (Rutherford et al. 2006) where rain falls predominately in the winter months (from May to September) coinciding with laying, incubation and much of the nestling stage. In contrast, previous studies on Verreaux's eagles in southern Africa (Allan 1988, Gargett 1990, Davies 1994) have been conducted in summer rainfall regions (from October to March), where most rain falls outside of the most sensitive breeding period, therefore effects of rainfall on nesting success are expected to be more pronounced in this study.

Comparative studies of subpopulations in contrasting environments can be useful in exploring the relative ecological importance of distinct populations (Pulliam 1988, Pulliam and Danielson 1991, Boal and Mannan 1999, Amar et al. 2003). To assess if agriculture negatively affects Verreaux's eagle demographics, we test the hypothesis that productivity is lower in the Sandveld than the Cederberg. We also compare our productivity measures to previous studies in southern Africa. We test the effects of weather on breeding performance, where increased rainfall during the nestling stage is expected to have a negative impact on nesting success. Additionally, we expect lower breeding productivity in our study areas compared to previous studies owing to the contrasting rainfall seasonality. Lastly, we used our demographic data from both sites to a construct a simple population model of the long-term population viability of these two populations, assuming both open and closed population scenarios.

Methods

Study area

The 2570 km^2 Sandveld study area (Figure 1) stretches from the coast of the Western Cape Province, South Africa, inland through agricultural plains and hills (altitudes of 0−1078 m). There is little formal conservation through statutory protected sites in the Sandveld and extensive agricultural conversion since the 1980s has transformed this region into an important area for the production of potatoes (Heydenrych 1993, Low et al. 2004, Franke et al. 2011). There is an average density of 1.2 pairs of Verreaux's eagles per 100 km^2 (n=30), with nests sites generally clustered around the available cliff habitat.

The Cederberg Mountains are located to the east of the Sandveld region (Figure 1). Covering 1178 km^2 (altitudes from 200−2027 m), this area is dominated by natural Fynbos vegetation and is largely protected by provincial conservation authorities (Maree and Vromans 2010). There are a similar number of Verreaux's eagles breeding here (n=42) as in the Sandveld, but they occur at nearly three times the density (3.0 pairs/100 km^2), due to a greater availability of nesting habitat availability.

Figure 1. Map of southern Africa showing locations of study areas for this study (Cederberg and Sandveld) represented as black dots and previous studies represented as circles (Matopos, Gargett 1900; Magaliesberg, Allan 1988; Karoo National Park, Davies 1994).

Study species and breeding terminology

Despite usually laying two-eggs (Gargett 1990), Verreaux's eagles almost invariably rear a single young per successful breeding attempt. Obligate siblicide occurs if both eggs hatch successfully (Rowe 1947, Gargett 1978, 1990; Steyn 1982). Consequently, breeding productivity is directly determined by the breeding rate and whether or not a nesting attempt produces a fledgling, with variation in brood size being irrelevant. Terminology is used here as follows; 1) breeding rate: the proportion of monitored occupied nests that make a breeding attempt, 2) nesting success: the proportion of breeding attempts that successfully rear a young, 3) breeding productivity: the proportion of monitored pairs that successfully rear a young (Steenhof and Newton 2007, Virani and Harper 2009).

Surveys and monitoring

Nests were monitored in four breeding seasons (2011−2014). Good prior knowledge of nest locations was available in the Sandveld (Rodrigues pers. comm.) and these were supplemented through additional ground surveys. Knowledge of nest locations in the Cederberg was relatively limited, and nests were located through ground surveys commencing in March 2011 prior to the first breeding season.

Aerial surveys were carried out in 2012 and 2013, at the end of each breeding season because of permit constraints on helicopter use. The interior of the Cederberg and the peripheries of both study areas were covered by aerial surveys along cliffs to ensure good coverage of nest locations in less accessible areas. These peripheral nests were not monitored for breeding productivity, but this information was important for accurate determining nest proximities (see nesting variables methods section). GPS locations and photographs were taken of all nests. Nests were considered occupied if eagles were seen close to a nest (<200 m) (n=11), there was a nestling on the nest (n=1), there was greenery on the nest (n=1), there was bright white wash on the cliff wall or a flattened nest platform indicative of a recent breeding attempt (n=8) or if occupation was confirmed post-survey (n=6).

Nest sites were observed from a distance (0.5−1.5 km) with a spotting scope every 2−3 weeks throughout the breeding season (late May−early November). Observations lasted for a target of three hours, although the length of each one varied according to the stage of breeding and ease of identification of breeding behaviours. Eagles were considered not to have initiated breeding when a pair was not sighted during observations lasting at least three hours, or were sighted but left the nest unattended regularly or for extended periods of time. Incubation was assumed when eagles appeared to be sitting (rather than standing) in a nest for the majority of an observation and not leaving the nest unattended for more than ~15 minutes. Occasionally (n=6) this was verified by observations of the nest contents. Hatching was assumed when an adult was observed feeding a nestling or moving prey on the nest. Precise hatching dates were obtained at nests that had cameras installed (Appendix 1) and these were used to validate our observations (n=8). Successful breeding was determined by seeing the fledged young close to the nest or a fully feathered nestling on the nest.

Because monitoring of some pairs commenced later in the season, deriving nesting success using these nests could bias our results, due to potential failure prior to the first visit (Steenhof and Kochert 1982). Therefore, we excluded nests from our analyses that were found with a nestling or were only monitored after July (n=22).

Our analysis is focused on those nests that were monitored from or prior to incubation and non-breeding pairs that were checked at least once in both June and July (*n*=112).

Explanatory variables

Lay date. The lay date was estimated to the nearest (Julian) day by methods in the following order of preference: 1) Hatching dates obtained from nest cameras minus the 44-day incubation period (Steyn 1982, Gargett 1990) from date of hatching (*n*=8). 2) The midpoint of visits less than two weeks apart when incubation began between the visits (*n*=12). 3) Back-calculated from hatching dates estimated from observations of nestling size and feather development (Steyn 1982) (*n*=31). 4) A combination of methods 2 and 3 when nest monitoring occurred more than 14 days apart (*n*=14). 5) In cases of nest failure, the earliest possible lay date was assumed to be the last date the nest was recorded as incubating minus 44 days, and the lay date was estimated as the mid point between the earliest possible lay date and the date incubation was actually first noted (*n*=2). A small number of failed nests (*n*=6) could not be assigned a lay date and were excluded from analyses that included this variable.

Nesting variables. The proximity index (PI), which is an index of the population density for each occupied nest, was calculated for each nest annually as the sum of reciprocals of the squared distance to all other occupied nests within 10 km (Amar and Redpath 2005, Arroyo et al. 2009). All nests known by the end of the surveys were included, except when new nests were detected in areas previously surveyed (*n*=1) and when territory abandonment occurred (*n*=1). Nest aspect (nearest of the four cardinal directions) was considered to be proxy for nest exposure to prevailing weather conditions and was estimated from 1:50,000 topographical maps.

Weather. Weather data were obtained from the South African Weather Service stations located at Clanwilliam and Lambert’s Bay, which are *c.* 20 km from the northwest edge of the Cederberg and the Sandveld study areas respectively. To investigate the influence of weather on nesting success we used weather variables around hatching and during the early nestling phase, when nestlings are most vulnerable to climatic extremes (Kostrzewa and Kostrzewa 1990). Hatch date was calculated from our lay date plus 44 days. The influence of weather was explored over three temporal scales: 7, 14, and 28 days starting from three days before the hatch date (to account for inaccuracy in the date). During these periods we calculated the following weather variables for each nest: the maximum number of consecutive days with rain (RainCon, days), the cumulative total of rainfall (RainTot, mm) and the average temperature (TempAv, °C).

Statistical analysis

Breeding rate. All statistical analyses were performed in R version 3.1.2 (R Core Team, 2015). The breeding rate was investigated using a Generalized Linear Mixed Effect Model (GLMM) specifying a logit link function and binomial response where 1= a breeding attempt was made, and 0= no breeding attempt was made. We included three fixed effects: area (Cederberg or Sandveld), year, and PI. Territory was included as a random term to account for pseudoreplication. To explore the most important variables we analyzed the data using model selection with Akaike's Information Criterion (AIC_c) using the 'MuMIn' package (Barton 2014). Models were ranked according to their AIC_c values and model averaging was performed across the top candidate models ($\Delta AIC_c < 2$). We could not perform a formal test of the effects of weather variables (rain and temperature) on breeding rate because of the lack of territory-specific data.

Nesting success. Nesting success was investigated using a Generalized Linear Model (GLM) specifying a binomial distribution and logit link function with the response variable being 1 or 0 for whether a pair was successful or not. The following covariates were included: study area, year, PI, nest aspect, lay date and the three levels of RainCon[7, 14, 28], RainTot[7, 14, 28] and TempAv[7, 14, 28]. RainCon and RainTot variables were also entered with an interaction term as a proxy for the intensity of rain. All terms were entered into the GLM and subsequently we performed model selection using the AIC_c ranking methods, with the specification that weather variables from different temporal scales (7-, 14-, 28 days) could not appear in the same model. Additionally, we analysed interactions with area between abiotic and climate variables (to look for area-dependent effects) in an ad-hoc way, but none of the models provided any strong evidence for any such difference, therefore no interactions with area were included in the analysis presented in the results.

Population viability analysis. Population viability was modelled using Vortex version 10 (Lacy and Pollak 2014), a commonly used software for modelling population dynamics (e.g.: Carrete et al., 2009; Jarić, Ebenhard & Lenhardt, 2009; García-Ripollés & López-López, 2011). Models were parameterized using our area-specific breeding productivity data and population sizes, assuming stable age distribution. Starting population sizes included all known occupied nests used in calculating PIs plus 5 % to account for the possibility of any missed territories. The carrying capacity was considered to be the population size plus the few known vacant territories in both study areas. We used survival rates from Vernon's (1972) predictions of life expectancy and survival in a stable population of Verreaux's eagles to create a baseline model. Additionally, we investigated the effects of a 10 % increase (PVA+10) in mortality, simulating a plausible low intensity anthropogenic effect such as the construction and operation of a wind farm nearby (García-Ripollés and López-López 2011), and a comparable 10 % decrease (PVA-10) in mortality, to investigate potential population growth around upper and lower bounds of biologically plausible ranges of mortality. Natal dispersal has rarely been investigated in Verreaux's eagles (but see Goodwin 2000). However, studies of dispersal and natal philopatry in similar sized raptors have indicated there is potential for natal dispersal between populations (Gonzalez et al. 1989, Whitfield et al. 2009, Weston et al. 2013), while dispersal of breeding adults is expected to be rare (Gargett 1990, Whitfield et al. 2009, Newton 1979). Therefore, due to our limited understanding of these movements, we ran all models assuming closed populations with no dispersal, allowing estimation of population-specific growth rates. We then specified 50 % dispersal of sub-adult birds between the populations to examine the influence of differential productivity on the overall metapopulation in the region given the potential for population connectivity due to natal dispersal. The predicted population growth rates are derived from 1000 iterations over 50 years for each model (Appendix 2).

Results

From 2011−2014, 112 occupied breeding years were monitored with an annual productivity of 0.52 ±0.27 young per pair per year (Table 1, Figure 2). However, all measures of breeding performance were greater in the Sandveld than in the Cederberg. The breeding rate in the Sandveld was double that of the Cederberg and the nesting success was 1.4 times higher in the Sandveld than the Cederberg. This was followed by overall breeding productivity, which was 2.7 times higher in the Sandveld (0.76 ±0.05) than the Cederberg (0.28 ±0.13).

Breeding rate

The GLMM analysis of the breeding rate included three top candidate models with $\Delta AIC_c < 2$ (Table 2). Following model averaging, the most important term (with a relative importance of 1.00) was ‘area’ (Table 3), reflecting the consistently higher breeding rate in the Sandveld (0.94 ±0.07) compared to the Cederberg (0.48 ±0.14) (Table 1, Figure 2). There was considerable year-to-year variation in breeding rate, with our ‘year’ term having a high relative importance value (0.72). ‘PI’ had a low relative importance value (0.21) and the confidence intervals for the parameter estimates overlapped zero suggesting no support for strong density dependence in breeding rates.

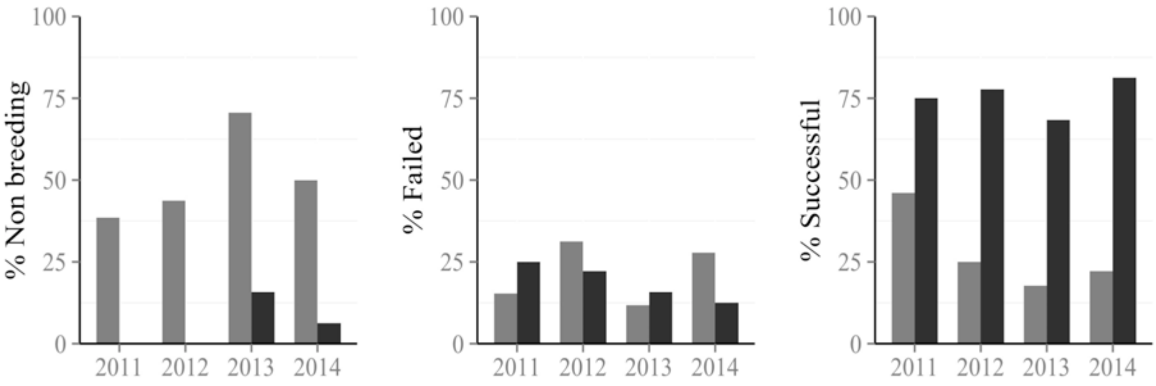

Figure 2. Breeding performance of Verreaux’s eagles in the Cederberg (grey, *n*=64) and the Sandveld (black, *n*=48), South Africa, from 2011-2014.

Table 1. Summary of Verreaux’s eagle pairs monitored and breeding parameters recorded in each area in each year of the study. Rate (breeding rate: the proportion of monitored occupied nests that make a breeding attempt); Productivity (the proportion of monitored pairs that successfully rear a young); Success (nesting success: the proportion of breeding attempts that successfully rear a young).

Area	Cederberg					Sandveld					**Both**
Year	2011	2012	2013	2014	**Total**	2011	2012	2013	2014	**Total**	**Total**
Pairs	13	16	17	18	**64**	4	9	19	16	**48**	**112**
Attempts	8	9	5	8	**30**	4	9	16	15	**44**	**74**
Young fledged	6	4	3	4	**17**	3	7	13	13	**36**	**53**
Rate	0.62	0.56	0.29	0.44	**0.48 ±0.14**	1.00	1.00	0.84	0.94	**0.94 ±0.07**	**0.71 ±0.27**
Productivity	0.46	0.25	0.18	0.22	**0.28 ±0.13**	0.75	0.78	0.68	0.81	**0.76 ±0.05**	**0.52 ±0.27**
Success	0.75	0.44	0.60	0.50	**0.57 ±0.13**	0.75	0.78	0.81	0.87	**0.80 ±0.05**	**0.69 ±0.15**

Table 2. Results from the top GLMMs (ΔAICc <2) comparing model fit for breeding attempts rate of Verreaux's eagles (*n*=112 observations from 2011−2014). Model parameters: area (Cederberg or Sandveld), year (2011−2014), PI (proximity index: a measure of the density of nests within 10km). Other column abbreviations: df, degrees of freedom; LogLik, Log liklihood; ΔAICc, change in AICc relative to the highest ranked model; ωi, AICc weight; ER, evidence ratio.

Models	df	logLik	AIC_c	ΔAIC_c	ω_i	ER
area+year	6	-52.35	117.50	0.00	0.50	-
area	3	-56.22	118.70	1.17	0.28	1.79
area+year+PI	7	-52.07	119.20	1.71	0.21	2.35

Table 3. Parameter estimates (β) from model averaged (with shrinkage) from the ranked models in Table 2 explaining the variation in breeding rate in Verreaux's eagles. Parameters include area (Cederberg or Sandveld), year (2011-2014), PI (proximity index: a measure of the density of nests within 10km). RI is the relative variable importance.

			Adjusted			Confidence intervals		
	β	SE	SE	*z*	*P*	2.5 %	97.5 %	RI
(Intercept)	0.38	0.77	0.78	0.49	0.63	-1.14	1.90	-
area	3.52	1.00	1.01	3.48	0.00	1.54	5.51	1.00
year2012	-0.11	0.76	0.77	0.14	0.89	-1.91	1.62	0.72
year2013	-1.43	1.19	1.19	1.20	0.23	-3.81	-0.17	0.72
year2014	-0.70	0.86	0.87	0.81	0.42	-2.71	0.75	0.72
PI	0.22	0.83	0.84	0.27	0.79	-2.00	4.08	0.21

Nesting success

The lay date and RainTot28 featured in all top candidate models explaining nesting success (Table 4) and consequently both contributed the highest relative importance (1.00) (Table 5) after model averaging. Nesting success decreased with later laying (Figure 3) and with increasing total rainfall up to 28 days after hatching (Figure 4). Nesting success was consistently higher in the Sandveld (0.80 ±0.05) than the Cederberg (0.57 ±0.13), however the relative importance of the term 'area' (0.55; Table 5) was lower than for lay date and RainTot28. Other terms that featured in our top candidate models had low relative importance values (PI: 0.24; Tempav28: 0.14; RainCon28: 0.11) and none of the weather variables at shorter temporal scales (up to 7 and 14 days) around the hatch date were featured in any of the models with an ΔAIC_c <2.

Table 4. Results from the top GLMs (ΔAICc<2) comparing model fit for nesting success of Verreaux's eagles (*n*=68 observations from 2011−2014). Model parameters: include LD (lay date), area (Cederberg or Sandveld), year (2011−2014), PI (proximity index: a measure of the density of nests within 10km), RainTot28 (total rainfall, mm), RainCon28 (number of consecutive rain days) and TempAv28 (average temperature, °C) all during 28 days around hatching (starting three days before the estimated date of hatching). Other column abbreviations: df, degrees of freedom; LogLik, Log likelihood; ΔAIC_c, change in AIC_c relative to the highest ranked model; ω_i, AIC_c weight; ER, evidence ratio.

Models	df	logLik	AIC_c	ΔAIC_c	ω_i	ER
area+LD+RainTot28	4	-27.47	63.60	0.00	0.28	-
LD+RainTot28	3	-28.83	64.00	0.45	0.22	1.26
area+LD+RainTot28+Temp28	5	-27.00	65.00	1.38	0.14	1.96
area+LD+RainTot28+PI	5	-27.09	65.10	1.57	0.13	2.21
LD+RainTot28+PI	4	-28.37	65.40	1.80	0.11	2.52
LD+RainTot28+RainCon28	4	-28.39	65.40	1.83	0.11	2.52

Table 5. Parameter estimates (β) from model averaged (with shrinkage) from the ranked models in Table 4 explaining the variation in nesting success in Verreaux's eagles. Parameters include LD (lay date), area (Cederberg or Sandveld), PI (proximity index: a measure of the density of nests within 10km), RainTot28 (total rainfall, mm), RainCon28 (number of consecutive rain days) and TempAv28 (average temperature, °C) all during 28 days around hatching (starting three days before the estimated date of hatching). RI is the relative variable importance.

			Adjusted			Confidence intervals		
	β	SE	SE	*z*	*P*	2.5 %	97.5 %	RI
(Intercept)	15.87	6.70	6.82	2.33	0.02	2.51	29.23	-
LD	-0.08	0.03	0.03	2.31	0.02	-0.14	-0.01	1.00
RainTot28	-0.09	0.04	0.04	2.15	0.03	-0.18	-0.01	1.00
area	0.63	0.77	0.77	0.81	0.42	-0.25	2.53	0.55
PI	-0.20	0.56	0.57	0.36	0.72	-2.60	0.91	0.24
TempAv28	0.05	0.20	0.20	0.27	0.79	-0.39	1.16	0.14
RainCon28	-0.03	0.13	0.13	0.23	0.82	-0.84	0.31	0.11

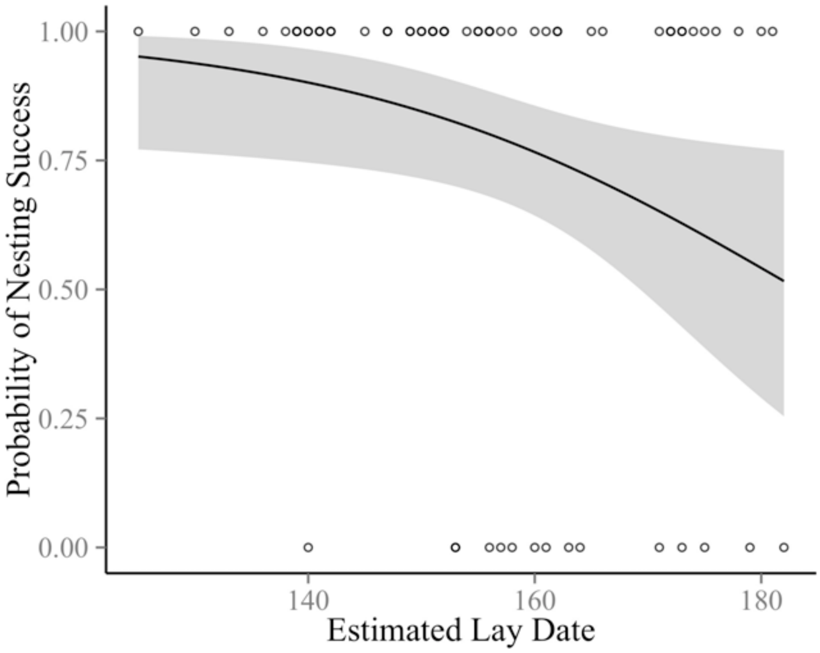

Figure 3. Line fitted from a Binomial Generalised Linear Model showing the probability of Verreaux's eagle nesting success against the estimate lay date (Julian days) with confidence intervals, in the Cederberg and Sandveld regions of South Africa. Circles show data points, where 0= an unsuccessful attempt and 1= a successful attempt.

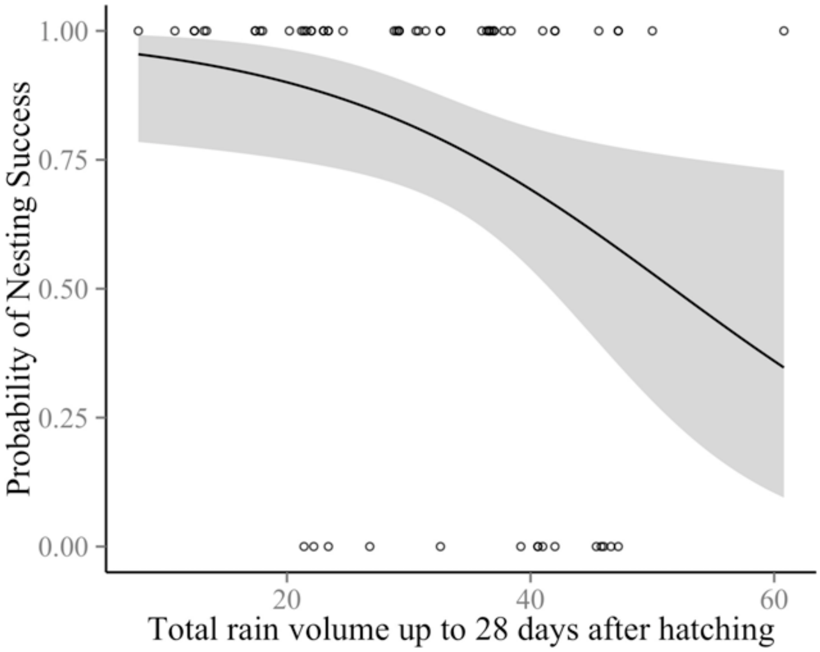

Figure 4. Line fitted from a Binomial Generalised Linear Model showing the probability of Verreaux's eagle nesting success against total rainfall (mm) recorded up to 28 days after hatching with confidence intervals, in the Cederberg and Sandveld regions of South Africa. Circles show data points, where 0= an unsuccessful attempt and 1= a successful attempt.

Comparison of breeding performance in other populations

All of the breeding parameters in the Sandveld were greater than in any of the previous studies reported, making it the most productive area for Verreaux's eagles currently known (Figure 5). In contrast, the Cederberg is considerably less productive than all other studied populations (Tarboton and Allan 1984, Allan 1988, Gargett 1990, Davies 1994). Between area differences are more pronounced for the breeding rate than the nesting success.

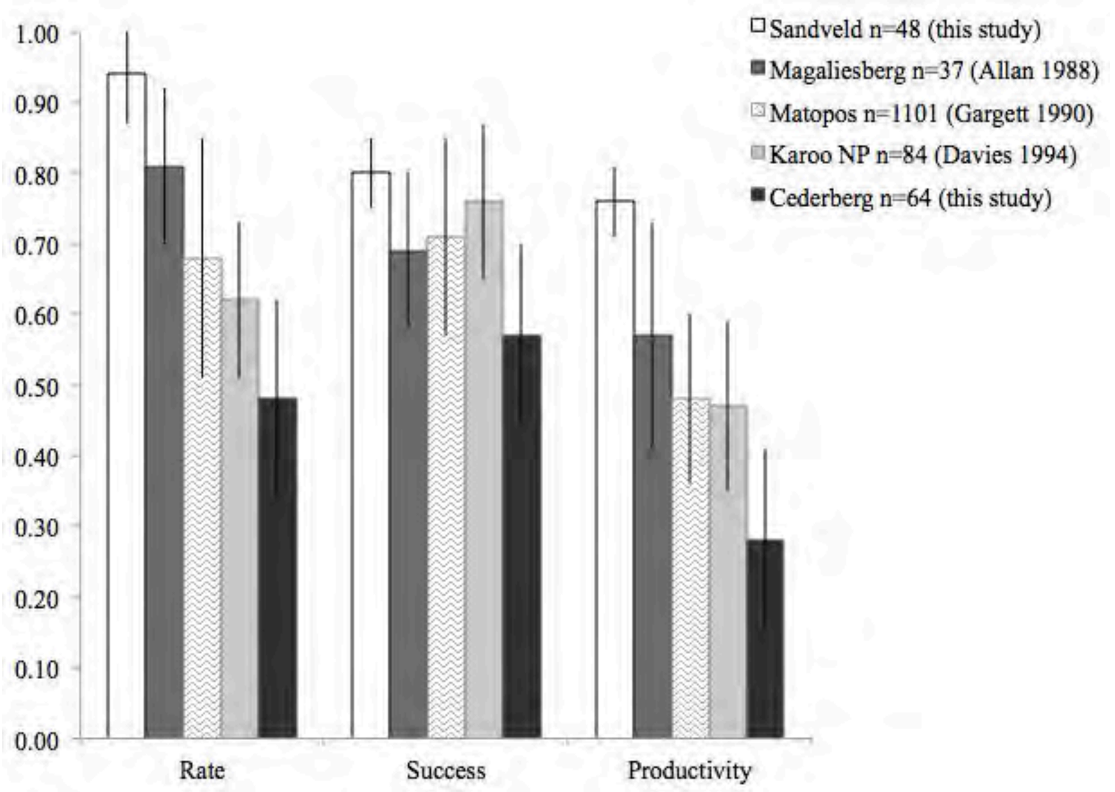

Figure 5. Mean annual breeding performance with standard deviation of Verreaux's eagles in five areas of Southern Africa (Gargett 1990, Davies 1994, Allan 1988). Breeding rate: proportion of monitored pairs which initiated incubation, success: proportion of breeding attempts which were successful and productivity: proportion of monitored pairs which were successful. Sample sizes of monitored occupied breeding years (n) given in legend. Study durations: this study 2011−2014; Magaliesberg 1982−1984; Matopos 1959−1984; Karoo NP 1986−1990.

Population viability

Stochastic growth rates (λ) indicated that as a closed population, in all survival scenarios, the Cederberg population would be unlikely to sustain itself (λ: 0.921−0.951). The Sandveld population was predicted to experience a positive growth rate in the baseline scenario (λ: 1.011), which increased further with a 10 % decrease in mortality (λ: 1.029). However, even within the more productive Sandveld population, a negative population growth was predicted when mortality was increased by 10 % (λ: 0.990) (Table 6; Figure 6).

Table 6. Stochastic estimates of annual rate of population growth (λ) with standard deviation (SD) for Verreaux's eagles over a 50-year time period in the Cederberg and the Sandveld, South Africa. λ equal to 1 represents a stable population, less than 1 is declining and more than 1 is increasing. Metapopulation growth rates are not included for closed populations due to the complete separation of the populations, therefore only the sum of individuals in the two populations is relevant. Other abbreviations: probability of extinction (PE) and predicted extant population size (N-extant) of eagles in the 50-year time frame. All variables are modelled as both closed (no dispersal between sites) and open (50 % dispersal of juveniles) populations with area specific breeding rates derived from this study. Population viability analysis (PVA) model scenarios: 'PVA Baseline' is a model with mortality rates derived from Vernon (1972), 'PVA-10' incorporates a 10 % decrease in mortality and 'PVA+10' is modelled on a 10 % increase in mortality.

Model		Population	λ ±SD	PE	N-extant ±SD
PVA -10 mortality	closed	Cederberg	0.951 ±0.10	0.19	10 ±5.6
		Sandveld	1.029 ±0.06	0.00	70 ±4.5
		Meta	-	0.00	78 ±7.6
	open	Cederberg	0.992 ±0.08	0.00	56 ±13.3
		Sandveld	1.000 ±0.09	0.00	54 ±12.2
		Meta	0.996 ±0.04	0.00	110 ±23.4
PVA Baseline	closed	Cederberg	0.935 ±0.12	0.54	6 ±3.0
		Sandveld	1.011 ±0.06	0.00	64 ±9.3
		Meta	-	0.00	68 ±10.0
	open	Cederberg	0.975 ±0.11	0.01	26 ±10.2
		Sandveld	0.979 ±0.11	0.01	26 ±10.9
		Meta	0.977 ±0.05	0.00	52 ±20.1
PVA +10 mortality	closed	Cederberg	0.921 ±0.13	0.84	4 ±1.6
		Sandveld	0.990 ±0.07	0.01	42 ±15.8
		Meta	-	0.00	42 ±16.0
	open	Cederberg	0.954 ±0.14	0.09	10 ±5.4
		Sandveld	0.958 ±0.15	0.13	10 ±5.6
		Meta	0.956 ±0.07	0.03	19 ±10.5

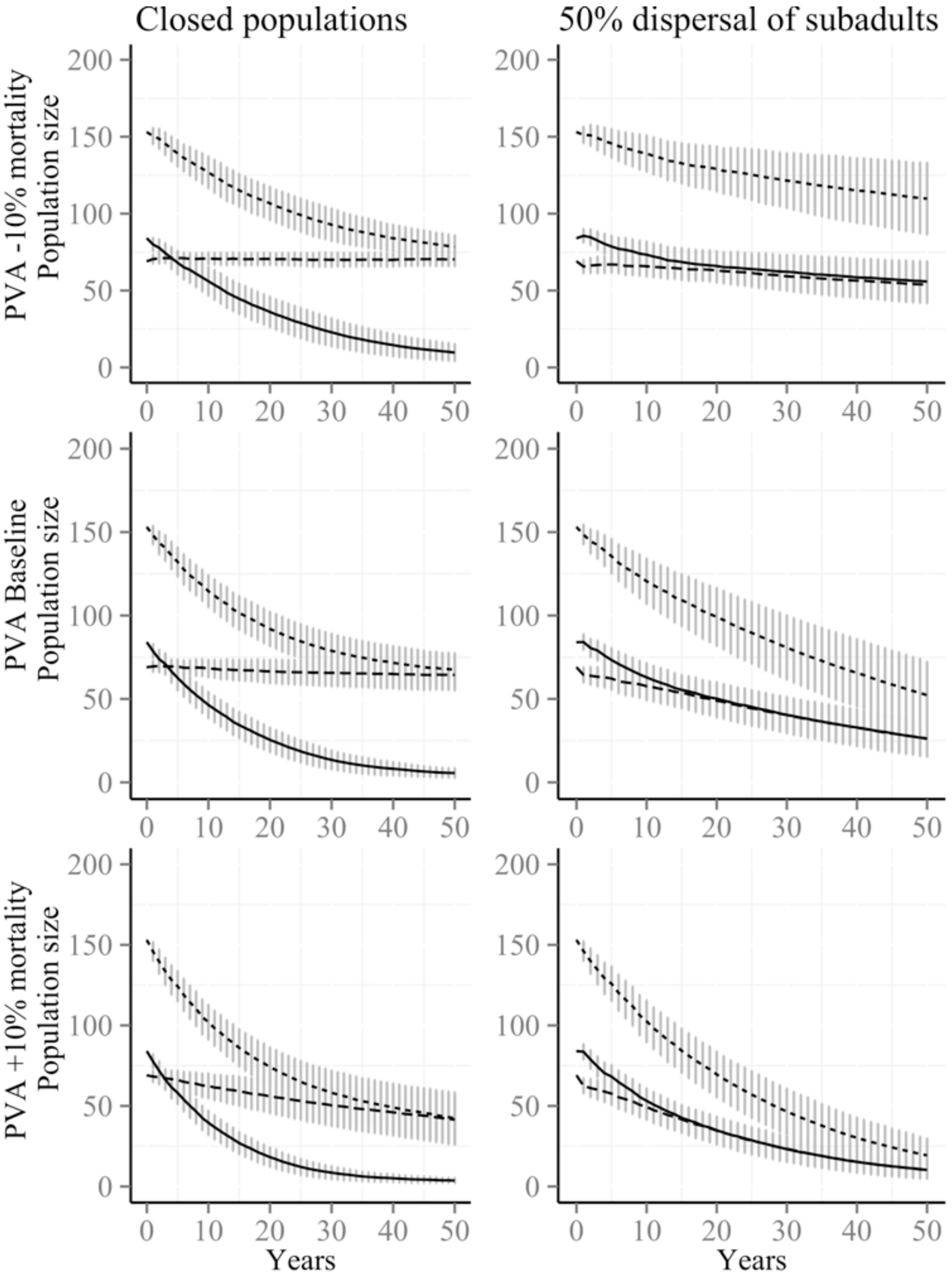

Figure 6. Graphical output for the population viability models, simulated population size of Verreaux's eagles over 50 years, for the Cederberg (solid lines), the Sandveld (dashed line) and the metapopulation across both areas (dotted lines) with standard deviation, modelled as both closed and open populations with area specific breeding rates derived from this study. 'PVA Baseline' is a model with mortality rates derived from Vernon (1972), 'PVA-10' incorporates a 10 % decrease in mortality and 'PVA+10' is modeled on a 10 % increase in mortality. Lines show the mean output for 1000 simulations.

In the open population models, the baseline model predicted a decrease across all populations (λ: 0.977) where negative growth rates in the Cederberg combined with dispersal between the populations results in a metapopulation decrease. This was exacerbated when mortality rates increased (λ: 0.956). Decreased mortality (PVA-10) stabilised the population growth rate in the Sandveld population (λ: 1.000) and slowed the decline in the Cederberg (λ: 0.992). However due to dispersal between the populations the overall metapopulation remained slightly in decline (λ: 0.996), but the probability of extinction within the tested timeframe was eliminated in this scenario (Table 6; Figure 6).

Discussion

In direct contrast to our predictions, we found a consistently greater breeding performance of eagles in the agriculturally transformed Sandveld area compared to the relatively pristine Cederberg. Breeding parameters for these two areas also differed markedly from previous studies of this species. Despite the limitations acknowledged (i.e.: sample size in some years of monitoring and that we do not know the productivity of the Sandveld area prior to agricultural conversion), these results indicate that some raptors can achieve high productivity in agricultural areas. Furthermore, in the scenario presented, this is actually sufficient enough to maintain the population viability.

The sample size of monitored nests was limited in 2011 and 2012, particularly in the Sandveld, owing to incomplete data sets where monitoring either commenced late or was not completed during the later stages of chick rearing. We chose to exclude these data to avoid introducing biases. Reflecting on the presumed outcomes of those excluded records; it is unlikely to affect the overall results of this study.

Between area differences

Differences in breeding performance between the areas were more prominent for the breeding rate than the nesting success, with less than half of the resident pairs making a breeding attempt annually in the Cederberg, but over 90 % of pairs attempting to breed in the Sandveld. The greater breeding rates in the Sandveld than the Cederberg could not be attributed to nesting densities or annual fluctuations. Nesting success was effected by rain and timing of laying and it remained consistently greater in the Sandveld than the Cederberg. Mean annual rainfall during our study was greater in the

Cederberg (213.8 ±47.8 mm) than the Sandveld (177.8 ±51.0 mm) and this might be a mechanism for the observed differences between the sites. Furthermore, these differences are expected to be exacerbated in reality, as data recorded more centrally to the study areas shows stronger differences (Cederberg: 706 ±174 mm, 2004–2014 Algeria weather station 32.374S, 19.058E, CapeNature 2015. Sandveld: *c.* 300 mm, 1990–2008 Graafwater weather station 32.155S, 18.603E, Franke et al., 2011) however these data were sparse and not available for the full analysis performed here. When compared with previous studies, the Sandveld is noted for being the most productive area for Verreaux's eagles currently known, while the Cederberg is the least productive area. This demonstrates the potential value of some agriculturally transformed areas to breeding eagles and begs the questions; what is so good about the Sandveld and what is so bad about the Cederberg?

Territory and individual adult quality are important in determining the probability of making a breeding attempt (Drent and Daan 1980, Sergio and Newton 2003) and this can be regulated by a balance between food availability and daily energy requirements (Widen 1994, Lohmus and Vali 2004, Shepard et al. 2011). Consequently, it may be that in the Cederberg either food availability is limited or that the topography requires greater energy consumption for daily movements compared to the Sandveld, resulting in the substantially lower breeding rate. The opposite might be true in the Sandveld, where agricultural transformation might be responsible for providing greater diversity or availability of prey (Ogada 2009, Kross et al. 2013) or the topography may be more conducive to a low energy consuming life style, although further research is clearly required to explore this explanation further. Davies (1994) observed that the apparently optimal habitat along upper cliff escarpments in the Karoo harboured high densities of Verreaux's Eagle pairs but these pairs experienced far lower breeding rate and success than pairs that had a greater proportion of bottom plains and farmland within their territories; resulting in breeding productivity being 66 % lower in upper escarpment pairs than lower escarpment pairs. This was attributed to a less reliable single-species (Rock Hyrax) prey base in the upper escarpments compared to the farmlands where there are alternate species available. Dietary differences or relative prey availability in each study site should be further investigated to assess the contribution it might have on breeding parameters.

Some raptors are known to exhibit fluctuating patterns in breeding productivity in which productivity follows patterns in prey abundance (Korpimaki and Wiehn 1998, Mcintyre et al. 1999, Steenhof et al. 1999, Millon et al. 2008, Moss et al. 2012) or the favourability of climatic conditions (Redpath et al. 2002, McDonald et al. 2004). However, our findings are likely to be representative of local trends owing to; i) The similarity of rainfall patterns during our study (Cederberg 213.8 ±47.8 mm; Sandveld 177.8 ±51.0 mm) and in the preceding decade (Cederberg 204.8 ±46.1 mm; Sandveld 185.9 ±53.9 mm) in both regions; ii) The slow life history of hyrax (Hoeck 1989, Barry et al. 2014); and iii) The absence of obvious cyclic trends in a 31-year study of Verreaux’s eagles (Gargett et al. 1995). Considering these factors and even with the addition of occasional ‘good’ years, the Cederberg is unlikely to become more productive than the Sandveld.

Other variables affecting breeding performance

We expected lower breeding productivity in our study areas compared to previous studies owing to the contrasting rainfall seasonality. The Cederberg and the Sandveld are both located in a winter rainfall region, while the previous studies were all undertaken in summer rainfall regions. Despite this, the breeding rate in the Sandveld exceeds that in summer rainfall regions, while the breeding rate of Cederberg eagles is substantially lower than all other studies (Figure 5), showing that eagles can breed successfully in winter rainfall regions.

Increased rainfall during nestling stage invariably causes reduced nesting success in raptors (Rodríguez and Bustamante 2003, Donald et al. 2004, Bionda and Brambilla 2011, Amar et al. 2012, Zabala and Zuberogoitia 2014). During heavy rainfall a nestling is more susceptible to starvation from decreased food provisioning and hypothermia particularly until it has developed the first insulating feathers. Furthermore the food requirements of nestlings increases during cold weather (Gargett 1990, Redpath et al. 2002) and rainfall is likely to impact adult hunting success negatively (Donald et al. 2004). The total rainfall up to 28 days after hatching was significant in predicting the outcome of a breeding attempt, whereas rainfall during shorter periods after hatching was less important, demonstrating the susceptibility to nest failure beyond just the first few weeks of nestling rearing. From a recent review of brooding behaviour in raptors, the allometric relationship predicts that for a bird of this size intensive brooding requirements should occur until the young are *c.* 27 days old (Katzenberger et al. 2015), which links well with our findings.

Our finding that the timing of breeding influences success was in agreement with multiple studies of raptorial species (Newton and Marquiss 1984, Margalida et al. 2003, McDonald et al. 2004, Martin et al. 2014). Increased rainfall as the breeding season progresses has been identified as a mechanism explaining this seasonal decline in nesting success in some species (Senapathi et al. 2011, Cartwright et al. 2014). However, lay date and rainfall were not correlated in our study, therefore we assume that these act independently with the greater success of early-breeding pairs potentially related to individual and/or territory quality. Although these effects are often difficult to separate, higher quality individuals or those inhabiting better quality territories can attain breeding condition earlier than poorer individuals or territories, and these pairs often have a greater probability of nesting success (Verhulst and Nilsson 2008, Zabala and Zuberogoitia 2014).

Population viability

Unfortunately, reliable survival estimates were not available for our populations. Differences in population trends between the modelled scenarios highlight the need to be cautious when assigning these predictions to real-life scenarios. Furthermore, although productivity was higher in the Sandveld, survival of adults or juveniles (Millsap et al. 2004), or the quality of offspring (Almasi et al. 2015) could be lower in this human-altered habitat and therefore the balance between productivity and survival may not be equal between the two areas. Accepting this limitation, population modelling indicated that differences in breeding productivity could have a profound effect on the long-term stability of each study population. In contrast to expectations of negative impacts of agricultural land use on breeding productivity of top predators, the closed baseline model shows an apparently healthy population in the Sandveld. On the other hand, it is unlikely the Cederberg population would be self-sustaining. Although little is known about natal dispersal and philopatry in Verreaux's eagles, potential for dispersal from natal areas has been seen in closely related Spanish imperial eagles (*Aquila adalberti*) (Gonzalez et al. 1989), golden eagles (*Aquila chrysaetos*) (Weston et al. 2013, Ogden et al. 2015) and Bonelli's eagles (*Aquila fasciata*) (Real and Manosa 2001, Cadahía et al. 2010). Dispersion between sub-populations can drive source-sink dynamics and often leads to a combined higher metapopulation than just the 'source' would alone (Pulliam 1988, Pulliam and Danielson 1991). However, dispersion from a productive population into decreasing population can cause an ecological trap situation (Purcell and Verner 1998, Battin 2004) and result in the decline of the metapopulation, as seen in the open baseline model.

The scenario-based approach highlights how any increment in mortality would be detrimental to the metapopulation, which is consistent with modelling in other long-lived raptors (Katzner et al. 2006, Carrete et al. 2009, García-Ripollés and López-López 2011, Rushworth and Krüger 2014). Although density dependent effects are usually expected to result in increased breeding performance as the population declines (Fasce et al. 2011), we did not include these effects in our models and believe it is unlikely there would be a significant change as our breeding analysis showed no relationship with the proximity index.

Conclusions

The measured differences in breeding performance between the natural and agriculturally-developed study areas was opposite to our predictions based on the fundamental idea that top predators are largely associated with natural and undisturbed ecosystems (Sergio et al. 2005, 2006). Our results challenge the assumption that the Cederberg represents prime habitat for this species and suggest that the Sandveld, in its current agriculturally transformed state, is in fact a more suitable area. Although agricultural intensification is often blamed for the loss of ecological heterogeneity (Benton et al. 2003, Flynn et al. 2009, Herrera et al. 2015), it can also provide resource opportunities that can be beneficial under some circumstances (Cardador et al. 2011, Buij et al. 2013). Despite not knowing whether breeding performance has changed in the Sandveld following agricultural development and a changing prey base or if the differences in breeding productivity between the areas already occurred prior to agricultural transformation of the Sandveld, our findings support the notion that Verreaux's eagles can maintain good breeding productivity in agriculturally transformed areas. However, there is likely to be a threshold of transformation tolerance where functional diversity and prey availability are not compromised (Magioli et al. 2015). Land use and climate change are the two major pressures facing biodiversity loss globally. There are potentially synergetic effects between these factors and understanding these is important for effective conservation strategies (Opdam and Wascher 2004, Mantyka-Pringle et al. 2015). The results from this study highlight the Sandveld as a regionally important area for conservation and preservation of Verreaux's eagles. Management actions should aim to identify and eliminate or avoid any current or future sources of unnatural mortality in this area. This may be particularly relevant to the growing wind energy industry in South Africa, which has been identified as a cause of mortality (Drewitt and Langston 2008, de Lucas et al. 2008) and disturbance-related decreases in breeding productivity of similar eagle species (Dahl et al. 2012). The maintenance of suitable heterogeneous conditions in the Sandveld is also likely to be important to secure viable populations in this region.

Acknowledgements

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Appendices

Appendix 1. Supplementary information on camera deployments information on Verreaux's eagle nests in the Cederberg and the Sandveld.

Area	Year	Camera make	Set up	Frame interval	Start date	End date	*n* photos
Cederberg	2012	Scoutguard 560	Motion-sensing	na	11-Jul	22-Jul	302
Cederberg	2012	Scoutguard 560	Motion-sensing	na	14-Jul	15-Jul	32
Sandveld	2012	Scoutguard 560	Motion-sensing	na	05-Jul	20-Jul	475
Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	29-Jun	25-Sep	18576
Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	22-Jul	13-Aug	5610
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	10-Jul	07-Sep	5268
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	05-Jul	11-Jul	1468
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	04-Jul	26-Aug	5287

Appendix 2. Input parameters from the simulated PVA scenarios of the Verreaux's eagles in the Cederberg and the Sandveld as modeled in Vortex.

Parameter	**PVA -10 % mortality**		**Baseline PVA**		**PVA +10 % mortality**	
Model settings	Cederberg	Sandveld	Cederberg	Sandveld	Cederberg	Sandveld
Number of iterations	1000	1000	1000	1000	1000	1000
Number of years	50	50	50	50	50	50
Extinction definition	Only 1sex remains		Only 1sex remains		Only 1sex remains	
Number of populations	2	2	2	2	2	2
Inbreeding depression	no	no	no	no	no	no
Reproductive system						
Pair system	Long-term monogamous		Long-term monogamous		Long-term monogamous	
Age at first breeding (female)	4	4	4	4	4	4
Age at first breeding (male)	4	4	4	4	4	4
Maximum age of reproduction	30	30	30	30	30	30
Maximum number of broods/year	1	1	1	1	1	1
Maximum number of progeny/year	1	1	1	1	1	1
Sex ratio at birth (m/f)	50/50	50/50	50/50	50/50	50/50	50/50
Density dependent reproduction	no	no	no	no	no	no
% adult females breeding successful/year[1]	28	76	28	76	28	76
EV in % adult females breeding successful/year[1]	13	5	13	5	13	5
Mean number of offspring/female/year[1] (± SD)	1 (±0.00)	1 (±0.00)	1 (±0.00)	1 (±0.00)	1 (±0.00)	1 (±0.00)
Mortality rates						
% mortality from age 0-1 (juveniles) ± SD	36.9 ± 2 3	36.9 ± 2 3	41 ± 2 [2]	41 ± 2 [2]	45.1 ± 2 4	45.1 ± 2 4
% mortality from age 1-2 (sub-adult) ± SD	16.2 ± 2 3	16.2 ± 2 3	18 ± 2 [2]	18 ± 2 [2]	19.8 ± 2 4	19.8 ± 2 4
% mortality from age 2-3 (sub-adult) ± SD	16.2 ± 2 3	16.2 ± 2 3	18 ± 2 [2]	18 ± 2 [2]	19.8 ± 2 4	19.8 ± 2 4
% mortality from age 3-4 (sub-adult) ± SD	16.2 ± 2 3	16.2 ± 2 3	18 ± 2 [2]	18 ± 2 [2]	19.8 ± 2 4	19.8 ± 2 4
% mortality from age 4+ (adult) ± SD	8.1 ± 2 3	8.1 ± 2 3	9 ± 2 [2]	9 ± 2 [2]	9.9 ± 2 4	9.9 ± 2 4
Initial population structure						
Initial population size	90	100	90	100	90	100
Stable age structure	yes	yes	yes	yes	yes	yes
Carrying capacity	90	100	90	100	90	100

[1] Results from this study, [2] estimates from Vernon (1972), [3] 10 % decrease in Vernon's estimates, [4] 10 % increase in Vernon's estimates

Chapter 3

Adaptability of a specialist predator: The effects of land use on diet diversification and breeding performance of Verreaux's eagles

A modified form of this chapter is published in The Journal of Avian Biology.
Murgatroyd, M., G. Avery, L. Underhill A. and Amar (2016). Adaptability of a specialist predator: The effects of land use on diet diversification and breeding performance of Verreaux's eagles. *Journal of Avian Biology*. 47:001-012. dio: 10.1111/jav.00944

Abstract

Specialist predators are generally negatively impacted by habitat change. Predators that inhabit transformed areas are usually forced to diversify their diet and this departure away from traditional resources can have negative consequences for fitness and demographic parameters. We consider this relationship as it applies to Verreaux's eagle *Aquila verreauxii*, which is typically considered to be a highly specialised predator of hyraxes (*Procavia* and *Heterohyrax* spp.). We investigate diet in relation to land cover in two adjacent areas of South Africa and explore the links between diet diversity, the percentage of hyrax consumed, and the breeding performance of eagles. We also examine these same patterns using data from other studies. We found that diet diversity was greater in the agriculturally developed Sandveld region compared to the natural Cederberg region. Proportions of the three main prey types were correlated with the proportion of agriculturally developed land around the nest site. Breeding performance was correlated with the diet, but not in the manner expected, with breeding productivity being greater in regions with large diet diversity and a small proportion of hyrax in the diet. We found similar patterns when placing our results into a broader geographical context using existing data for the species, suggesting our results were not unique to our study system. Thus, our results suggest that diet diversification does not necessarily impinge on breeding performance in the presence of adequate alternative prey resources. This research adds to the growing number of studies suggesting that some specialist predators may be able to cope or even benefit up to a threshold level of habitat transformation. These results have implications for predicting changes on such species by anthropogenic habitat transformation and highlight the potential for agriculturally developed areas to maintain a conservation value when habitat heterogeneity is preserved.

Introduction

The global decline of specialist species has been associated with human-induced landscape degradation (Julliard et al. 2004, Ewers and Didham 2006, Devictor et al. 2008, Clavel et al. 2011). Land use change can reduce or degrade foraging habitats and alter food supplies, thereby forcing a change in diet (Glue 1967, Amar and Redpath 2005, Palma et al. 2006). Such changes in diet can affect life-history traits, including individual fitness and breeding performance (Lourenço et al. 2015, Senior et al. 2015); therefore understanding these relationships can provide an important tool in conservation biology. It is generally considered that, as the availability of preferred prey decreases, diet diversity increases and this increased diet breadth has adverse demographic impacts on specialist predators (Elmhagen et al. 2000, Sumasgutner et al. 2013, Resano-Mayor et al. 2014). For example, in Montagu's harriers *Circus pygargus* diet diversification, as a consequence of reductions of traditional prey resources, has been correlated with lower nesting success (Arroyo and Garcia 2006). However, responses are variable and important factors to consider are the level of intensification of land use and the ability for individual specialisation or diversification to occur within the species of concern.

For predators in agricultural landscapes, the more intensively managed that an area is, the less likely it will be able to support an adequate prey base (Flynn et al. 2009). While occasionally, low intensity agriculture can actually increase the availability of suitable alternative resources (Ogada 2009, Kross et al. 2013), which is usually dependent on maintaining habitat heterogeneity (Tews et al. 2004). Furthermore, generalist-specialist traits will determine an individual's capacity to utilize alternative resources. Foraging success by specialists declines with a decrease in abundance of preferred prey (Terraube et al. 2011) and the pursuit of alternative prey is expected to be more costly in terms of search time or net calorific value (Macarthur and Pianka 1966). Therefore, spatial or temporal declines in preferred prey availability incur an energy cost, and this can have negative consequences for demographic parameters such as survival (Resano-Mayor et al. 2015), breeding density (Graham et al. 1995) and reproductive performance (Korpimaki and Wiehn 1998, Arroyo and Garcia 2006, Otterbeck et al. 2015). In contrast, generalists have wide dietary niches and can switch prey resources, making them less susceptible to the negative demographic and individual fitness-related effects caused by changes in prey availability than specialists (Reif et al. 2001, Whitfield et al. 2009).

Verreaux's eagle *Aquila verreauxii* is often considered to be one of the most specialised raptors, with up to 98 % of their diet in some studied populations consisting of a single prey type, hyraxes (*Procavia capensis* and *Heterohyrax brucei*) (Gargett 1990). Furthermore, the distribution of Verreaux's eagle in Africa closely follows the availability of mountainous habitat and the distribution of hyrax species (Davies and Allan 1997). Consequently, we might expect that in regions where inert-individual diet diversification has occurred there would be negative consequences for the fitness and demography of individuals with the most diverse diets. Within our study area, in south-western South Africa, Verreaux's eagles occupy areas with vastly contrasting land use and the breeding performance in these areas also differs between the populations (Chapter 2). Contrary to expectations of a specialized predator, breeding productivity is greater in the agriculturally transformed area (the Sandveld) than the predominately natural area (the Cederberg) (Chapter 2).

This study investigates how diet composition of the Verreaux's eagle differs between these areas to better understand links between habitat transformation, dietary niche, and demography. Firstly we examine diet diversity in relation to land use cover diversity and in particular, the extent of agricultural land use. Secondly, we assess the contribution of the main prey types in relation to agricultural transformation. Thirdly, we relate diet diversity to breeding performance. Lastly, to examine whether the findings from this study were consistent at a broader scale, we compare diet diversity and breeding performance revealed by this study with studies elsewhere in southern Africa. We predict that either (a) in line with traditional views of a dietary specialist, Verreaux's eagles in the more productive (agricultural) area successfully maintain a specialised diet or (b) diet diversification does not have a negative effect on breeding performance in this species, and is likely to be related to prey availability in the environment.

Methods

Study area

This study was carried out in two regions in the Western Cape Province, South Africa: the Cederberg (centred at 32.495°S, 19.264°E) and the Sandveld (centred at 32.426°S, 18.669°E). The Cederberg is a relatively pristine mountainous area, largely under legislative protection, and dominated by natural Fynbos vegetation (Maree and Vromans 2010). In contrast, the Sandveld is a heterogeneous environment that has been transformed for agriculture, with the main period of habitat transformation being the 1980s (Heydenrych 1993). Important land use activities include irrigated crops, small livestock grazing and fallow land for potato rotations and this is interspersed by remaining patches of natural vegetation (Low et al. 2004, Franke et al. 2011).

Diet data

Prey remains collections

Remains of prey were collected (*n*=41 collections) opportunistically from under and on nests during and after the breeding season (*n*=20 unique territories) from 2011−2014. At each collection all items were removed. Skulls and postcranial components were identified to family or species level by comparison with osteological reference materials at the Iziko Museum, Cape Town. The minimum number of individuals (MNI) of each species in each sample was taken as the maximum frequency of unique skeletal components (either identified bones or, for tortoises, unique components of the plastron) (Marti 1987, Davies 1994). Collections from all nests within the same territory and in the same year were pooled before calculation of MNIs, those collected in subsequent years were pooled by territory after calculation of MNI. Only nests with at least seven MNI were included in diet analyses. We checked for biases in diet diversity caused by the sample size at each nest and found no correlation between diet diversity and MNI in either study area (Sandveld: r=0.12; Cederberg: r=0.40), suggesting that larger diet diversity was not a result of larger sample size.

Nest cameras

Nest cameras (Scoutguard 560 & Ltl Acorn 6210MG/C with 32GB SD memory card; Appendix 1) were installed 2−4 m above the nest during incubation to record prey brought to the nest during the chick-rearing period (*n*=9). In the 2012 season four motion-sensing cameras were installed (Cederberg *n*=2; Sandveld *n*=2), these were programmed with a two-minute delay so that a maximum of one image was recorded every two minutes although generally the frequency of images was much less. In 2013, five time-lapse cameras were installed with a schedule of one image every three minutes (Cederberg *n*=2; Sandveld *n*=3). All cameras were programmed to switch off from 19:00−07:00, during darkness, to conserve batteries (AA), which were replaced a maximum of once during the season and supplemented with small solar panels (12x7.5 cm) in 2013. Data collected in different years at the same territory were pooled to determine the percentage contribution of species to the diet. Eight items (5 % of all camera items) recorded on cameras were not identifiable and were excluded. This method provides an unbiased representation of prey brought to the nest (Margalida et al. 2005, García-Salgado et al. 2015).

Prey remains versus camera data: Correction indices

Prey remains from nest sites have been found to be biased (Real 1996, Redpath et al. 2001, Sánchez et al. 2008). To ascertain whether prey remains reflected an accurate representation of prey delivered to the nest, we compared prey remains with the information obtained from nest cameras, which were not subjected to the same kinds of bias.

For both methods, prey were grouped into broad taxonomic categories: Rock hyrax (*Procavia capensis*), mole-rats (*Bathyergus suillus, B. janetta*), tortoise (*Chersina angulata*), birds (Columbidae, *Numida meleagris, Pternistsis capensis* and other small-medium sized birds), lagomorphs (*Lepus capensis, L. saxatillis, Pronalagus rupestris*), small antelopes (*Oreotragus oreotragus, Raphicerus* spp., *Sylvacapra grimmia*), livestock (Ovis/Capra) and other (*Papio ursinus, Herpestes pulverulenta, Octocyon megalotis*, Mustelidae, *Felis* sp., fish sp.).

A linear regression with intercept forced through the origin was performed to compare the percentage contribution of prey groups assessed by the two methods (prey remains versus cameras). Adjusted R-squared values (R^2) were used to assess the strength of the correlation between the two methods. The regression through the origin has a single coefficient and this was used as the correction factor for prey remains for prey groups which showed biases between methods and an $R^2 > 0.60$.

In order to increase the sample size and reliability of individual prey remains collections, at nests where prey remains and camera data were both available we quantified all other prey groups by averaging the results from prey collections and camera data weighted by the size of the camera study (n items recorded) and the prey collection (n MNI) to derive a mean contribution of the prey group (Appendix 2).

After the application of correction factors, the diet diversity was estimated for each territory using the Shannon diversity Index (H) where p_i is the proportion of prey represented in each taxonomic group (Shannon and Weaver 1949).

$$H = -\sum_{i=1}^{R} p_i \ln p_i$$

The maximum potential diversity value can be calculated as the natural logarithm of the maximum number of species or species groups possible, in this case eight, therefore the most diverse diets will tend towards the maximum of 2.08, while the least diverse diets will tend towards a value of zero.

Breeding performance

Breeding performance was monitored by nest observations over four breeding seasons from 2011−2014 (Chapter 2). In brief, nests were visited every two−three weeks and observed for approximately three hours, depending on the ease with which breeding behaviour could be identified. We measured three breeding parameters, which might be impacted differently by the diet composition and are described as follows; the breeding productivity is the proportion of the monitored nest years that successfully fledge a chick, the breeding rate is the proportion of the monitored nest years in which a breeding attempt is made (incubation is initiated), and the nesting success is the proportion of breeding attempts that successfully rear a chick (Steenhof and Newton 2007, Virani and Harper 2009). These parameters were monitored for 2−4 years for each territory.

Land cover

Percentage land cover type within a 3 km circular buffer of nests was derived in QGIS (Quantum GIS Development Team 2014) from a layer that had been digitized at scales 1:10,000–50,000 (Kirkwood 2010). This was based on previous estimates of home range size (Chapter 4) and for territories with multiple nest cliffs we centred this on the nest that was most frequently active (alternative nest cliffs were <1 km apart). Four habitats were considered: natural (pristine habitat), near-natural (close to pristine), degraded (those areas which have been severely impacted but could be rehabilitated at great cost) and no natural habitat (areas which have been irreversibly transformed through development) (Maree and Vromans 2010), which were the same habitats used in Chapter 4. Owing to the negligible urban development in the Sandveld, departure from natural habitat is largely associated with agriculture, and in this case the latter category of “no natural habitat” is considered to be areas with complete agricultural transformation. Using these measures we calculated a land use cover diversity index within each nest buffer, also using the Shannon diversity Index. From this index, territories with a predominant coverage of natural habitat will have small land use cover diversity despite supporting an inherent large diversity of flora and fauna. This measure of land use cover diversity therefore measures only the broad heterogeneity of land cover classes. Likewise would be true for territories with predominately no natural habitat, however such scenario does not arise in this study (Appendix 2).

Regional data

Regional correlations, on a southern African scale, between breeding parameters and both diet diversity and the proportion of hyrax in the diet were also explored using data from the two areas in this study (Cederberg, Sandveld) and previous research on this species elsewhere (Figure 1, Appendix 5). Diet data were derived in four other

Figure 1. Map of the locations of current (1. Sandveld; 2. Cederberg) and previous (3. Karoo; 4. Magaliesberg; 5. Former Transvaal region; 6. Matopos; 7. Walter Sisulu Botanical Gardens, Johannesberg) studies on the diet and breeding performance of Verreaux's eagles in southern Africa.

areas of South Africa; from prey remains in the Karoo (Davies 1994), and the former Transvaal province (Tarboton and Allan 1984), from camera studies in the Magaliesberg (K. Padayachee unpubl. data), and from observations of prey deliveries at a closely monitored nest in the Walter Sisulu National Botanical Garden, Gauteng (Symes & Kruger, 2012), as well as from prey remains at one well studied site in Zimbabwe, the Matopos Hills (Gargett 1990). Shannon's diversity indices were calculated from data for each study according to the same taxonomic groups described above. Breeding parameters were derived from the maximum available data for each area (Appendix 5).

Statistical analysis

All statistical analyses were performed in R version 3.1.2 (R Core Team 2015). We used multiple linear regression (General Linear Models with a gaussian error distribution and an identity link function) to explore associations between diet diversity and land cover characteristics within the 3 km buffer of the nest site. Two models were performed for the response variable, diet diversity, testing firstly for an association with land use cover diversity and secondly for an association with the percentage of agricultural (no natural) land cover (Table 1, Analysis i). In both models the explanatory variables were initially included as quadratic terms to investigate for non-linear relationships and then ranked by AIC_c values against the null model (not including the quadratic term). Following this the most parsimoniousmodel was selected to describe diet diversity. Using the same method, we also explored the relationship between the proportions of the three dominant prey items in the diet (hyrax, tortoise, mole-rats) and the percentage of agricultural land cover within the nest buffers (Table 1, Analysis ii). The size of each prey remains collection was incorporated into each analysis by weighting each observation by the log of the MNI in the collection.

Variations in breeding parameters (rate, success & productivity) were investigated using Generalized Linear Models with a quasibinomial error distribution (to correct for extra-dispersion) and a logit link function (Table 1; Analysis iii; Data set A). The response variables were modelled as a two-vector response calculated from the breeding parameters and the sample size of monitored breeding events (i.e.: for breeding rate: the number of years an attempt was made or the number of years an attempt was not made; breeding productivity: the number of years a chick was produced successfully or no chick produced; nesting success: the number of years a successful breeding attempt was made or an unsuccessful one). In this way the number of years that a breeding territory was monitored is accounted for in this analysis by weighting those with more uncertainty (or fewer years monitored) less heavily than those with more years monitored. The log of the MNI in diet analyses was also used as a weighting factor in these analyses to improve model reliability. Each of these response variables was tested separately for an association with two explanatory variables: diet diversity and percentage of hyrax in the diet. These models were run for all breeding territories in the study areas (n=14). The relationship between regional breeding parameters and diet variables (diet diversity and percentage of hyrax in the diet) was investigated in the same way, using additional data from previous studies (Table 1; Analysis iii, Data set B and Appendix 5).

Table 1. Descriptions of the response variables and model structures used in analyses of diet and breeding parameters of Verreaux's eagles. ^2 signifies the inclusion of the variable as a quadratic term, (+^2) signifies initial inclusion of a quadratic term that did not occur in the final model. "-" is non applicable. Land use cover (l.u.c) diversity and % agricultural land cover were calculated in a 3km buffer around the nest sites. Diversity indices were calculated following Shannon's diversity index. All models were weighted by the minimum number of individuals in the prey remains collections.

Analysis	Response Variable	Response variable		Distribution (link)	Explanatory variable	Data set	
		Vector 1	Vector 2			A	B
i)	Diet diversity	-	-	gaussian (identity)	L.u.c diversity (+ ^2)	All nests	-
	Diet diversity	-	-	gaussian (identity)	% agriculture + ^2	All nests	-
ii)	% hyrax in diet	-	-	gaussian (identity)	% agriculture + ^2	All nests	Sandveld
	% tortoise in diet	-	-	gaussian (identity)	% agriculture + ^2	All nests	Sandveld
	%mole-rat in diet	-	-	gaussian (identity)	% agriculture (+ ^2)	All nests	Sandveld
iii)	Breeding rate	Breeding attempt	No breeding attempt	quasibinomial (logit)	Diet diversity	All nests	Regional
	Breeding productivity	Young produced	No young produced	quasibinomial (logit)	Diet diversity	All nests	Regional
	Breeding success	Successful attempts	Unsuccessful attempts	quasibinomial (logit)	Diet diversity	All nests	Regional
	Breeding rate	Breeding attempt	No breeding attempt	quasibinomial (logit)	% hyrax in diet	All nests	Regional
	Breeding productivity	Young fledged	No young fledged	quasibinomial (logit)	% hyrax in diet	All nests	Regional
	Breeding success	Successful attempts	Unsuccessful attempts	quasibinomial (logit)	% hyrax in diet	All nests	Regional

Results

Prey items were analysed from nine nests in the Sandveld and five nests in the Cederberg where the MNI >7. Difficulties experienced with collecting remains at nests in mountainous terrain limited the sample size achieved in the Cederberg. The two methods (camera and prey remains) were considered correlated ($R^2 > 0.60$) for the most frequently occurring prey groups (hyrax, tortoise and mole-rats) and the regression line coefficients were used as correction factors for tortoise and mole-rats, which deviated from the 1:1 line, with prey remains over-representing tortoises and under-representing mole-rats (Figure 2).

Diet composition and diversity

Rock hyrax was the dominant prey species at all Cederberg nests (*n*=5) (mean: 97.8 %; range: 91.7−100 %), whereas at the Sandveld nests (*n*=9) hyrax contributed on average a quarter of all prey (25.0 % range: 5.9−51.9 %). Mole-rats (31.0 % ±18.8) and tortoises (10.6 % ±5.8) were the most frequently recorded prey in the Sandveld; neither of these prey types featured in the diet at any of the nests in the Cederberg (Figure 3, Appendix 2).

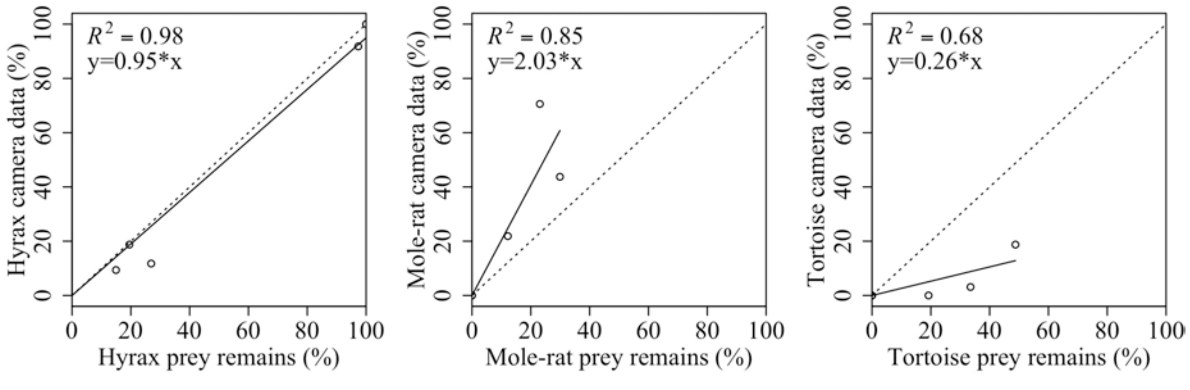

Figure 2. Comparative percentage contribution of rock hyrax, mole-rats and tortoise as assessed by prey remains collections and camera studies at five Verreaux's eagles nests from 2012-2013 in our study areas. Solid lines show linear relationships and dotted lines show 1:1 relationships. Points above the dotted line indicate under-representation in prey collections, points below the dotted line indicates over-representation in the prey collections.

Diet diversity (H) was higher in the Sandveld (Diet H= 1.34±0.20) than in the Cederberg (Diet H= 0.14±0.13) (X^2= 96.3, p<0.01). In the most parsimonious model (Appendix 3) diet diversity was positively and linearly related to land use cover diversity (Figure 4a, Slope coefficient estimate (β) ± Standard error (SE)= 1.31±0.13, t= 9.78, p<0.01) and the quadratic term was not featured. In general, diet diversity was also positively associated with the percentage of agricultural land within nest buffers (Figure 4b, β±SE= 0.095±0.013, t= 7.29, p<0.01) and the quadratic term was significant (β±SE= -0.00165±0.00034, t= -4.83, p<0.001), with a rapid increase in diet diversity in territories with up to 20 % of agricultural land cover around the nest followed by a levelling off, or even a small decrease, at sites above this level (Figure 4b).

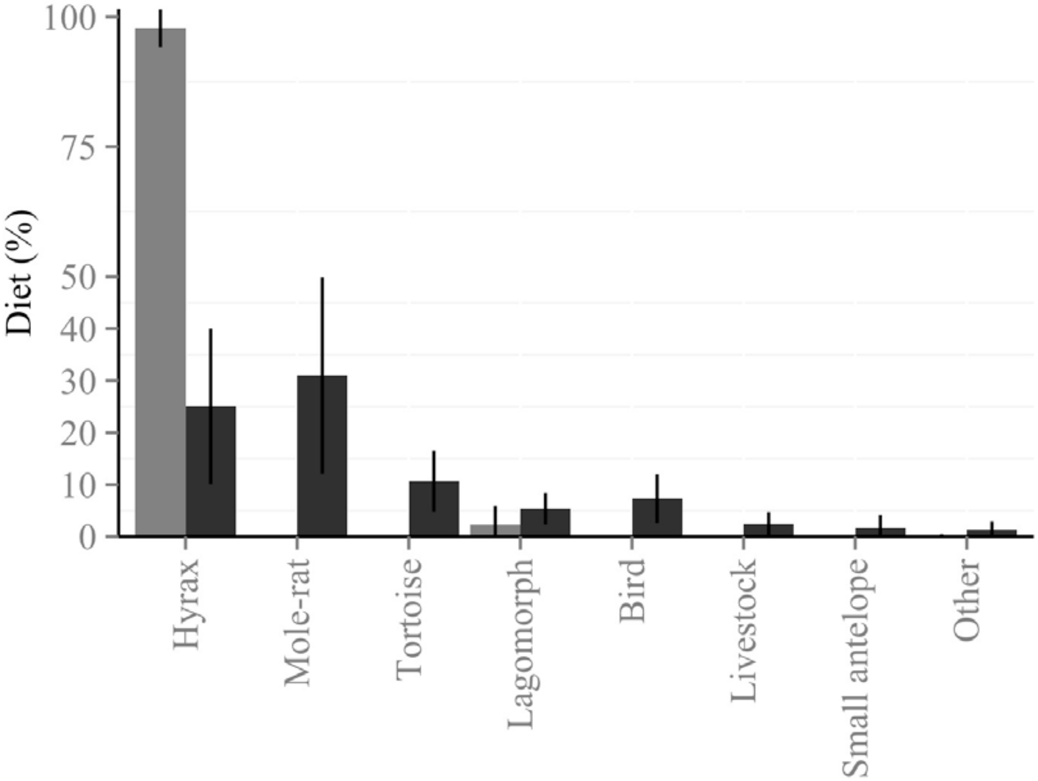

Figure 3. Diet composition (mean ±standard deviation) of Verreaux’s eagles in the Cederberg (grey, n=5) and the Sandveld (black, n=9). Determined by prey remains collections below nests, with correction factors introduced from camera studies.

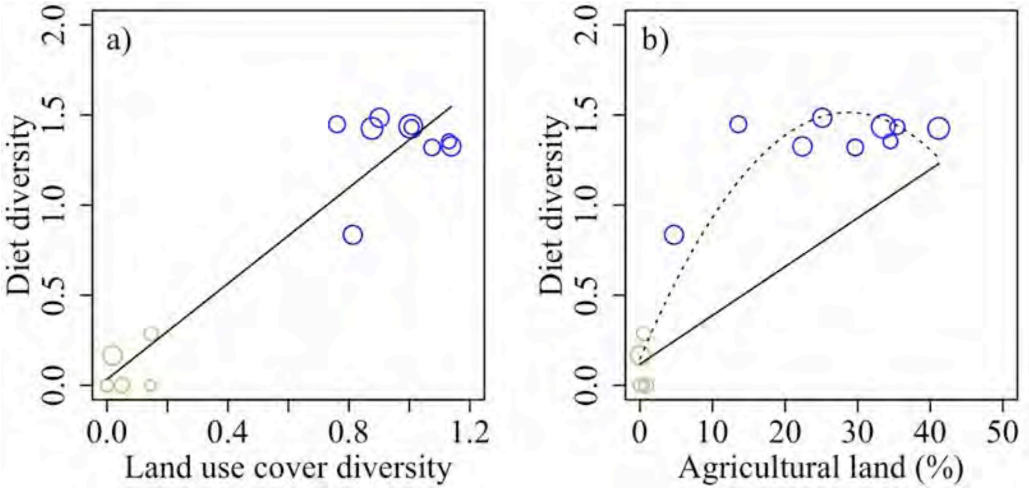

Figure 4. Diet diversity of Verreaux's eagles (ascertained by prey remains collections from nests (*n*=14) and corrected with indices from camera diet study) in the Sandveld (blue, *n*=9) and the Cederberg (green, *n*=5) in relation to a) land use cover diversity and b) the percentage of agriculturally converted habitat [no natural] within a 3 km buffer around the nest. Circle size represents the log of the minimum number of individuals in each prey remains collection. Solid lines represent linear regresions, dotted line is the significant quadratic term. Diet and land use cover diversity were determined with the Shannon diversity Index (*H*).

Prey proportions and agriculture

There was a negative relationship between the proportion of hyrax in the diet and the proportion of agricultural land in the nest buffers (Figure 5a, β±SE= -6.36±1.60, *t*= -3.97, *p*= <0.01). However, within the Sandveld this relationship was reversed so that, as the proportion of agriculture around the nest increased, the proportion of hyrax in the diet also increased and this was evident in the significant quadratic correlation (Appendix 4, Figure 5a, β±SE= 0.133±0.042, *t*= 3.15, *p*= <0.01). The proportion of mole-rats in the diet was positively correlated with agriculture (Figure 5b, β±SE= 1.16±0.22, *t*= 5.30, *p*<0.01). The proportion of tortoise in the diet was positively correlated with agricultural land cover overall (β±SE= 0.14±0.41, *t*= 2.77, *p*= >0.05). However, within the Sandveld the proportion of tortoise in the diet was lower in territories with a greater proportion of agriculture and this was reflected by the significant negative quadratic term (Appendix 4, Figure 5c, β±SE= -0.02±0.01, *t*= -2.61, *p*<0.05).

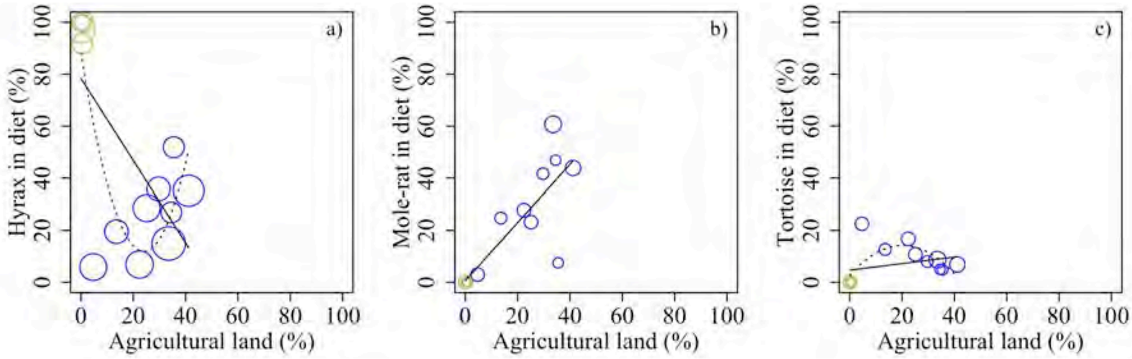

Figure 5. Percentage of prey in the diet of Verreaux's eagles (ascertained by prey remains collections from nests (*n*=14) and corrected with indices from camera diet study) in the Sandveld (blue, *n*=9) and the Cederberg (green, *n*=5) in relation to the percentage of agriculturally converted habitat [no natural] within a 3km buffer around the nest. Circle size represents the log of the minimum number of individuals in each prey remains collection. Solid lines are linear regression lines to show trends across both areas, and dotted lines show significant quadratic trends.

Diet and breeding performance

Breeding productivity was positively related to diet diversity (Figure 6a, β±SE= 1.35±0.56, *t*= 2.43, *p*= 0.03) and negatively related to the percentage of hyrax in the diet (Figure 6b, β±SE= -0.03±0.01, *t*= -2.76, *p*= 0.02). Nesting success was positively related to diet diversity (Figure 6c, β±SE= 1.60±0.69, *t*= 2.31, *p*= 0.04) and a corresponding tendency was shown by the negative relationship between nesting success and hyrax in the diet (Figure 6f, β±SE= -0.02±0.01, *t*= -2.01, *p*= 0.07). Relationships between diet and the breeding rate showed similar tendencies but they did not reach significance (Figures 6c and 6d).

Regional data from across southern Africa included 7059 prey items (MNI) and 1457 breeding records (Appendix 5), and similarly to our study areas revealed significantly lower breeding productivity with a larger proportion of hyrax in the diet (Figure 7b, β±SE= –0.02±0.01, *t*= –2.71, *p*= 0.04). Furthermore, tendencies for lower breeding rate (Figure 7d, β±–SE= –0.02±0.01, *t*= -1.94, *p*= 0.11) and nesting success (Figure 7f, β±SE= –0.008±0.004, *t*= –1.98, *p*= 0.11) with increasing hyrax in the diet were found, although these were non-significant. Similarly, some trends were present between the breeding performance and diet diversity (Figure 7c, 7e, 7a), where there was a tendency for greater breeding performance with increased diet diversity, reflecting the negative relationship between diet diversity and the proportion of hyrax in the diet, although these also did not reach significance.

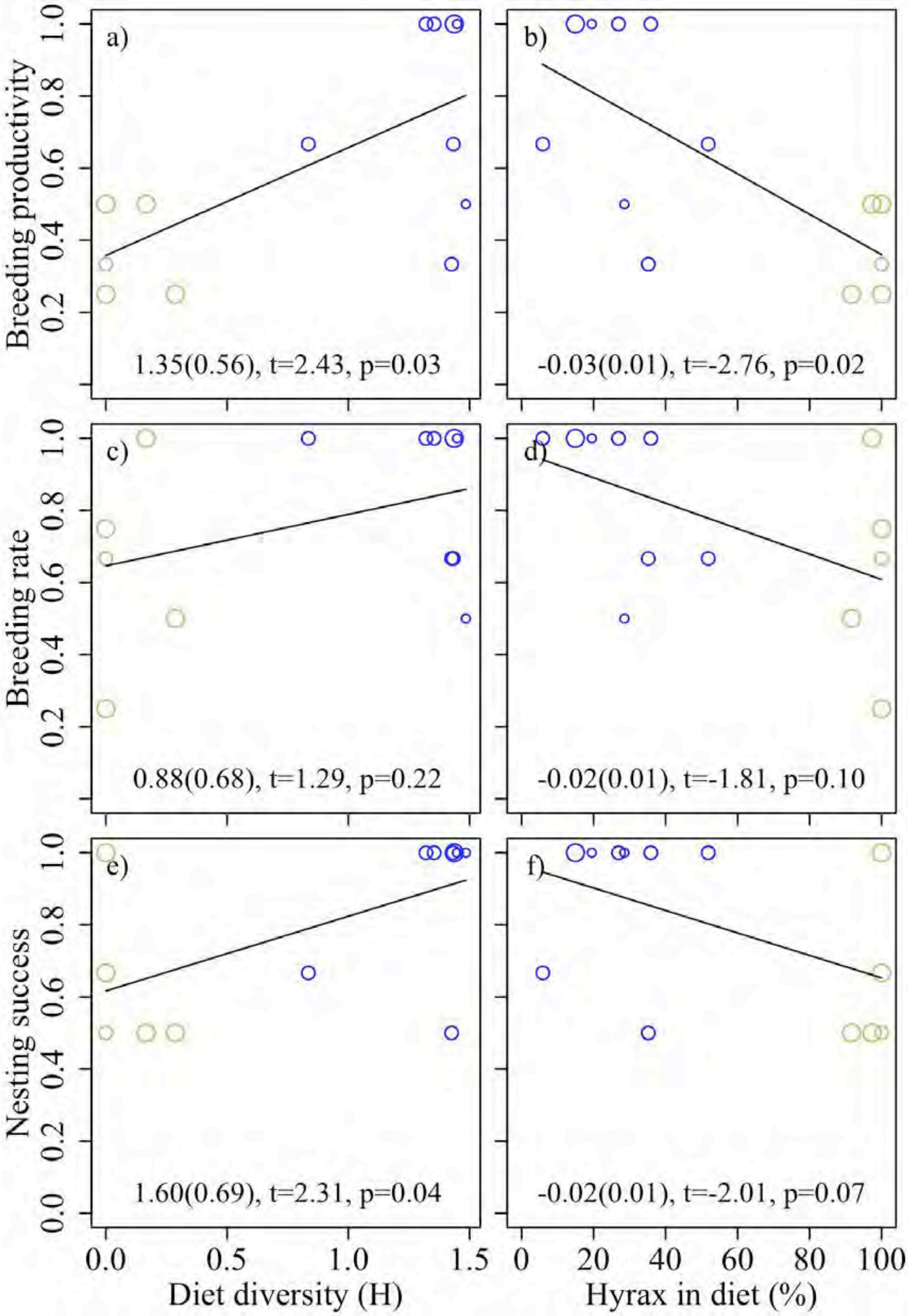

Figure 6. Breeding performance of Verreaux's eagles (between 2011−2014 for 2−4 years per nest, reflected by circle size) in the Sandveld (blue, *n*=9) and the Cederberg (green, *n*=5) in relation to a) diet diversity (Shannon's diversity Index, H) and b) the percentage of rock hyrax *Procavia capensis* in the diet. Solid lines show linear regression trends across both areas and GLM coefficients (Standard error), t-value, p-value results are given for this.

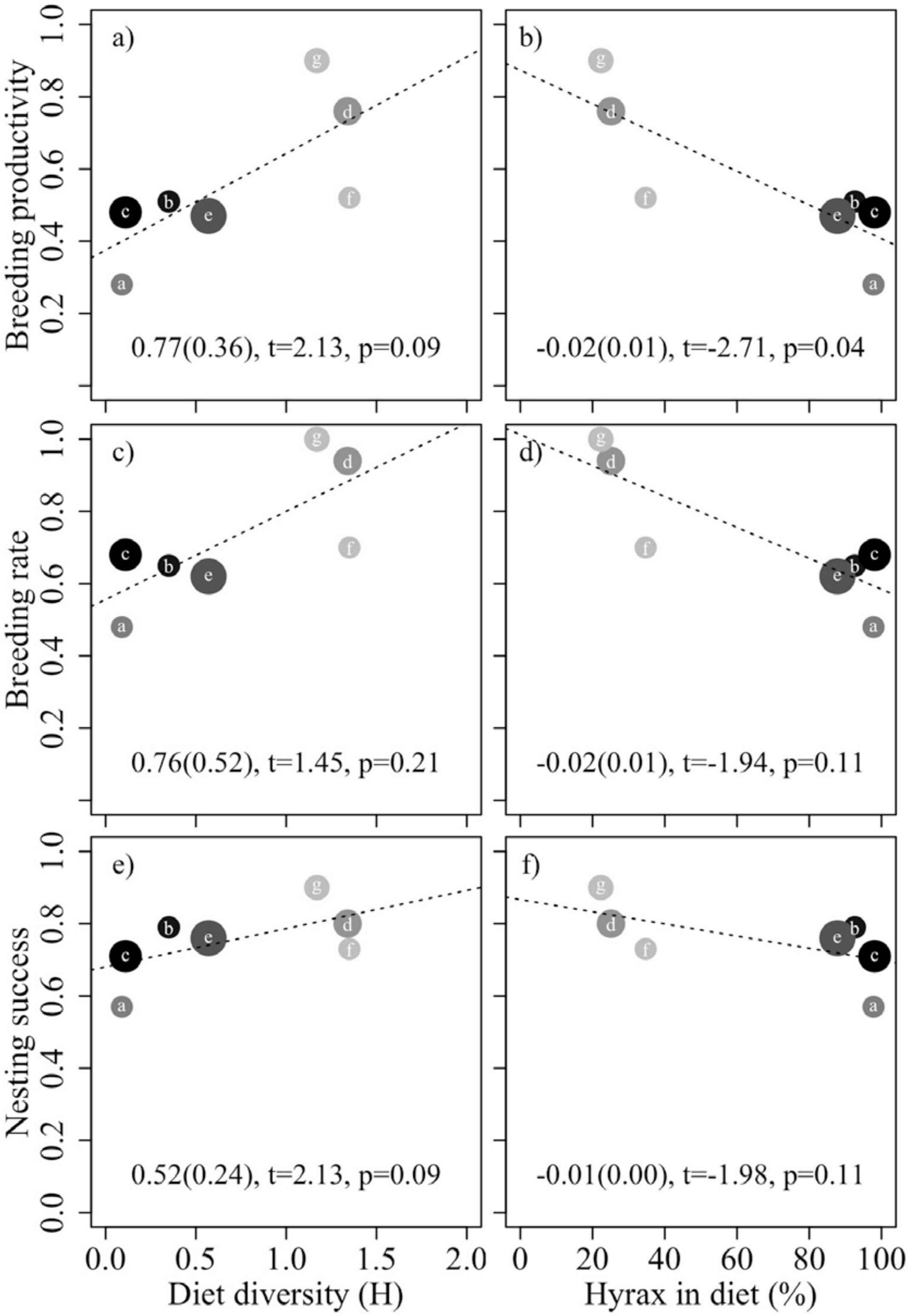

Figure 7. Diet diversity (Shannon's diversity Index, H) and percentage of hyrax in diet of Verreaux's eagles in relation to breeding parameters. Each point is weighted (size) by the log of the minimum number of prey items identified in each diet study and (grey-scale) the number of breeding events monitored, whereby darker points contain more breeding years. Dotted lines show regression trends and GLM coefficient (Standard error), t-value, p-value results are given. a) Cederberg (this study), b) former Transvaal (Tarboton and Allan 1984), c) Matopos (Gargett 1990), d) Sandveld (this study), e) Karoo (Davies 1994), f) Magaliesberg (Whittington-Jones et al., 2013, Padayachee unpub. data), g) Walter Sisulu (Symes and Kruger 2012).

Discussion

Despite long being thought of as a ‘highly specialised’ predator (Siegfried 1968), diet diversity of Verreaux’s eagles varies greatly between regions (Boshoff et al., 1991; this study). In this study, diet diversity and contributions of main prey types contrasted between the Cederberg and the Sandveld. There was evidence that this may have been related to prey availability within the territory, as indicated by relationships between diet and surrounding habitat composition. Rock hyrax formed the overwhelming majority of the eagles’ diet in the Cederberg, where the landscape is dominated by untransformed mountainous habitat suitable for hyraxes (Sale 1966). In the Sandveld, only 25 % of the diet comprised of hyrax and this was less than all previous multi-nest studies (49–98 % hyrax, Boshoff et al., 1991; Davies, 1994; Gargett, 1990; Tarboton and Allan, 1984). One exception to this is an isolated pair nesting in a suburban area with fragmented and degraded habitat, where hyrax made up 22 % of the diet (Symes and Kruger, 2012).

Diet diversity

The presence of mole-rats and tortoises in the diet of Sandveld eagles demonstrated generalist utilization of available resources. Mole-rats and tortoise were not available in the Cederberg and this is reflected by their absence in the diet of eagles in this area. Different levels of land transformation, from natural to completely transformed for agriculture, create a mosaic of habitats which provide different niches and support a greater variation of prey species (Benton et al. 2003, Tews et al. 2004). This is likely to drive the positive relationship between land use cover diversity and diet diversity. The positive correlation between diet diversity and agricultural land cover also reflects the provision or increase in availability of suitable alternative prey species sometimes associated with productive agricultural land use (Ogada 2009, Kross et al. 2013). However, the quadratic relationship indicated that at higher levels of agricultural conversion diet diversity did not continue to increase. Although our data only reached a plateau, this prediction supports the idea of a threshold effect, whereby further agricultural conversion may result in a decline of resource diversity which could incur negative ecological impacts (Flynn et al. 2009, Magioli et al. 2015). This pattern has been recorded in saw-whet owls *Aegolius acadicus* where low levels of habitat loss and fragmentation can be beneficial, potentially by increasing prey abundance but further habitat loss reduces foraging efficiency and reproductive success demonstrating the ultimately negative impacts of unrestrained intensive land use change (Hinam and St Clair 2008).

Prey proportions and agriculture

There was evidence for a relationship between prey availability and habitat availability (Ontiveros et al. 2005, Palma et al. 2006, Romanowski and Zmihorski 2008). This relationship was apparent in the correlation between the proportions of the three predominant prey groups (mole-rats, hyrax, tortoise) and the proportion of agriculturally converted land around the nest site. Mole-rats were the most frequent item in the diet of eagles in the Sandveld, and their importance in the diet increased with increasing amounts of agricultural land surrounding a territory. Virani (1999) found that mole-rat density was positively correlated with grass height in Kenya and suggested that this could be related to spatiotemporal increases in food availability for mole-rats. Other variables which are likely to interact and affect mole-rat abundance include rainfall, grazing regimes and irrigated cultivation (Virani 1999). Rainfall and irrigated cultivation are both likely to increase soil softness and primary productivity, which is conducive to mole-rat activity. Grazing decreases vegetation cover, increasing prey visibility and accessibility to avian predators, which ultimately reduces mole-rat density (Faulkes et al. 1997, Virani 1999). In the Sandveld, irrigated potato agriculture (Franke et al. 2011) is likely to enhance mole-rat abundance, while intermittent grazing regimes (Franke et al. 2011) could increase their availability to eagles. These factors could be a mechanism for the observed positive relationship between the proportion of agriculturally converted land within a territory and the proportion of mole-rats in the diet.

The trend for an increase in the proportion of tortoise in the diet with an increase in agriculture is largely due to their complete absence in the diet of eagles in the Cederberg, because of the avoidance of mountainous Fynbos habitat by angulate tortoises (du Toit 2015). However, within the Sandveld, there were fewer tortoises in the diet in territories with more agricultural land use and this was reflected in the significant quadratic trend. Although angulate tortoises occupy a wide variety of habitat types (Joshua et al. 2010), their preference for vegetation cover (Branch 1984) probably reduces their abundance in highly transformed landscapes and likely explains this negative relationship in the Sandveld.

Overall, the proportion of hyrax in the diet decreased with increasing agriculture. The high percentage of hyrax in the diet in predominately ‘natural’ territories is either the result of their high abundance or a relatively low abundance of alternative prey species. Surprisingly, the within the Sandveld the proportion of hyrax in the diet increased in territories with a greater proportion of agriculturally developed land around the nest. These contrasting scenarios were reflected in the significant quadratic trend. Although rock hyrax are usually associated with habitat providing refuges from predation, they have generalist feeding behaviour and have been considered an agricultural pest in parts of their range (Lensing 1983, Barry et al. 2014). Therefore, it is plausible that agricultural transformation in the Sandveld increases food resources for this species and can result in increased hyrax abundance. Alternatively, prey accessibility and encounter rates can depend upon habitat (Terraube and Arroyo 2011) and therefore agricultural transformation might leave hyraxes more exposed, facilitating accessibility and the ease of capture. To understand this relationship fully it will be important to quantify prey abundance in different habitats taking into account factors including rock refugia and grazing availability to hyrax in future research.

Diet and breeding performance

In the case of dietary specialists, diet diversification is expected to cause reduced breeding performance, whereby lower numbers of preferred prey type or broader dietary niches are thought to reduce hunting success (Katzner et al. 2005, Terraube et al. 2011, 2014) and lead to fewer breeding attempts (Steenhof et al. 1997) or reduced nesting success (Katzner et al. 2005, Arroyo and Garcia 2006, Sundell et al. 2014). We found no evidence for such an effect in our study. In fact there was support for the opposite effect, both within our own study and between different regions. Firstly, the diet was more diverse and contained a lower proportion of hyrax in the Sandveld than the Cederberg, despite considerably greater reproductive output in the Sandveld. When examining these relationships in more depth we found positive correlations between breeding productivity and diet diversity and an inverse relationship with the proportion of hyrax in the diet, similar to that found in systems characterized by high spatial or temporal variability in prey availability (Margalida *et al.*, 2012). In single-young-rearing species breeding productivity is determined by the proportion of pairs that initiate breeding (breeding rate) and the number of these which are successful (nesting success); brood size being irrelevant. We found some evidence that nesting success, rather than the breeding rate, was more strongly affected by diet diversity. Nesting success showed a significant positive relationship with diet diversity and a negative relationship with the percentage of hyrax in the diet. This may be incidental owing to the underlying correlation between these two diet variables. Although similar relationships were present in our study between breeding rate and these dietary components they did not reach the same significance level. Imperial eagles *Aquila heliaca* show regional differences in nesting success, which are thought to be driven by variation in diet diversity, while the decision to initiate breeding is independent (Katzner et al. 2005). In our study, greater diet diversity is probably important in allowing adequate chick provisioning resulting in better nesting success (Olsen and Olsen 1989). While the breeding rate could be further affected by other factors, including age (Sánchez-Zapata et al. 2000) and mate changes (Margalida et al. 2003).

Biases between different methods of diet analysis (Lewis et al. 2004, Margalida et al. 2005, Sánchez et al. 2008) used in other studies and also supplementary feeding during some years at Walter Sisulu National Botanic Gardens (Symes and Kruger 2012) may present some limitations to the regional analysis. Nonetheless, this does not negate the fact that eagles in transformed environments (agricultural: Sandveld and suburban: Walter Sisulu) consumed a smaller proportion of hyrax, had a wider diet breadth and maintained relatively high breeding performance compared to other areas. Although these trends were largely not statistically significant, partly due to the weighting factors we introduced in attempt to minimize method biases, they were contrary to expectation and fitted with our localized results. This further supports the notion that some top predators can successfully adapt to changes in resources availability.

Conclusions

Although we are unable to determine if i) diet diversification has occurred in the Sandveld in response to agricultural transformation or ii) this area has always supported greater prey diversity, eagles breeding in this area successfully utilize the currently diverse availability of resources. Our findings are in agreement with a growing body of research that suggests diet generalism does not necessarily result in reduced reproductive output in raptors. Golden eagles *Aquila chrysaetos* (Whitfield et al. 2009), Egyptian vultures *Neophron percnopterus* (Margalida *et al.*, 2012) and Eurasian eagle-owls *Bubo bubo* (Penteriani, Gallardo & Roche, 2002) are other raptors which have shown positive relationships between breeding performance and diet diversity. There is evidence across multiple taxa that mean fitness, particularly as measured by longevity and reproductive capacity, can be higher in organisms with a mixed diet than a single-species one, due to the easier fulfilment of nutritional requirements (Senior et al. 2015).

Our findings support the view that diet composition in raptors is determined by local prey abundance and/or availability (Graham et al. 1995, Salamolard et al. 2000, Amar et al. 2004, Ontiveros et al. 2005, Terraube and Arroyo 2011, Cardador et al. 2012) and indicate that Verreaux's eagles can successfully adopt a generalist foraging strategy. The general view of this species being a hyrax specialist is likely to be due largely to their morphological adaptations to mountainous habitat and tendency to nest on cliffs, which often ties their distribution to areas where hyrax are common or abundant (Sale 1966, Simmons 2005). In reality, there is a probably a continuum of traits from generalist to specialist and within a species range individuals can adapt differently to the prevailing resources (Salamolard et al. 2000, Terraube and Arroyo 2011). On review, prey availability, rather than foraging behaviour, is likely to be the main predictor of diet composition in this species. These findings have significant implications for predicting the effects of changes in land use, which is a primary driver of biodiversity loss globally. Adaptation to changing resources is evidently possible but threshold effects are likely to be of significance to many species worldwide. This research also supports the emerging view that agriculturally developed areas can maintain a high conservation value when managed effectively to maintain habitat heterogeneity (Norris 2008).

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Appendices

Appendix 1. Summary of camera data recorded at Verreaux's eagle nests in the Cederberg and the Sandveld.

Nest ID	Area	Year	Camera make	Set up	Frame interval	Start date	End date	Photos (n)	Reason for end	Prey deliveries (n)
1	Cederberg	2012	Scoutguard 560	Motion-sensing	na	11-Jul	22-Jul	302	nest failed	3
2	Cederberg	2012	Scoutguard 560	Motion-sensing	na	14-Jul	15-Jul	32	camera failed	1
1	Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 minute	29-Jun	25-Sep	18576	fledged	57
2	Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 minute	22-Jul	13-Aug	5610	chick died	15
5	Sandveld	2012	Scoutguard 560	Motion-sensing	na	05-Jul	20-Jul	475	camera failed	0
4	Sandveld	2012	Scoutguard 560	Motion-sensing	na	06-Jul	26-Jul	520	camera failed	10
3	Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 minute	10-Jul	07-Sep	5268	camera failed	27
4	Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 minute	05-Jul	11-Jul	1468	camera failed	7
5	Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 minute	04-Jul	26-Aug	5287	camera failed	31
									Cederberg	76
									Sandveld	75
									TOTAL	151

Appendix 2. Summary of dietary data collected at Verreaux's eagle nests in the Sandveld (n=9) and the Cederberg (n=5) by means of prey remains collections, with adjusted percentage of each prey group corrected by correction factors devised from camera data. Diet and habitat diversity were determined with the Shannon diversity Index (*H*).

Area		**Sandveld**										**Cederberg**					
Nest		1	2	3	4	5	6	7	8	9	**Mean ±SD**	10	11	12	13	14	**Mean ±SD**
Prey remains collection (MNI)	Hyrax	14	4	20	29	14	8	44	7	5	**16.1 ±13.2**	22	11	73	19	26	**30.2 ±24.5**
	Mole-rats	1	1	8	58	8	5	27	6	10	**13.8 ±18.3**	0	0	0	0	0	**0 ±0**
	Tortoise	5	59	29	65	12	20	33	5	47	**30.6 ±22.5**	0	0	0	0	0	**0 ±0**
	Birds	2	2	1	20	3	2	3	4	4	**4.6 ±5.9**	0	0	0	0	0	**0 ±0**
	Small Antelopes	1	0	5	5	0	0	2	0	0	**1.4 ±2.1**	0	0	0	0	0	**0 ±0**
	Lagomorphs	1	1	4	10	1	6	12	4	2	**4.6 ±4.1**	2	0	1	0	0	**0.6 ±0.9**
	Livestock	2	1	3	5	1	0	2	0	2	**1.8 ±1.6**	0	0	0	0	0	**0 ±0**
	Other	1	0	0	2	0	0	2	0	3	**0.9 ±1.2**	0	0	1	0	0	**0.2 ±0.4**
	TOTAL	27	68	70	194	39	41	125	26	73	**73.7 ±54.6**	24	11	75	19	26	**31 ±25.3**
Corrected prey in diet (%)	Hyrax	51.9	5.9	28.6	14.9	35.9	19.5	35.2	26.9	6.8	**25.0 ±14.9**	91.7	100.0	97.3	100.0	100.0	**97.8 ±3.6**
	Mole-rats	7.5	3.0	23.2	60.7	41.6	24.8	43.8	46.8	27.8	**31.0 ±18.8**	0.0	0.0	0.0	0.0	0.0	**0 ±0**
	Tortoise	4.8	22.6	10.8	8.7	8.0	12.7	6.9	5.0	16.7	**10.6 ±5.8**	0.0	0.0	0.0	0.0	0.0	**0 ±0**
	Birds	7.4	2.9	1.4	12.4	7.7	12.3	2.4	14.0	5.5	**7.3 ±4.6**	0.0	0.0	0.0	0.0	0.0	**0 ±0**
	Small Antelopes	3.7	0.0	7.1	2.7	0.0	0.0	1.6	0.0	0.0	**1.6 ±2.4**	0.0	0.0	0.0	0.0	0.0	**0 ±0**
	Lagomorphs	3.7	1.5	5.7	5.3	2.6	8.2	9.6	9.3	2.7	**5.4 ±3**	8.3	0.0	2.9	0.0	0.0	**2.2 ±3.6**
	Livestock	7.4	1.5	4.3	2.2	2.6	0.0	1.6	0.0	2.7	**2.4 ±2.2**	0.0	0.0	0.0	0.0	0.0	**0 ±0**
	Other	3.7	0.0	0.0	0.9	0.0	1.4	1.6	0.0	4.1	**1.2 ±1.6**	0.0	0.0	0.7	0.0	0.0	**0.1 ±0.3**
Diet diversity (H)		1.43	0.84	1.48	1.44	1.32	1.45	1.43	1.35	1.33	**1.34 ±0.18**	0.29	0.00	0.17	0.00	0.00	**0.09 ±0.11**
Habitat availability (%)	Natural	54.0	71.0	65.5	55.5	52.5	75.5	54.1	47.1	19.1	**54.9 ±16.4**	97.3	97.3	99.8	100.0	99.1	**98.7 ±1.3**
	Near Natural	4.1	2.6	2.6	3.6	2.3	1.1	2.3	4.1	5.1	**3.1 ±1.2**	0.4	0.1	0.2	0.0	0.0	**0.1 ±0.2**
	Degraded	6.4	21.8	6.8	7.3	15.5	9.8	2.5	14.3	53.4	**15.3 ±15.4**	1.8	2.1	0.0	0.0	0.0	**0.8 ±1.0**
	No Natural	35.5	4.7	25.1	33.5	29.7	13.6	41.2	34.5	22.4	**26.7 ±11.6**	0.5	0.5	0.0	0.0	0.8	**0.4 ±0.4**
Habitat diversity (H)		1.01	0.81	0.90	1.00	1.08	0.76	0.88	1.13	1.14	**0.96 ±0.13**	0.15	0.14	0.02	0.00	0.05	**0.07 ±0.06**
Years monitored		3	3	2	4	3	2	3	3	NA	**2.9 ±0.6**	4	4	4	3	4	**3.8 ±0.4**
Mean breeding	Productivity	0.67	0.67	0.50	1.00	1.00	1.00	0.33	1.00	NA	**0.77 ±0.26**	0.25	0.50	0.50	0.33	0.25	**0.36 ±0.12**
	Success	1.00	0.67	1.00	1.00	1.00	1.00	0.50	1.00	NA	**0.89 ±0.19**	0.50	0.67	0.50	0.50	1.00	**0.63 ±0.21**
	Rate	0.67	1.00	0.50	1.00	1.00	1.00	0.67	1.00	NA	**0.85 ±0.2**	0.50	0.75	1.00	0.67	0.25	**0.63 ±0.28**

Appendix 3. Results from GLMs comparing model fit for diet diversity of Verreaux’s eagles described by land use cover diversity (H.l-use) and the proportion on agricutral land (No.nat) within a 3 km of the nest and its quadratic term. Other column abbreviations: df, degrees of freedom; LogLik, Logit link; ΔAICc, change in AICc relative to the highest ranked model; ωi, AICc weight; ER, evidence ratio.

Response variable	Explanatory variables	df	logLik	AIC_c	ΔAIC_c	ω_i	ER
Diet diversity	H.l-use	3	2.61	3.20	0.00	0.50	-
	H.l-use + H.l-use ^2	4	4.62	3.20	0.03	0.49	1.01
Diet diversity	No.nat + no.nat^2	4	5.28	1.90	0.00	1.00	-
	No.nat	3	-2.68	13.80	11.88	0.00	332.33

Appendix 4. Results from GLMs comparing model fit for the proportion of main prey in Verreaux’s eagles diet described by the proportion of no natural habitat (No.nat) within a 3 km buffer of the nest and its quadratic term. Other column abbreviations: df, degrees of freedom; LogLik, Logit link; ΔAICc, change in AICc relative to the highest ranked model; ωi, AICc weight; ER, evidence ratio.

Response variable	Explanatory variables	df	logLik	AIC_c	ΔAIC_c	ω_i	ER
% hyrax	No.nat + no.nat^2	4	-62.08	136.60	0.00	0.90	-
	No.nat	3	-66.59	141.60	4.97	0.08	12.00
% mole-rat	No.nat	3	-54.33	117.10	0.00	0.74	-
	No.nat + no.nat^2	4	-54.02	120.50	3.42	0.14	5.51
% tortoise	No.nat + no.nat^2	4	-43.07	98.60	0.00	0.42	-
	No.nat	3	-46.80	98.70	0.10	0.40	1.05

Appendix 5. Summary of data used in regional analysis of diet correlations with breeding parameters. MNI= Minimum Number of Individual Prey Items. H= Shannon's index for diet diversity. Breeding data: Rate, success and productivity are given as mean values with (SD) where possible.

	Diet data				Breeding data					
Study	MNI	H	Hyrax (%)	Source	Rate	Success	Productivity	Events	Years	Source
Cederberg	155	0.09	97.8		0.48 (0.14)	0.57 (0.13)	0.28 (0.13)	64	4	
Sandveld	663	1.34	25.1		0.94 (0.07)	0.8 (0.05)	0.76 (0.05)	48	4	
Karoo	3823	0.57	87.8		0.62 (0.11)	0.76 (0.11)	0.47 (0.12)	84	4	
Matopos	1748	0.11	98.1		0.68 (0.17)	0.71 (0.14)	0.48 (0.12)	1101	26	
Magaliesberg	158	1.35	34.7		0.70 (0.26)	0.73 (0.12)	0.52 (0.23)	28	3	
Transvaal	176	0.35	92.6		0.65	0.79	0.51	111	5	
Walter Sisulu	336	1.17	22.3		1	0.9	0.9	21	21	

[1] This study; [2] Davies 1994; [3] Gargett1990; [4] Padayachee unpub.; [5] Tarboton and Allan 1984; [6] Symes and Kruger 2012; [7] Chapter 2; [8] Whittington-Jones et al. 2013 and unpub.; [9] Roodekrans Project 2015.

Chapter 4

Ranging behaviour and foraging patterns of Verreaux’s eagles in areas of contrasting land use

Abstract

The Verreaux's eagle *Aquila verreauxii* has experienced loss of natural habitat to agricultural intensification within parts of its range. This is expected to affect ranging behaviour by increasing the effort associated with trips away from the nest or forcing eagles to select for remaining patches of natural habitat. We used GPS tracking technology to obtain spatially (within 3 m) and temporally (*c.* 3 min) high-resolution movement data on a small sample of these birds (n=5). To understand space use, the first home range estimate for this species derived from GPS data are presented. Following this, we examine temporal (timing, duration and speed) and spatial (total path length and maximum distance from nests) patterns of trips away from the nest. Comparison of movement patterns between birds tracked in the Cederberg (natural habitat) and the Sandveld (agriculturally transformed) showed that temporal and spatial measures of trip parameters were not greater in the agriculturally transformed area. However, there was a narrower peak of activity around midday in the Sandveld than the Cederberg, possibly due to topographic differences driving dissimilar lift availability. Furthermore, a habitat selection analysis in the Sandveld found that eagles selected for near-natural and degraded habitat over natural or completely modified areas. Habitat transformation does not appear to have extended eagles in the Sandveld beyond the routine flight behaviour of eagles in the Cederberg, in terms of trip duration or distances travelled. Furthermore, preferential use of partially degraded habitat indicates that Sandveld birds might be adjusting foraging patterns to exploit new opportunities presented by land use change.

Introduction

Changes in land use can have profound impacts on habitat structure and composition, with extreme repercussions for local biota (Ryall and Fahrig 2006, Haines-Young 2009, Gonthier et al. 2014). The current rate of anthropogenic habitat change is unprecedented (Lambin et al. 2001, Britton 2013) and an understanding of the impacts of these changes is vital for the conservation of biodiversity (Fahrig et al. 2011). How an organism responds to changes in the environment depends on its ability to adapt and exploit changes in resource availability. As a result, agricultural intensification tends to favour more common, generalist species while rarer specialist species are usually negatively impacted (Mangnall and Crowe 2003, Ryall and Fahrig 2006). Specialist predators are mostly restricted to feeding on a limited number of prey types and are therefore vulnerable to environmental changes affecting prey availability. In contrast, generalist predators exploit a variety of prey species and can therefore adequately adapt their diet (Terraube et al. 2011). Models predict that generalists might actually benefit from fragmentation and land use change because they might be able to exploit new resources that arise (Swihart et al. 2001, Ewers and Didham 2006). For example, the dramatic increase in urban populations of red foxes *Vulpes vulpes* in European cities demonstrates the ability of a generalist predator to adapt to and benefit from anthropogenic resources (Deplazes et al. 2004, Baker and Harris 2007). Likewise, the ability of avian predators to increase in population size or range in response to the availability of a new resource has been demonstrated by the expansion of northern goshawks *Accipiter gentilis* and black sparrowhawks *Accipiter melanoleucus* into urban areas (Rutz 2008, Martin et al. 2014), and the increase in abundance of marsh harriers *Circus aeruginosus* in response to agricultural development (Cardador et al. 2011). Nevertheless, declines in raptor populations have been seen worldwide (Ferrer and Negro 2004, Balbontin 2005, Cuthbert et al. 2006, Thiollay 2007, Burfield 2008). Within South Africa, raptors and scavengers appear to have undergone the greatest losses among avian guilds in agriculturally dominated habitats (Child et al. 2009, Loftie-Eaton 2014). The depletion of habitats supporting traditional prey resources is considered to be one of the primary drivers for these declines (Amar and Redpath 2005, Butet et al. 2010).

The ranging behaviour of a species is often correlated with food availability within the home range (Corp et al. 1997, Dussault et al. 2005, Pérez-García et al. 2013, Watson et al. 2014) and while on migration (García-Ripollés et al. 2010, Trierweiler et al. 2013). Declines in prey availability invariably result in increased hunting effort in avian predators. Greater strike rates at prey have been noted in pallid harriers *Circus macrourus* in years of low vole abundance (Terraube et al. 2011) and longer foraging trips, in terms of both duration and distance travelled, have been associated with reduced prey availability in African penguins *Spheniscus demersus* (Petersen et al. 2006). As such, changes in foraging behaviour might even be an early warning signal of a stressed species.

The Verreaux's eagle *Aquila verreauxii* is a large, territorial raptor which captures most of its prey in open habitats and has been documented to be a specialist hunter of hyraxes *Procavia capensis* and *Heterohyrax brucei* when available (Gargett 1977, Steyn 1982, Davies 1994), with regional variations in diet associated with prey availability (Chapter 3; Boshoff et al. 1991). It is a year-round resident, and although their nesting sites on steep cliffs are relatively immune to disturbance, their dependency on a localized prey base and their usually specialized diet could leave them susceptible to the knock-on effects of land use change (Chiweshe 2007). Globally, the Verreaux's eagle is listed as a Species of Least Concern given its extensive range throughout much of eastern and southern Africa (BirdLife International 2014). However, within South Africa the species has recently been classified as "Vulnerable" (Taylor 2015) due to decreases in range and abundance recorded by the Southern African Bird Atlas Projects (Loftie-Eaton 2014). The Verreaux's eagle is considered vulnerable to increasing human pressures (Gargett 1990, Simmons et al. 2007, Symes and Kruger 2012). For example, decreases in the number of resident pairs on the Cape Peninsula, South Africa, have been related to the loss of prey resources and disturbance caused by urbanization (Jenkins and van Zyl 2005, Simmons et al. 2007). A loss of traditional prey resources has also been related to a diet shift, reduced breeding productivity and the need for supplementary feeding of a pair on the outskirts of Johannesburg (Symes and Kruger 2012). On communal lands in Zimbabwe, nest abandonment and reduced breeding productivity have been associated with reduced hyrax numbers and increased disturbance (Gargett 1990). Hyraxes feed on a wide range of plants, meaning they can inhabit a range of environments (Hoeck 1975, Olds and Shoshani 1982, Chase et al. 2012). However, they are dependent on rocky refuges to provide protection from predators (Davies 1994, Kotler et al. 1999) which is the primary limitation in their distribution (Chase et al. 2012).

Despite considerable historical research on many aspects of the Verreaux's eagle ecology (Rowe 1947, Siegfried 1968, Vernon 1972, Allan 1988, Boshoff and Palmer 1988, Brown 1988, Gargett 1990, Davies 1994, Goodwin 2000), little is known about the ranging behaviour, foraging patterns and habitat selection of this species, with almost no information available on behaviour away from the nest site (but see Davies 1994). Recent advances in GPS tracking technologies have enabled data collection on these aspects for a number of other raptor species (Soutullo et al. 2008, Shepard et al. 2011, Pérez-García et al. 2013). On-going technological developments in this field are providing progressively higher-resolution data giving unprecedented insights into ranging behaviour away from the nest (Kays et al. 2015). These advances in the temporal and spatial resolution of data have also been followed by developments of analytical methods. Analyses of home range sizes using kernel densities (Worton 1989) have come under particular scrutiny regarding the inherent temporal and spatial autocorrelation in high-resolution data sets (Hemson et al. 2005, Byrne et al. 2014). However, the dynamic Brownian Bridge Movement Model (dBBMM) provides an alternative analytical framework to quantify the utilization distribution of an animal based on the GPS path rather than independent positions and is therefore well suited to high-resolution data sets (Kranstauber et al. 2012). In addition to enhancing our knowledge of ranging behaviour and the likely impacts of agricultural transformation (Cardador and Manosa 2011), these types of data can be useful for understanding the possible impacts of energy infrastructure developments, which are increasing throughout sub-Saharan Africa (Rushworth and Krüger 2014, Watson et al. 2014, Reid et al. 2015).

In the Western Cape Province, South Africa, large areas of natural habitat have been transformed by agriculture (Fairbanks et al. 2000, Rouget et al. 2003). Studies from other, similarly affected habitats suggest that such transformation is likely to have had a negative impact on the distribution and/or abundance of small animals that typically feature in the diets of raptorial birds (Butet and Leroux 2001, Moulton et al. 2005, Heroldová et al. 2007, Flynn et al. 2009). Hence, Verreaux's eagles breeding in areas of intensive agriculture may have experienced some depletion of their natural prey base, and altered their ranging behaviour accordingly in order to meet their food requirements (Terraube et al. 2011, Pérez-García et al. 2013, Trierweiler et al. 2013, Watson et al. 2014). This study compares aspects of Verreaux's eagle foraging behaviour between two locations: the Sandveld, which is an agriculturally developed area; and the Cederberg Mountains, which are relatively pristine. Using GPS tracking technology, we firstly describe the home ranges and their core use by territorial adult Verreaux's eagles. Secondly, we investigate detailed movement patterns, specifically exploring the temporal (trip timing, duration and speed) and spatial (total path length and maximum distance from nest) patterns of trips away from the nest. Thirdly, for birds tracked in the more heterogeneous Sandveld habitat, we explore habitat selection in relation to land use type and topography. Following our assumption of reduced prey availability related to agricultural transformation, we hypothesize that eagles in the Sandveld make trips away from the nest of greater distance (total path length or distance from the nest), duration, or speed, indicative of greater energetic requirements, than eagles in the Cederberg. Furthermore, in the habitat selection analysis, we expect preferential use of remaining patches of natural vegetation to exploit restricted prey resources.

Methods

Study area

This study was conducted in the Cederberg and Sandveld regions in the Western Cape Province, South Africa. Both areas are located within the Cape Floristic Region, which is recognized as a biodiversity hotspot (Cowling et al. 2003). Land use and conservation protection are contrasting between the areas. The Cederberg falls largely under the management of CapeNature, the statutory conservation body of the province, within this protected area no recent land use change has occurred and there is limited human presence (Maree and Vromans 2010). The vegetation type is predominantly mountain Fynbos. The mean annual rainfall (2004–2014 Algeria weather station 32.374S, 19.058E) is 706 ±174 mm (CapeNature 2015). Peak rainfall occurs from May to August (Saul et al. 2011) during the austral winter and coincides with the breeding season of the eagles. Elevation ranges from 150 m to 2027 m. (SAEON 2014). In contrast, the Sandveld region has little formal conservation protection and agricultural expansion has caused loss of endemic vegetation and its associated biota (Low et al. 2004). Following the installation of electricity distribution infrastructure in the 1980s, centre-pivot cultivation (allowing for large scale irrigation) increased dramatically (Heydenrych 1993) and, by the first decade of the 21st century the Sandveld was one of the most important potato production areas in South Africa (Franke et al. 2011). Approximately 50–70 % of the area has had its original vegetation removed (Myers et al. 2000, Archer et al. 2009, Franke et al. 2011) and it is characterized by a mosaic of habitats ranging from potato circles (with no remaining natural habitat) to natural patches of pristine vegetation. There is comparatively low mean annual rainfall, 298 mm (1990–2008 Graafwater weather station 32.155S, 18.603E) (Franke et al. 2011) and rainfall also occurs predominantly during the austral winter months. Within the Sandveld, the topography is also generally much flatter, with elevation ranging from sea level up to about 1000 m.

GPS tracking

Adult Verreaux’s eagles were caught using Bal-chatri traps (Berger and Mueller 1959) (n=4) or Dho Gaza nets (Bloom et al. 1992) (n=1) close to known nest sites, before breeding (n=3) or during the chick rearing stage (n=2). Trapping was done between April 2012 and April 2013 in the Cederberg (n=2) and Sandveld (n=3) (Table 1). Although attempts were made to trap at similarly spaced neighbouring nests in each area, final territory selection was based on accessibility and trapping success. GPS loggers were attached using a back-pack style harness (Buehler et al. 1995) made from 0.45” tubular Teflon Ribbon® (Bally Ribbon Mills, Pennsylvania).

Table 1. Summary of all Verreaux's eagles tracked and the GPS fixes obtained.

Eagle id	Study area	Sex	Tag date	End track	Eagle fate	*n* total fixes
721	Cederberg	male	06/04/2012	10/07/2013	ousted	117839
722	Cederberg	male	26/09/2012	11/05/2013	unknown	393926
723	Sandveld	male	25/08/2012	11/09/2012	died	31144
726	Sandveld	female	10/04/2013	18/05/2013	killed in territorial dispute	14643
727	Sandveld	female	13/04/2013	18/05/2013	killed in territorial dispute	10538

We used University of Amsterdam Bird Tracking System (UvA-BiTS) GPS loggers. UvA-BiTS loggers were developed and manufactured specifically for fine-scale monitoring of avian movements and behaviour (Bouten et al. 2013). The loggers weighed 44 g and were attached to an aluminium baseplate to aid in their fitting, bringing the total weight of the logger to 55 g (1.7 % of the body weight of the lightest eagle tagged). Loggers recorded the 3D locations up to every three seconds during optimal battery conditions. However, recording frequency was dependent on solar charge and we aimed to collect data every two minutes in daylight hours, with hourly recordings during the night (usually 19:00−07:00 SA Standard Time) and higher resolution data for limited segments of the day. Data recorded by the loggers were downloaded in the breeding area through a ground-based antenna network or a portable base-station (Bouten et al. 2013).

All tagged adult eagles were one of a resident breeding pair when trapped and all tagged eagles were from different territories. However, none of our tracked eagles completed a full year within their initial home range (see Discussion). We excluded data collected on the day of tagging from our analyses since it might not reflect normal daily activity. Days where more than 2.5 hours of data were missing during daylight hours were also excluded. Following this, the maximum number of tracking days available per eagle for all individuals was 22 days. Therefore the data analysed in each case were limited to a subset of 22 days for each eagle to allow for more direct comparisons of behaviour. Individual subsets were selected on the basis of the most comparable season available for each eagle (April−May, pre-breeding *n*=4). Concurrent data were not available for one eagle in the Sandveld (Eagle id 723, Table 2), which was only tracked while chick rearing (Aug−Sept). Although we present data on the home range and trip parameters of the chick rearing individual, it has not been

Table 2. Summary of the tracking data subsetted for use in the analysis of Verreaux's eagle ranging behaviour and habitat preferences.

Eagle id	Status	Date range	*n* fixes	*n* daylight fixes	mean daylight fix interval	mean fixes / day
721	Pre-breeding	10/04/2012−08/05/2012	6231	4888	2 min 47 sec	222
722	Pre-breeding	11/04/2013−03/05/2013	6407	5693	2 min 25 sec	259
726	Pre-breeding	11/04/2013−03/05/2013	5186	4245	3 min 24 sec	193
727	Pre-breeding	14/04/2013−07/05/2013	5579	4644	3 min 12 sec	211
723	Chick rearing	26/08/2012−20/09/2012	6341	5529	2 min 41 sec	251

included in any analyses of trip parameters between the study areas or estimates of home ranges. However, this eagle was included in the habitat selection analysis of birds in the Sandveld region. The other four pre-breeding eagles used in our analyses appeared to be representation of their population in terms of breeding performance (Chapter 2) and diet (Chapter 3). In all analyses only fixes made between sunrise and sunset (based on nautical twilight) were used. The temporal resolution of the data was standardized by sub-setting to fixes that were more than 115 seconds apart to get comparable average fix rates for all eagles (mean ±SD: 2 min 54 sec ±0 min 24 sec) (Table 2).

Home range analysis

We estimated home ranges as Minimum Convex Polygons (100 % MCPs) (Mohr 1947) using the adehabitatHR package (Calenge 2011) in R v.3.0.2 (R Core Team 2015). Although this method is useful for exploratory purposes and comparison with other studies (Brown 1988), it tends to overestimate the home range size and does not account for the relative intensity of space use within the total area used (Cumming and Cornélis 2012). Due to these limitations, we also estimated home ranges, in terms of utilization distributions (UDs) using a dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber et al. 2012). This method quantifies the UD of an animal based on the movement path rather than individual points, by accounting for the time between locations, therefore it can process high-resolution temporally autocorrelated data (Kranstauber et al. 2012). Further to the original Brownian Bridge Movement Models (BBMM: Horne et al., 2007), the dBBMM uses a moving window to dynamically calculate changes in variance of the Brownian motion which is related to the mobility of an animal and therefore better describes the space use of behaviourally heterogeneous tracks (Kranstauber et al. 2012). dBBMM UDs were calculated using the R package 'move' (Kranstauber and Smolla 2014). We used a window size of 31 locations with a margin of 11 locations, which equated to a window length of one hour. The UD was mapped over a grid with cell size of 90 m. Bouten *et al.* (2013) reviewed the positional error of UvA-BITS tags and reported that a stationary tag recording positions every 60 seconds had a mean positional error of 3.23 m (Bouten et al. 2013) and data collected at shorter intervals has significantly reduced the positional error, thus a location error of the GPS logger of 3 m was used in the estimations. Using this method, we estimated UDs at two levels (50 % and 90 %) and projected home range polygons into the UTM coordinate system (WGS 1984 UTM zone 34) in QGIS (version 2.2.0) (Quantum GIS Development Team 2014) for spatial mapping.

Defining trips from the nest

A 400 m buffer was placed around each nest, and a 'trip' was defined as the eagle leaving this buffer between 07:00 and 19:00, for at least three minutes, travelling at least 1 km and excluding any overnight trips when the eagle did not return to the nest site to roost. These conditions mean that we have excluded short pseudo trips when an eagle might be flying back and forth over the nest ridge, which are likely to be territorial display flights. Eagles were considered perched when the distance moved between consecutive points was less than 3 m, and these distances were zeroed in order to reduce possible error in the accumulated trip distance due to positional error in the GPS reading (Ryan et al. 2004).

Total trip duration (minutes), path length (km), maximum distance from the nest (km) and average trip speed (km h^{-1}) was calculated for each trip. Temporal patterns of these parameters were visually explored by plotting the parameters from each trip against the start time of the trip with locally weighted polynomial curves and 95 % confidence intervals. This is a non-parametric method that does not rely on the assumption of a linear relationship between the predictor and response variables.

Therefore, such plots allow for the exploration of the expected non-linear temporal trends in eagle trip behaviour.

To investigate when eagles were most often away on trips during the day, we calculated a measure of ‘trip probability’, which reflects the daily temporal distribution of eagle activity. This was calculated per minute of the day and is inclusive of the full duration of all active trips.

Statistical analysis of trips from the nest

Differences in mean trip parameters (duration, path length, maximum distance from nest and speed) between the study areas were analysed using Generalized Linear Models (GLM) in R. Additionally, to investigate differences in trip parameters through the day we used Generalized Additive Models (GAM) within the ‘mgcv’ package in R (Wood 2006). We included the start time of each trip on a decimal scale as a smoothing term and study area and eagle identity were included as fixed effects. GAMs were considered to be more appropriate since the relationship was not expected to be linear. GAMs were also used to test for differences in trip probability between the areas and through the day with decimal time included as a smoothing term. Differences in these probabilities were further validated at hourly intervals by GLMs. Due to the non-normal distribution of the data quasi-Poisson family was specified in all models.

Habitat selection data

We explored habitat selection for the three birds that were tracked in the Sandveld. In addition to habitat type, we investigated the influence of distance from the nest and topography. Habitat type was derived in QGIS from a layer that had mostly been digitized at scales 1:10,000–50:000 (Kirkwood 2010). Four habitats were considered (Chapter 3): natural (pristine habitat), near-natural (close to pristine), degraded (those areas which have been severely impacted but could be rehabilitated at great cost) and no natural habitat (areas which have been irreversibly transformed through development and as a result, no longer contribute to the biodiversity of the area) (Maree and Vromans 2010). Owing to the negligible urban development in the

Sandveld, departure from natural habitat is considered to be associated with agriculture, and the latter category of “no natural habitat” is considered to be areas with complete agricultural transformation. Topographic variables were extracted from a 30 m-resolution Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM). These included altitude, slope, terrain ruggedness index and aspect. Aspect was categorized into the four cardinal directions. The terrain ruggedness index is a quantitative measurement of terrain heterogeneity, which uses the difference between the altitude of a cell and the mean of the eight surrounding cells to describe the relief of the ground (Riley et al. 1999).

Statistical analysis of habitat selection

Temporal autocorrelation is a problem for data that are not uniformly sampled. In this case, the *c*. 3 min sampling frequency throughout means that data were sufficiently regular and over the entire period that they can be assumed to fairly approximate the activity of the eagles from which they were derived (Reid et al. 2015). To investigate the locations of fixes in relation to the explanatory variables, we first created a series of pseudo-absence points; these were random points generated for each eagle within the MCP. For each eagle we generated 3 times as many pseudo-absence points as we had tracking fixes. We used a GLM specifying a binomial response variable (eagle points = 1; pseudo-absence points = 0) and pairwise comparisons generated in the ‘lsmeans’ package (Lenth 2014). A correlation matrix showed strong co-linearity between the slope and terrain ruggedness values (0.989) due to being derived from one underlying measure, therefore terrain ruggedness was excluded from the model (Green 1979, Sergio et al. 2006). Consequently, explanatory variables entered into the GLM included eagle id, distance from nest (m), habitat type (four levels), slope (degrees), aspect (four cardinal directions) and elevation (m) and elevation squared (m^2) to explore for a quadratic relationship with this term.

To explore which variables best explained habitat selection we used a model selection approach using Akaike’s Information Criterion (AIC_c) with the ‘MuMIn’ package (Barton 2014). Models were ranked according to their AIC_c values and the suitability and efficiency of our final model were reviewed using the Area Under the Curve

(AUC) value of a Receiver Operating Characteristic (ROC) plot, which provides a measure of overall model accuracy. AUC values can range from 0.5-1, where 1 represents perfect model fit, and 0.5 indicate a complete lack of predictive power (Swets 1988, Robin et al. 2011).

Results

Home range

From the dBBMM UDs of the four pre-breeding eagles, we estimated average home range size (90 % UD) of 27.7 ±14.5 km^2 (mean ±SD) and core home range (50 % UD) of 1.4 ±1.6 km^2. All 50 % UDs were small, mutually exclusive and largely centred around the nest. Average MCP for pre-breeding eagles was 195.6 ±107.2 km^2 (Figure 1, Table 3).

For another eagle (723), nesting in the Sandveld, the three home range measures during the chick rearing period were approximately four times larger than that found for the other birds tracked during the pre-breeding period (90 % UD: 112.9 km^2; 50 % UD: 5 km^2; MCP: 775.9km^2) (Figure 1, Table 3).

Trips from the nest

During the 22 days of pre-breeding data we identified 369 trips from the nest across the four eagles and an additional 174 trips by the chick rearing eagle which are not included in averages or area comparisons (Table 4, Figure 2). Average trip duration and path length were 70 ±82 min (95 % confidence limits= 1−276 min) and 11.5 ±15.9 km (95 % CL= 0.7−37.0 km), respectively. The average trip speed was 15.2 ±12.4 km h^{-1} (95 % CL= 1.2−38.5 km h^{-1}). The mean maximum distance travelled from the nest per trip was 2.8 ±2.8 km (95 % CL= 1.0−6.9 km). There was high variability in all trip parameters, evident from the standard deviation usually being greater than or similar to the mean values (Table 4). No significant differences between areas or individual eagles were found between these trip parameters.

Figure 1. Map of home ranges (50 % and 90 % UDs estimated by the dynamic Brownian Bridge Movement Model (dBBMM) and Minimum Convex Polygons (MCPs)) for adult Verreaux's eagles in the Sandveld (*n*=3) and the Cederberg (*n*=2) in the Western Cape Province, South Africa. Red filled areas are 50 % UDs; other colours are 90 % UDs with the legend indicating individual eagle ID number. The Sandveld region is in the west and the Cederberg in the east of the map.

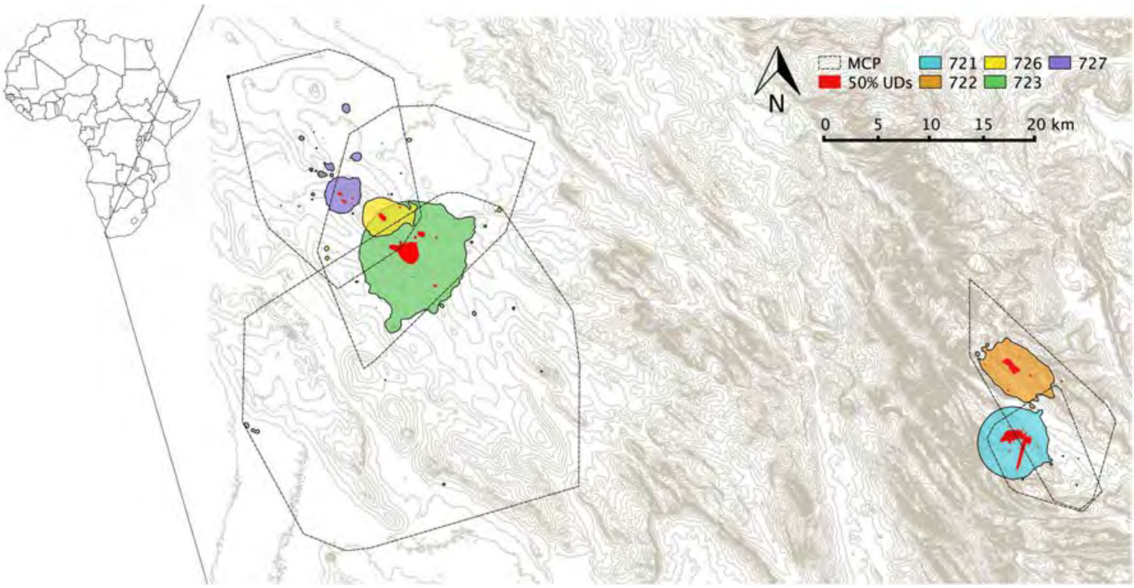

Table 3. A comparison of home range estimates (km^2) for individual resident Verreaux's eagles. 50 % and 90 % utilization distributions were calculated by the dynamic Brownian Bridge Movement Model (Kranstauber et al. 2012). Minimum Convex Polygon abbreviated to MCP. Average (mean ±standard deviation) home range estimates are given for each study area and overall for pre-breeding eagles only (April-May) (excluding 723 in all averages).

Eagle id	Status	Area	50 %	90 %	MCP
721	Pre-breeding	Cederberg	3.7	45.4	75.1
722	Pre-breeding	Cederberg	1.1	33.5	136.1
726	Pre-breeding	Sandveld	0.4	17.4	297.1
727	Pre-breeding	Sandveld	0.3	14.5	273.9
723	Chick rearing	Sandveld	5.0	112.9	775.9
		Cederberg	2.4 ±1.8	39.5 ±8.4	105.6 ±43.1
		Sandveld	0.4 ±0.1	16.0 ±2.1	285.5 ±16.4
		Pre-breeding	1.4 ±1.6	27.7 ±14.5	195.6 ±107.2

No differences were identified between the study areas for trip duration, path length or trip speed by the GAMs. The duration of trips was found to decrease through the day (F=26.65, p<0.001; Figure 3). Birds appeared to fly further overall during the middle of the day, with path length showing a significant uni-modal relationship with time of the day (F=4.66, p<0.001; Figure 3), peaking in trips which were initiated approximately one hour before 12:00. Trip speed increased through the day (F=7.014, p<0.001; Figure 4), with faster trips occurring in the afternoon compared to the evening. Maximum distance from the nest was the only trip parameter that showed variability between the study areas (t=–2.062, p<0.05), the peak in the maximum distance from the nest being more pronounced and occurring earlier in the Sandveld than the Cederberg (Figure 2c).

Table 4. Average (mean ±standard deviation) parameters for trips from nests made by Verreaux's eagles individually and grouped by study area during the pre-breeding stage (April−May) (excluding 723 in all averages).

Eagle id	Path length (km)	Trip duration (minutes, seconds)	Max. distance from nest (km)	Trip speed (km h^{-1})	*n*
721	11.02 ±12.56	79m16s ±78m55s	2.19 ±1.59	11.83 ± 8.01	79
722	12.66 ±12.80	67m42s ±78m07s	3.29 ±2.54	17.40 ±13.44	103
726	12.02 ±21.62	64m16s ±78m55s	2.94 ±3.41	16.34 ±14.56	108
727	9.82 ±13.08	72m21s ±92m36s	2.74 ±3.03	14.10 ±10.72	79
723	12.22 ±19.90	47m47 ±65m35s	3.45 ±4.43	20.54 ±11.24	174
Cederberg	11.95 ±12.69	72m43s ±77m36s	2.81 ±2.24	14.96 ±11.70	182
Sandveld	11.09 ±18.49	67m41s ±84m49s	2.85 ±3.25	15.39 ±13.09	187
Pre-breeding	11.51 ±15.88	70m10s ±81m40s	2.83 ±2.79	15.18 ±12.41	369

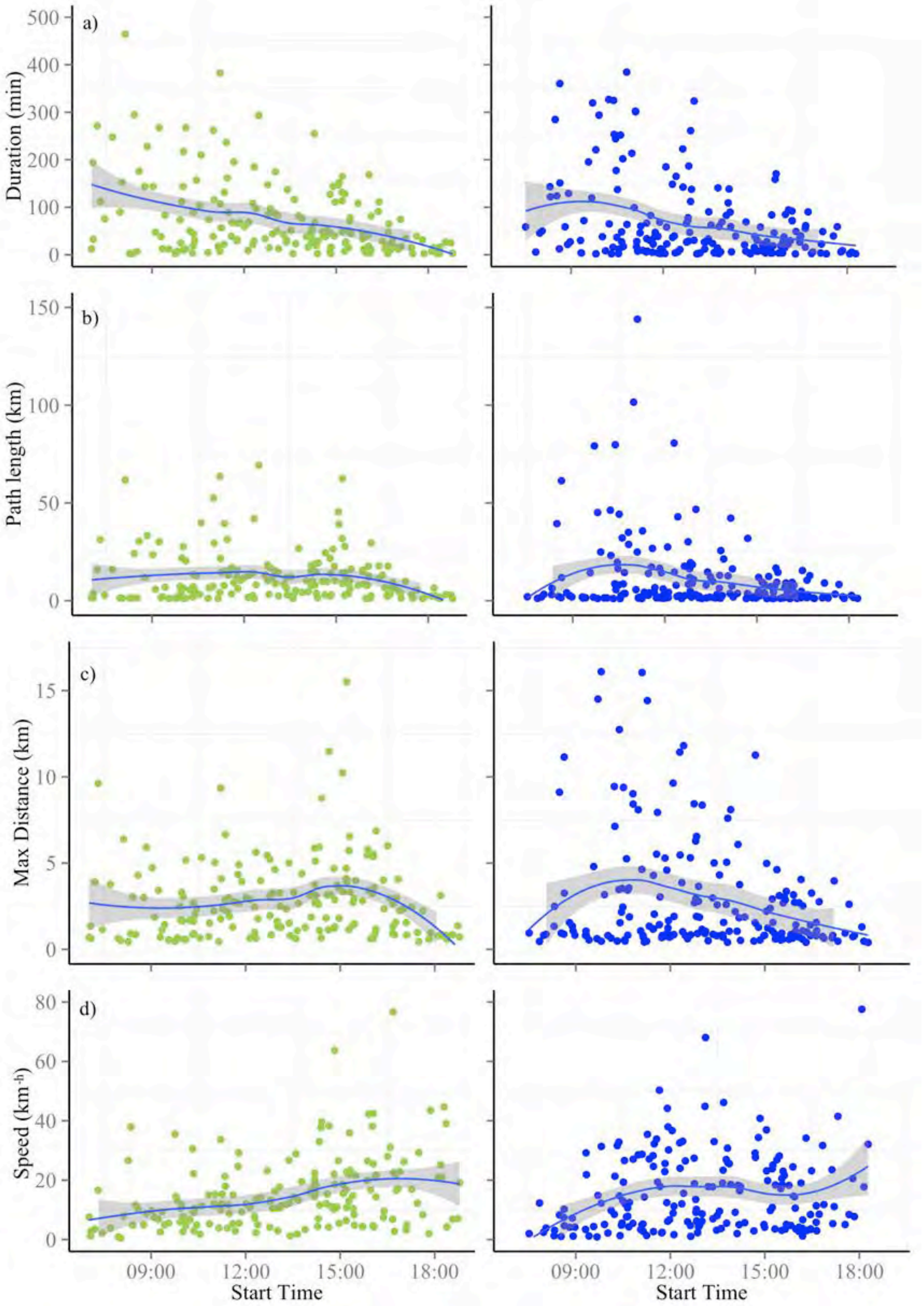

Figure 2. Parameters of trips from the nest by Verreaux's eagles in the Cederberg in green (*n*=2) and the Sandveld in blue (*n*=2) over 22 days of tracking. a) Trip duration b) path length c) maximum distance travelled from the nest d) trip speed. All plotted against the time the trip was initiated and with locally weighted polynomial curves and 95 % confidence interval.

As a general trend, trip probability increased through the morning as more flights were initiated and declined again in the afternoon. However, the trends varied significantly between the study areas (t=–0.046, p<0.001), with the Sandveld birds showing a narrower and more pronounced peak around midday compared to the Cederberg. These results were corroborated by GLMs at hourly intervals, which confirmed trip probability was significantly higher in the Cederberg than the Sandveld before 11:00 and after 15:00 and was significantly higher in the Sandveld than the Cederberg from 11:00 to 15:00 (Figure 4).

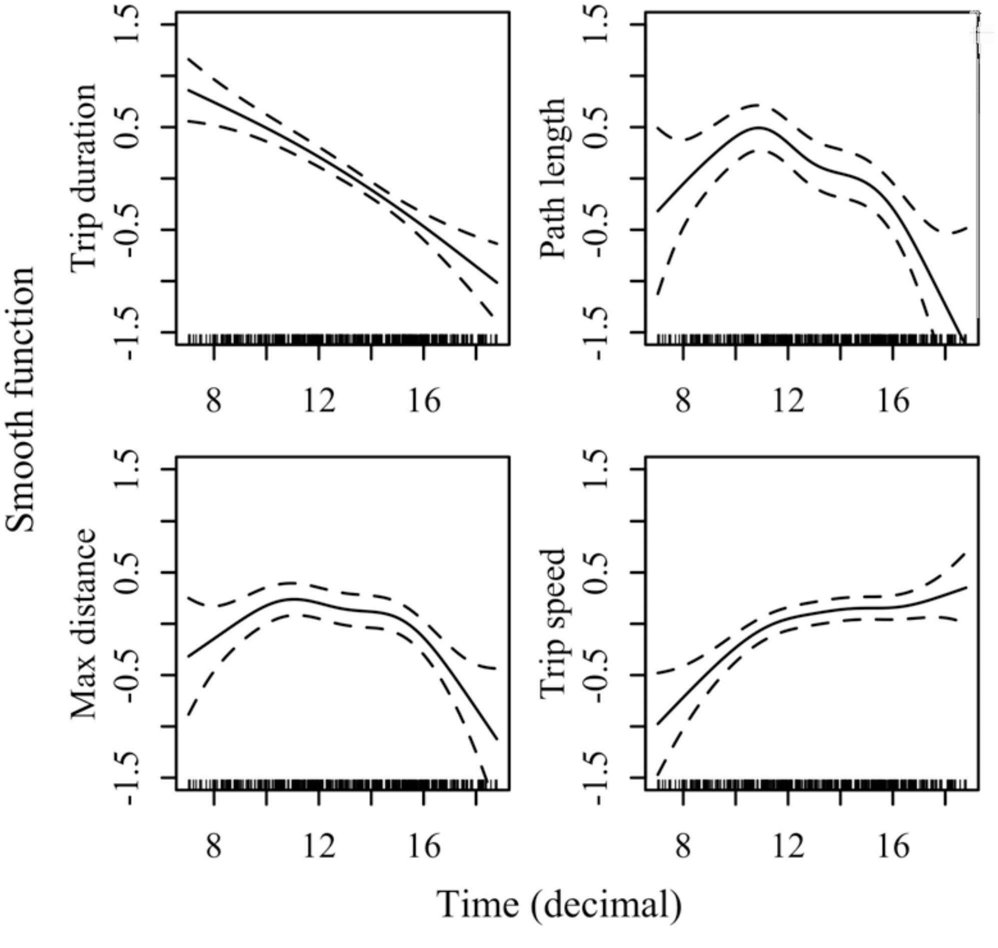

Figure 3. Plotted Generalized Additive Model (GAM) outputs showing the relationship between time of day (displayed as a decimal scale) and mean trip parameters (trip duration, path length, maximum distance from nest, trip speed) for pre-breeding Verreaux’s eagles in the Cederberg and the Sandveld combined (*n*=4). The solid line is the predicted variable and the dashed lines are the standard error.

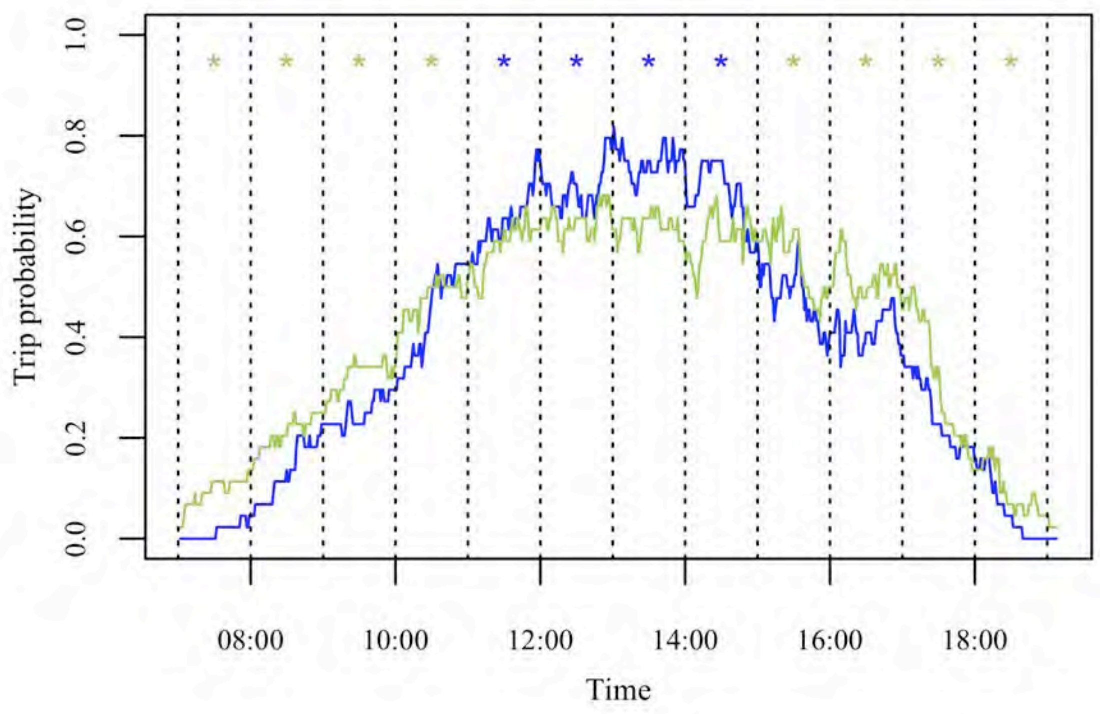

Figure 4. Probability of an active trip away from the nest, calculated per minute of the day, by Verreaux's eagles in the Cederberg (*n*=2) and the Sandveld (*n*=2). *Significant differences p <0.001 tested by a GLM at hourly intervals, colour coded for highest mean.

Habitat selection

Our most parsimonious model received substantial support (W_i =1.00), this model included all model parameters, i.e. the quadratic elevation term (elev and elev^2), eagle id, distance from the nest, slope, aspect and habitat type (Table 5). The AUC for this model was 0.94 suggesting a very good model fit.

Habitat selection was shown for the intermediate habitat conditions of degraded and near-natural, over areas with natural or no remaining natural habitat, confirmed by pairwise comparisons (Figure 5, Table 6). The probability of an area being used by an eagle within its MCP declined further away from the nest site, where probability of use of an area decreased by 50 % at 3.5 km from the nest site (Figure 6a). Eagle use increased with the steepness of the topographical slope (Figure 6b). There was a quadratic relationship with elevation, whereby the probability of eagle use increased with elevation up to about 400 m and decreased at higher elevations (Figure 6c).

Table 5. Results from the top five GLMs comparing model fit for habitat selection of Verreaux's eagles. Model parameters abbreviations: elev, elevation; elev^2, elevation squared for quadratic inference; asp4, cardinal aspect; egl_id, eagle id; hab_typ, habitat type; nst_dst, distance from nest; slp, slope. Other column abbreviations: df, degrees of freedom; logLik, log likelihood; ΔAIC_c, change in AIC_c relative to the highest ranked model; w_i, AIC_c weight. The top model is shown in bold.

Model	df	logLik	ΔAICc	*W_i*
Elev+elev^2+asp4+egl_id+hab_typ+nst_dst+slp	**13**	**-14093.84**	**0**	**1**
Asp4+egl_id+hab_typ+nst_dst+slp	11	-14118.2	44.71	0
Elev+asp4+egl_id+hab_typ+nst_dst+slp	12	-14118.2	46.71	0
Elev+elev^2+asp4+egl_id+nst_dst+slp	10	-14129.93	66.18	0
Asp4+egl_id+nst_dst+slp	8	-14149.71	101.73	0

Table 6. Slope coefficients (β) from most parsimonious model predicting habitat selection of Verreaux's eagles in the Sandveld region of South Africa.

					Confidence Intervals	
	β	Std. Error	z value	p value	2.5 %	97.5 %
(Intercept)	1.38	1.19E-01	11.55	< 2e-16	1.14	1.61
Natural	-0.40	4.85E-02	-8.27	< 2e-16	-0.50	-0.31
Near Natural	-0.15	8.65E-02	-1.68	0.09	-0.32	0.02
No Natural Habitat	-0.34	5.29E-02	-6.44	0.00	-0.44	-0.24
Nest distance	-0.36	4.77E-03	-76.08	< 2e-16	-0.37	-0.35
Slope	0.17	3.21E-03	51.96	< 2e-16	0.16	0.17
Elevation	-0.01	1.02E-03	-6.92	0.00	-0.01	-0.01
Elevation^2	1.90E-05	2.65E-06	7.18	0.00	1.38E-05	2.42E-05
Eagle_i.d 726	-1.40	4.00E-02	-35.07	< 2e-16	-1.48	-1.32
Eagle_i.d 727	-1.37	3.87E-02	-35.29	< 2e-16	-1.44	-1.29
Aspect N	-0.09	4.84E-02	-1.77	0.08	-0.18	0.01
Aspect S	0.09	4.90E-02	1.78	0.07	-0.01	0.18
Aspect W	0.39	4.64E-02	8.40	< 2e-16	0.30	0.48

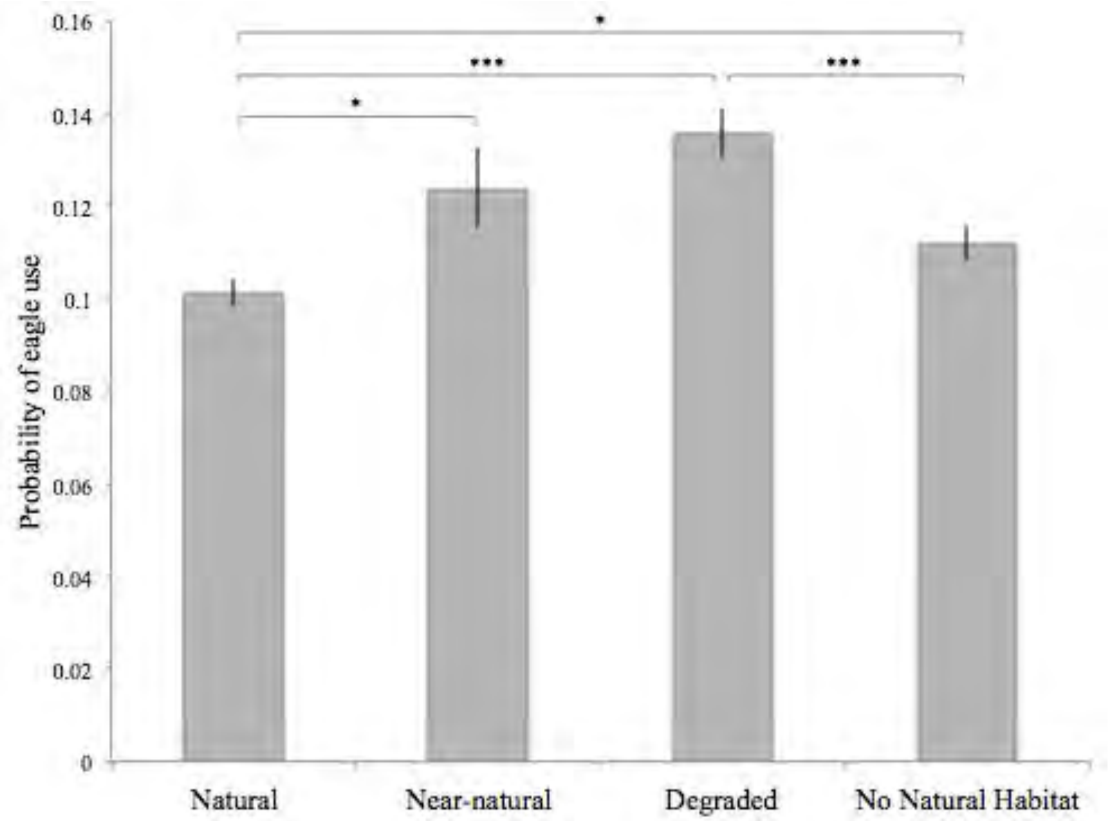

Figure 5. The use of four habitat types (natural, near-natural, degraded, no natural habitat) by Verreaux's eagles in the Sandveld, taking into account distance from nest and topographic variables, with standard error bars. * p<0.05; *** p<0.005 indicating significance of pairwise differences in least-squares means.

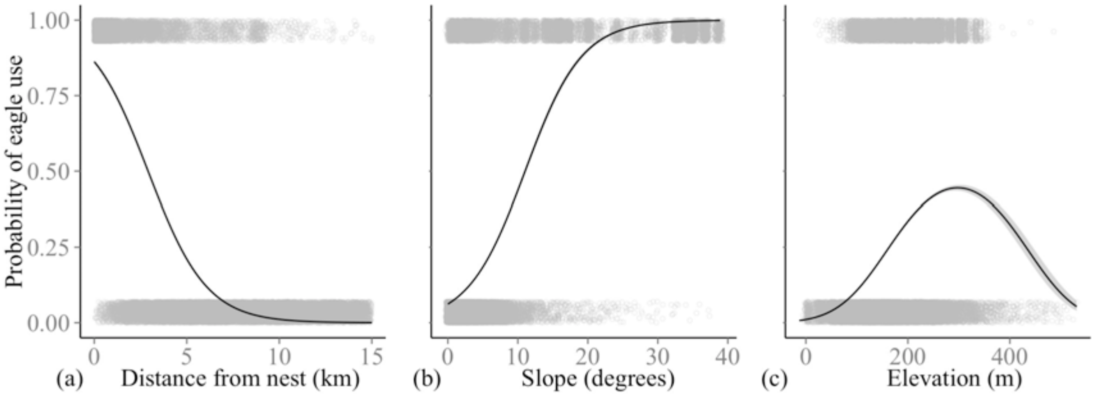

Figure 6. Lines fitted from a binomial Generalised Linear Model showing the probability of eagle use in the Sandveld where "1" is eagle derived data and "0" is pseudo-absent points, with (a) distance from nest (b) slope and (c) elevation fitted as a quadratic variable. Confidence intervals could not be displayed due to their minimal size in (a) and (b).

Discussion

Using high-resolution GPS fixes this study provides information on the spatial and temporal ranging behaviour of the Verreaux's eagle. Although GPS data have regularly been used to investigate coarse migratory routes and home range size in raptorial species (Katzner et al. 2012, Moss et al. 2014), with only a few exceptions, the use of high-resolution tracks derived from free-living raptors remains rare (Lanzone et al. 2012, Duriez et al. 2014, Katzner et al. 2015). We know of no studies that have attempted to investigate accurate parameters of trips away from the nest made by any territorial raptor. This kind of information has regularly been achieved for other avian groups, notably seabirds (Grémillet et al. 2004, Petersen et al. 2006, Moseley et al. 2012), which are easier to repeatedly trap and handle and are relatively robust to disturbance. This allows repeated deployments of tags, overcoming the compromise which most raptor studies need to make between sampling frequency and tracking duration (as determined primarily by device weight and battery capacity) (Rodríguez et al. 2012). Ethical concerns are also important. Owing to the fact most raptors are endangered, it is not easy or ethical to frequently re-trap large numbers of raptors as researchers are able to do on seabirds. Although we acknowledge that our sample size is small, owing principally to these challenges, the analyses presented in this paper were made possible by the resolution of the GPS data. Platform Transmitter Terminal satellite tags (PTTs) commonly used in other studies record fixes once an hour (Mellone et al. 2012, Moss et al. 2014), which would not have been adequate to describe these trips given that average entire trip duration was close to one hour (i.e. 70 minutes).

Our results for the 90 % UD (27.7 ±14.5 km^2) for pre-breeding eagles is comparable to previous estimates based on visual observations and inter-nest distances, which range from 10.5–64.4 km^2 (Brown 1988, Gargett 1990). The mean core home range use, considered as the 50 % UD, was small (1.4 ±1.6 km^2), mutually exclusive and centred around the nest, typical of territorial raptors. Due to our small sample size it was not possible to compare home range sizes between seasons, and it is evident from the larger home range of the chick rearing eagle (90 % UD: 112.9 km^2) that the home range size is likely to be subject to seasonal variation. Further research should go into assessing the home range size throughout the full annual cycle and identifying if regional differences occur. However, the mean 90 % UD value represents an important area outside of the breeding season, which can contribute to conservation planning and should be considered the absolute minimum area for conservation around a nest. As a circular value this would equate to a 3km buffer for exclusion of sensitive developments. This value is supported by the mean maximum distance from the nest (2.8 km) and the decrease in eagle use of an area with increased distance from the nest (0.5 probability of use: 3.5 km). In the absence of any site-specific information we recommend exclusion of high intensity development, including further agricultural intensification and the placement of wind turbines, from a buffer of 3 km around any occupied nest site.

Similar studies investigating foraging trip parameters in seabirds identified longer duration trips, longer path lengths and greater maximum distances from colonies as indicators of a greater foraging effort driven by prey declines (Grémillet et al. 2004, Petersen et al. 2006). Our data provided little support for our hypothesis that eagles inhabiting the Sandveld exhibit trips from the nest with larger parameters of duration, path length, maximum distance from the nest or speed analogous with a reduced prey availability and increased hunting effort. Although energetics of different flight techniques, topography and climatic conditions also contribute to overall energy expenditure (Duriez et al. 2014), under the current level of land transformation in the Sandveld, eagles are not displaying typical signs of increased energetic outputs when compared to those in a pristine habitat. However, caution is required when interpreting these results because; (1) they are based on a limited sample size of birds and (2) other dissimilarities are present between the contrasting study areas, primarily topography, which could obscure the effects of land use and create contrasting uplift situations.

Some interesting patterns were observed in the trip parameters, and these were largely present in both study areas. Trips tended to be longer in duration (but not path length) earlier in the day and the mean trip speed increased through the day. These results indicated that trips in the morning were either slower or included more time spent perched compared to trips made later in the day. The decrease in trip duration throughout the day may be driven by the decreasing availability of daylight flying time or by the fulfilment of foraging requirements as the day progresses. The total path length peaked in trips that were initiated approximately one hour before 12:00, which could be related to prey behaviour and availability or thermal lift availability. Although there were no differences between the study areas for the average maximum distance from the nest per trip, the daily temporal distribution of trips further from the nest was different between the study areas, with an earlier peak in maximum distances travelled in the Sandveld compared to the Cederberg (Figure 2c). Trips further away from the nest site, and consequently generally away from the isolated nest cliffs and orographic lift sources, are also initiated before 12:00 in the Sandveld, meaning that most are ongoing around midday. This is likely to be related to temporal and spatial differences in lift availability, driven by topographic differences (Chapter 5). The Sandveld is generally much flatter than the rugged terrain of the Cederberg Mountains. Raptors utilize both orographic lift and thermal lift (Duerr et al. 2012) for energy-saving flight modes (such as soaring) (Duriez et al. 2014). Orographic lift is generated by air movements over steep slopes and cliffs, and it is well established that eagles in mountainous areas exploit these opportunities (Pennycuick 1972, Chalmers 1998, Bohrer et al. 2012, Katzner et al. 2012). Thermal lift is generated by solar radiation heating the ground, which in turn heats patches of air creating thermal lift (rising patches of warmer lower density air). Thermal lift develops in strength with increasing temperatures, therefore the availability of thermals is likely to increase around midday. Changes in the temporal availability of thermal lift is expected to be more important to eagles in the flatter Sandveld region than the Cederberg, due to relatively fewer opportunities for orographic soaring (Chapter 5).

There were also significant differences in the temporal patterns in trip probability between the two study areas. It follows that these differences were also likely to be driven by the topographic differences between the study areas driving dissimilar lift availability. The centring of greater trip probability around midday, later increase of trip probability in the morning and the earlier decrease in trip probability in the afternoon in the Sandveld compared to the Cederberg might be explained by their greater reliance on thermal lift for flight activity. The availability of orographic lift in the Cederberg is relatively independent from the time of day so these eagles can initiate flights earlier and continue flying later into the day. However, we cannot exclude the possibility that these differences are associated with differences in temporal patterns in prey behaviours between the study areas (Davies 1994).

Habitat selection within agriculturally transformed landscapes has been examined in various raptorial species including golden eagle *Aquila chrysaetos* (Marzluff et al. 1997), Spanish imperial eagle *Aquila adalberti* (Ferrer and Harte 1997), lesser kestrels *Falco naumanni* (Donazar et al. 1993, Tella et al. 1998, Ursua et al. 2005), marsh harrier *Circus aeruginosus* (Cardador et al. 2011) and hen harrier *Circus cyaneus* (Amar and Redpath 2005), where preferences are usually determined by food abundance or availability (Donazar et al. 1993, Ursua et al. 2005). Within the Sandveld we were able to use the tracking data to build habitat models describing space and habitat use by three eagles. Unsurprisingly, given the territorial nature of the species and the fact that they are central place foragers, we found that eagles were more likely to use areas closer to the nest than further away. This also demonstrates the importance of minimising travel costs of foraging behaviour. Eagles were also found to select steeper areas and intermediate elevations, which probably reflect the species' use of slopes for soaring on updrafts where available, their tendency to perch on cliffs, and potentially the availability of hyrax on rocky slopes. This is relevant to suitable planning of developments, in particular wind farms in the vicinity of nest sites, which should ideally avoid slopes and other topographic features (de Lucas et al. 2008) to reduce collision risks. Although the sample size of birds used was limiting in the analysis and also the observed differences in habitat use were small, after controlling for these important constraining variables (i.e. nest distance and topography) the habitat selection analysis did not show a selection for remaining natural vegetation. In fact, contrary to our predictions, eagles tended to select for partially converted habitat types (i.e. near-natural and degraded), suggesting that Verreaux's eagles may be more resilient to agricultural transformation than previously thought. Foraging theory predicts that raptors will forage preferentially in patches offering the highest net energy gain (Stephens and Krebs 1986). This can be determined by prey abundance or availability, whereby prey availability to a predator can be determined by the physical accessibility in different habitat structures (Wakeley 1978, Preston 1990). Although we have no information on prey abundance in these different habitats, near-natural and degraded habitats are likely to feature intermediate levels of ground cover, and offer more visible or accessible hunting opportunities than natural vegetation, while still maintaining an adequate prey base. The avoidance of areas with no natural habitat, suggests that the suitability of the habitat mosaic for Verreaux's eagles is delicately balanced, and further agricultural development could reduce the suitability of the area. This reflects patterns seen elsewhere in other systems, whereby some agricultural transformation may be of benefit to avifauna (Fairbanks et al. 2002, López-López et al. 2006, Amar et al. 2011, Cardador et al. 2011, Camacho et al. 2014) but over a certain threshold level of intensification the balance is tipped and can lead to rapid species declines or loss (Donazar et al. 1993, Butet and Leroux 2001, Donald et al. 2001). In lesser kestrels low level agricultural transformation has been associated with an increase in abundance of breeding lesser kestrels (Tella et al. 2004). However, beyond a threshold of habitat conversion for agriculture, suitable foraging habitat and an adequate prey base are not maintained (Tella et al. 1998, Rodríguez et al. 2006) resulting in a decrease in abundance of this species (Tella et al. 1998, 2004; Rodríguez et al. 2006).

Considerations for future research

Sex was not used as an explanatory variable for any of these analyses although it should be accounted for, particularly as in this case it is confounded with study area. However, a study of golden eagle ranging behaviour found that males and females travelled similar distances (Marzluff et al. 1997) and observations of Verreaux's eagles indicate that they spend 95 % of the day together outside of the breeding season (Gargett 1990). Currently, the major limitation of this study remains the small sample size of eagles. Further research would ameliorate this limitation and might identify seasonal and regional changes in ranging behaviour. However, we believe that it is unlikely that a larger data set would vastly change our conclusions.

The effects of transmitters on the breeding productivity, longevity and behaviour of raptors should be subject to further consideration and research. The duration of the present study was curtailed by the loss of three eagles within the first 40 days of tagging, one of which was found dead 21 km away from its nest, while two neighbouring tagged eagles are believed to have killed each other, which was inferred from information from their GPS tags. This showed the two eagles were in the same place at the same time on their territory boundary and after returning to their respective nest cliffs contact was lost with both eagles. In addition, one eagle was ousted from its territory and although it survived, further contact was intermittent because of its massively expanded range and the constraints of the download system (Murgatroyd 2013). Birds carrying back-mounted tracking units have been known to experience increased energy costs, although these energetic demands might not be reflected in their normal daily behaviour (Godfrey and Bryant 2003). However, trapping and tagging of golden eagles has shown that these methods can cause reduced reproductive success or alter the frequency of use of nest sites where trapping occurred (Gregory et al 2003, Lockhart and Kochert 1978). Nevertheless, these impacts are variable and might be related to other factors including: the annual availability of prey, the sex of the bird tracked and the timing of capture as opposed to the tag itself (Marzluff and Vekasy 1997). Our sample size remains small and we are uncertain if this seemingly high turnover of adults was the product of a natural process, perhaps driven by a large population of ‘floaters’ (unpaired eagles) in the two areas, or was caused by the physical effect of the transmitters on the study birds. Although Verreaux’s eagles are generally considered to be monogamous, with pairs remaining together for many years (Steyn 1982, Gargett 1990, Simmons 2005), no adequate colour marking or DNA study has ever been undertaken to confirm this and there is some evidence to suggest that mate changes may be more frequent than believed (Gargett 1990, Murgatroyd 2013).

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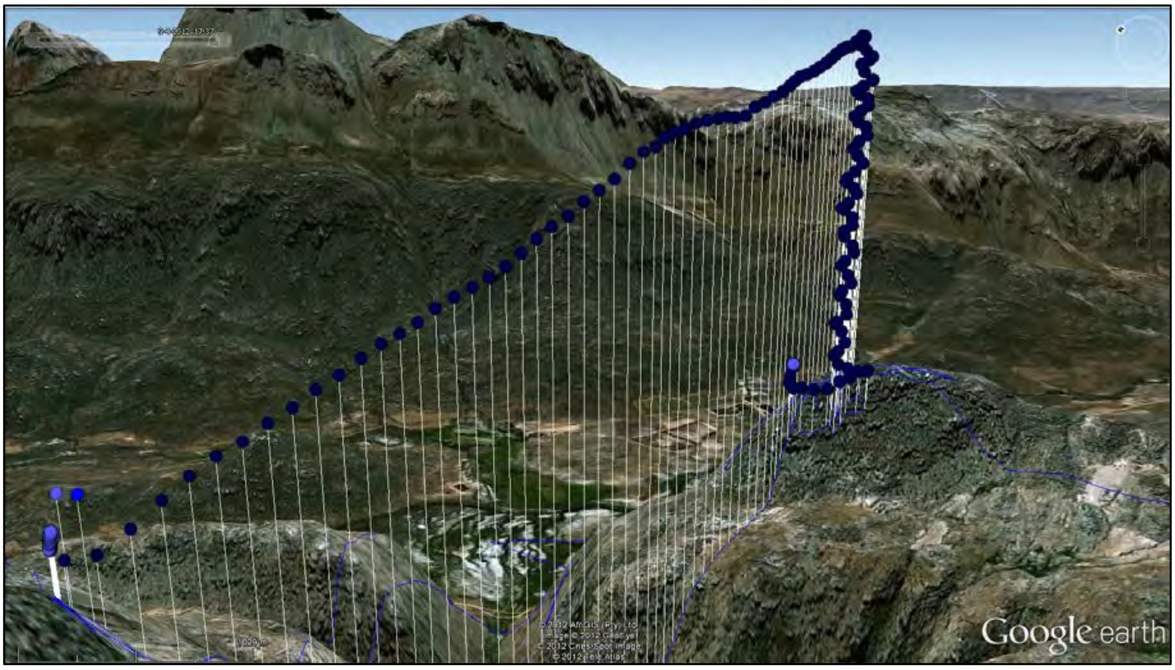
Chapter 5

Predicting soaring flight behaviours of Verreaux's eagles and lift availability in contrasting landscapes



Abstract

Unlike smaller raptors, which can readily use flapping flight, large eagles and vultures rely on lift for energetically efficient flight. Soaring strategies are determined by the underlying topography and meteorological conditions driving lift availability, which can be broadly categorised as orographic or thermal lift. Verreaux’s eagles are a typically mountainous species where orographic lift is likely to be prevalent owing to air movement over slopes and ridges. However, some populations of Verreaux’s eagles inhabit flatter regions and these populations may rely on thermal lift to a greater extent than their mountainous counterparts. In this study, we develop methods to identify behaviour states in high-resolution GPS tracking data and to predict the distribution of lift availability both spatially (across the landscape) and temporally (among months through the year). We demonstrate these methods with data derived for the Verreaux’s eagle and we use the predictions to understand lift availability for this species in topographically contrasting regions in South Africa. In the Cederberg Mountains we expect good orographic lift availability. In comparison to the Cederberg, the Sandveld is relatively flat and therefore we expect poor orographic lift availability, but enhanced thermal lift availability. The total lift availability is expected to be greater in the Cederberg than the Sandveld as mountains are thought to represent optimal habitat for this species. Additionally, the profitability (altitude gained) and strength (speed of altitude gain) of thermal and orographic soaring were examined in bouts of soaring flight, to ascertain which lift source is likely to be more beneficial to eagles. In line with expectations, we found that the Sandveld region had greater predicted thermal lift availability than the Cederberg, whereas, the predicted availability of orographic lift differed between areas and months depending largely upon the prevailing wind direction. Contrary to expectations total predicted lift opportunities were consistently greater in territories in the Sandveld region than the Cederberg. Assessments of soaring bouts suggest that thermal lift is more profitable and stronger than orographic lift although it’s relative usefulness in day-to-day activity, such as foraging, needs further assessment. Lift availability in the Sandveld may provide an overall improved ‘energy landscape’ and may in part explain why this population has higher breeding performance compared to the Cederberg.

Introduction

The physical environment influences the energetic cost of animal locomotion on land, in water and in air (Spaar and Bruderer 1996, Ganskopp et al. 2000, Wall et al. 2006, Wilson et al. 2011). Unlike land, air and water are dynamic environments, where flow and resistance to movement changes through time. The path of least cost usually determines the route of navigation through a landscape (Shepard et al. 2013). For soaring birds, the route, method and cost of flight are greatly affected by the availability of lift, which provides a harvestable energy form for movement (Lanzone et al. 2012, Katzner et al. 2015). Uplift used by large soaring birds can be broadly classified into two groups. (i) Thermal lift, which is driven by solar radiation heating the ground and warming the nearby air, thus creating rising columns of warm air (Akos et al. 2010), also referred to as 'thermals'. (ii) Orographic lift, which is upwards air movement generated by wind deflected over topographic features. Birds can exploit thermals by circling inside the upwards-moving columns to gain altitude. Large soaring birds rely on thermals for lift in flat terrain. Owing to the dependence of thermals on solar heating and their dissipation by strong winds, thermals are temporally variable (Shepard and Lambertucci 2013). In contrast, orographic lift is often concentrated along ridgelines and is thought to provide favourable conditions for flight within the breeding home range of large soaring raptors, during sub-adult dispersal and during the migration of some species (McLeod et al. 2002, Brandes and Ombalski 2004, Bohrer et al. 2012, Reid et al. 2015, but see: Duerr et al. 2012, 2015; Katzner et al. 2015). Mountainous areas are usually associated with high lift availability, owing to their ability to generate orographic lift even in low wind conditions (Shepard and Lambertucci 2013).

For obligate soarers, flight modes are limited by the availability of suitable soaring conditions. In a heterogeneous landscape soaring flights can be concentrated in space and/or in time (e.g. midday peaks of trip probability; Chapter 4) and are modulated by weather conditions (Spaar and Bruderer 1996, Shamoun-Baranes et al. 2006, Dodge et al. 2014, Vansteelant et al. 2014b, a; Treep et al. 2015) and seasonal differences in lift availability (Duerr et al. 2015). For example, when wind speeds increase, golden eagles *Aquila chrysaetos* change from thermal soaring to orographic soaring to reduce the energetic costs of migration (Lanzone et al. 2012). The altitude gained via lift is a form of potential energy that reduces the need for powered flight, enabling gliding flight and providing calorific savings (forwards movement while spending potential energy) (Pennycuick 2008). Therefore, preferential use of areas that maximise net energy gain is expected. Although there is good theoretical understanding of lift availability and its use for soaring (Pennycuick 2008, Bohrer et al. 2012), empirical studies using modern technology to investigate if birds utilise lift in line with these expectations is only now emerging (Shepard et al. 2011, Lanzone et al. 2012, Katzner et al. 2015).

‘Where’, ‘when’, ‘why’ and ‘how’ are basic components defining animal movement (Nathan et al. 2008). Questions around where animals move, such as home range size and habitat selection, can be readily answered in conventional tracking studies (Marzluff et al. 1997, McGrady et al. 2002, Bosch et al. 2010). To better understand ‘where’, ‘when’ and ‘why’ movement occurs we need to recognise ‘how’ movement is achieved by differentiating between specific behaviours. In highly mobile species, such as birds, this requires high-resolution data to detect particular behaviours and identify the spatiotemporal variables that drive them. Recent advances in technology are increasingly allowing the identification of such behaviours in free-living animals (Kays et al. 2015). Given these technological advances and the discrete nature of updrafts, we are now in a position to model energy landscapes for soaring species both spatially (driven by topography) and temporally (with changing meteorological conditions) (Wilson et al. 2011, Shepard et al. 2013). This advance will be important for a number of applications; for example, the ability to predict the distribution and likelihood of behaviours will be critical in mitigating anthropogenic risks associated with specific behaviours (Colchero et al. 2011, Camacho et al. 2014, Reid et al. 2015) and will enhance our understanding of resource availability to animals. For soaring birds spatial or temporal variations in lift availability are likely to confer fitness advantages, including reproductive outputs and body condition or to influence how species are distributed (Weimerskirch et al. 2012, Shepard and Lambertucci 2013). Thus, understanding flight behaviours in response to environmental variables can provide insights into the conditions under which large raptor species will struggle or benefit (Shepard and Lambertucci 2013).

In this study we aim to advance statistical methods for classifying and predicting flight behaviour from high resolution GPS data. Behavioural states were identified from high-resolution (temporally and spatially) GPS tracking data derived from a small sample of Verreaux’s eagles *Aquila verreauxii* in the Western Cape, South Africa. The topographical and meteorological correlates of the two lift-generated flight modes (thermal soaring and orographic soaring) were examined. Following this, we use these relationships to predict the availability of thermal and orographic lift within known active eagle territories in two topographically contrasting regions (Cederberg Mountains and the relatively flat Sandveld) throughout the year. Finally, to investigate whether thermal or orographic soaring is more beneficial to gaining potential energy we investigated the profitability (i.e. height gain) and strength (i.e. speed of vertical travel) of lift during consecutive bouts of soaring flight behaviours. Although our dataset was limited and consequently the ecological inferences that are drawn should be treated with caution we demonstrate the potential for these methods to further our understanding of the drivers of flight dynamics.

To the best of our knowledge, this study represents the first attempt to model such fine scale behaviour distributions using precise data derived from free-living non-migratory raptors. Based on current knowledge of lift availability and the effects of weather on soaring behaviour in birds we predict that: i) thermal soaring is correlated with warm still climate (favouring the formation of thermals) and flat topography; ii) orographic soaring is correlated with windy conditions and slopes provided by mountainous topography; iii) thermal lift availability is greater in the Sandveld than the Cederberg driven by its generally flatter topography; iv) orographic lift availability is greater in the Cederberg than the Sandveld driven by its mountainous topography and both will be subject to seasonally fluctuating patterns in availability. Lastly, the profitability (i.e. height gain) and strength (i.e. speed of vertical travel) of lift are investigated during bouts of consecutive behaviour and are used as an indicator of the most beneficial lift source (orographic or thermal lift).

Methods

Study area

This study was carried out in the Cederberg Mountains and the Sandveld regions in the Western Cape, South Africa. The climate of both regions is Mediterranean with hot dry summers and cool wet winters. The Cederberg forms the northern end of the Cape Fold Mountains and altitude ranges from *c.* 150−2027 m. This study area is dominated by natural Fynbos vegetation and is largely protected by provincial conservation authority, CapeNature (Maree and Vromans 2010). Topography in the Sandveld is generally much flatter, with elevation ranging from sea level up to *c.* 1000 m (see Introduction 'Figure 2'). Nests in this region are generally located on isolated rocky outcrops interspersed through relatively flat plains. There is little formal conservation in the Sandveld, which is consequently highly fragmented for agriculture (Heydenrych 1993, Franke et al. 2011). Nevertheless, this region maintains an important breeding population of Verreaux's eagles (Chapter 2).

GPS data

Adult Verreaux's eagles were caught close to known nest sites between April 2012 and April 2013 in the Sandveld (n=3) and the Cederberg (n=2) (See Chapter 4). Eagles were equipped with University of Amsterdam Bird Tracking System (UvA-BiTS) GPS-loggers (Bouten et al. 2013) using a Teflon backpack-style harness. The tags were scheduled to record a position every two minutes on average during daylight hours. This could be increased to collect high-resolution data for an hour or more daily, depending on the battery capacity and the availability of solar charge. Through the night hourly recordings were made (usually 19:00−07:00 SA Standard Time). The high-resolution segments are the focus of this study, these provide fixes once every 3 seconds, although due to occasional delays in making a GPS fix we include up to 6 seconds as "high-resolution".

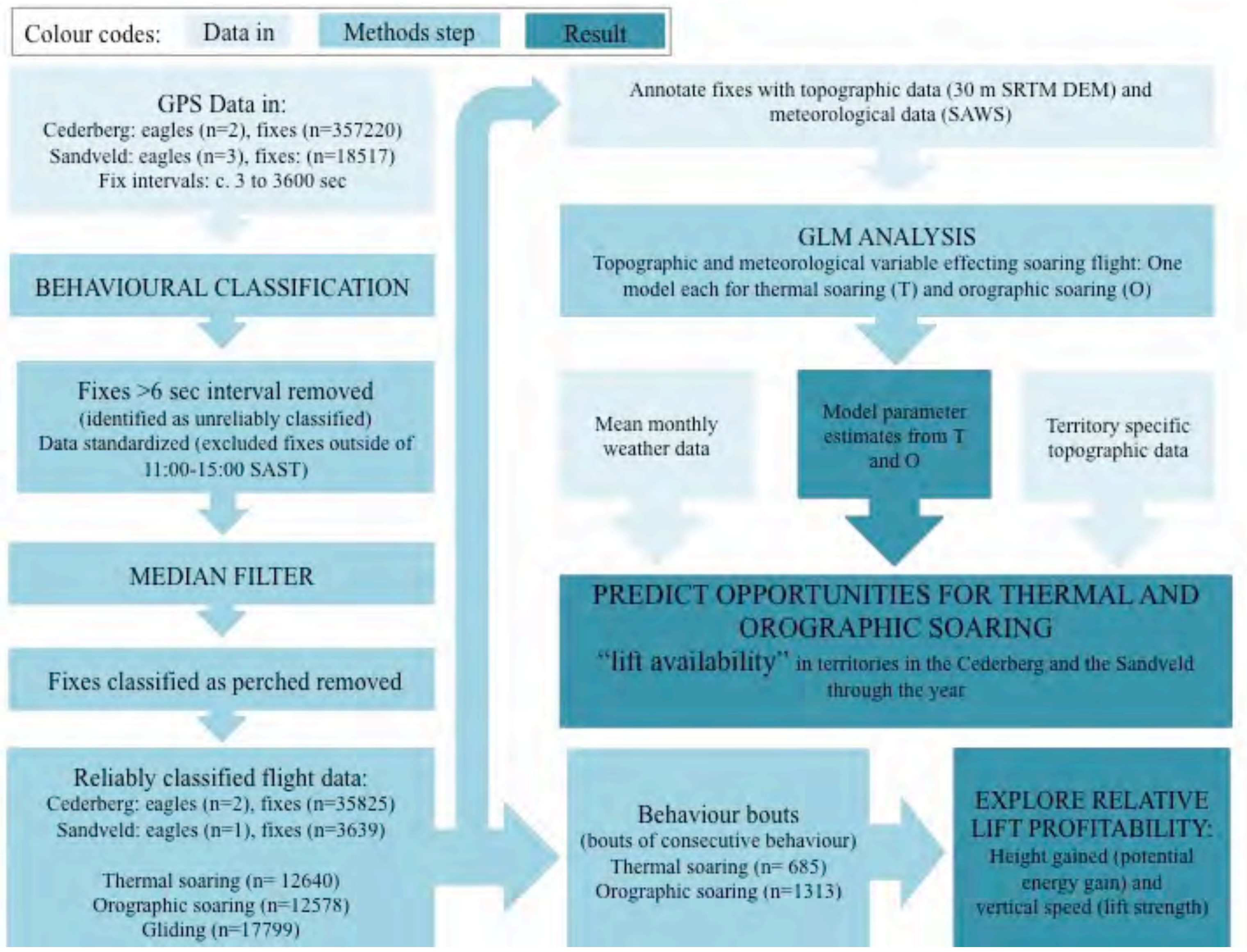


Figure 1. Flow chart showing steps described in methods for understanding flight behaviour of Verreaux's eagles. Abbreviations used: SRTM DEM; 30 m-resolution Shuttle Radar Topography Mission digital elevation model. SAWS; South African Weather Services, this data was recorded every hour at two nearby (*c.* 30 km) weather stations.

Behavioural classification

GPS data from days that featured at least some locations sampled at high-resolution were used for the behavioural classification. The dataset included over 386 000 GPS locations representing 178 days, from five eagles though the contribution of each bird was highly variable (Appendix 1, Figure 1). Although we knew that not all lower resolution data could be accurately classified prior to making behavioural classifications, we were unsure what temporal resolution cut-off point would be necessary to obtain accurate classifications. This meant that some low-resolution data were included in the sample to be classified and we later filtered these out appropriately.

We chose four categories to identify within the tracking data, representing broad behaviours: perched (little change in altitude or horizontal location), gliding (flying and losing altitude), orographic soaring (flying in a roughly straight trajectory without losing altitude) or thermal soaring (spiral-like flying with increasing altitude, and relatively little horizontal movement). Each GPS point was classified as belonging to one of the four behavioural categories, based on features extracted from the adjacent points. Features were extracted from all data points within a window extending 45 seconds either side of the location being considered (i.e. 90 seconds behavioural bouts), referred to as a ‘track segment’, this made it possible to resolve identifiable behaviours with short duration. This was done in order to capture the context of each point along the movement track, instead of considering it in isolation, because this method does not formally acknowledge the time series nature of the data.

A random forest ensemble learning method for classification was used to predict the behaviour associated with each point due to its efficiency and low error rate (Breiman 2001). The supervised learning version of the algorithm was implemented since visualisation of GPS tracks and their movement parameters readily allows for classification of sections into behavioural categories to form a training set. The training set consisted of a random sample of locations representing 10 % of all eagle tracking days including some high-resolution data from all tagged birds. This was done to ensure that individual and temporal differences were represented as adequately as possible in the training set. Training was carried out manually by visualising the tracks and identifying sections corresponding to a category. The movement features used in the random forest as predictors were identified during exploratory data analysis to reflect distinctive characteristics of the different behaviours. For example, a high correspondence between altitude above sea level and altitude above ground level was a good predictor of thermal soaring as these parameters increased in a linear fashion relative to each other. Low speeds were associated with little activity and expected to indicate perching. Regular, cyclical changes in direction were associated with the spiral tracks associated with thermalling behaviour (see Appendix Figure 1 for examples of the movement characteristics typical of each behaviour classifications). Segment length (number of locations in a segment) and the variance of the sampling interval were used to flag potentially unreliable segments. Although these were not used in the behavioural classification, flagged data points such as those with a large sampling interval were used later to help decide the reliability of behavioural classifications.

Although it is easy to pick out by eye the collection of characteristics that describe each of the behaviours, such as the periodic change in direction characteristic of thermalling, it was necessary to describe these formally to include them in the random forest as a predictor. On this basis, six movement features were extracted for each segment of track. First, (i) the mean of the three-dimensional instantaneous speed was calculated. Second, a linear regression model was fitted to altitude above sea level as a function of time, and altitude above ground level as a function of altitude above sea level. A total of four features were extracted from these two linear regression models and used as predictors in the random forest; (ii) the rate of change of altitude above sea level, (iii) the rate of change of altitude above ground level, (iv) the squared correlation coefficient (R^2) for the linear regression model of altitude above sea level against time, and (v) the R^2 for the linear regression model of altitude above ground level against altitude above sea level. The R^2 is a measure of the variability explained by the model and ranges from 0 to 1. A model that explains a high proportion of the variability in the data will have an R^2 close to 1. Lastly, the ‘spectrum’ function in R (R Core Team 2015) was used to estimate the spectral density of the time series of directions within the track segment. Spectral density estimation is a way of breaking down a pattern in a time series that displays sinusoidal periodicity (such as direction during thermalling), and, more specifically, identifying the different frequencies that make up the overall signal (Chatfield 2003). For the sixth movement feature, (vi) the dominant frequency in the time series of direction was extracted, where periodicity in direction results in high dominant frequency, whereas travelling in a relatively straight trajectory results in a low dominant frequency.

Following the behavioural classification, data with sampling intervals less than or equal to 6 seconds were extracted for further analysis, since these data were thought to have the most reliable behavioural classifications. This did not cause any bias towards the detection of any specific behaviour as it occurred independently from the behavioural classification. Due to the tag capabilities and schedules, this dataset was in fact largely (>99 %) data sampled at 3−4 second intervals. It was not possible to reliably resolve behaviours, particularly thermalling, at intervals more than or equal to 10 seconds and no data were collected at 7−9 second intervals. Data were further subsampled into those collected between 11:00−15:00 SAST daily, coinciding with when eagles are most active (Chapter 4) and this is also the period when most high-resolution data were collected. Owing to this subsampling, data from only three of five eagles were reliably classified and used in further analyses.

Meteorological and topographical variables

Topographical variables (elevation (m), slope (°) and aspect (°)) were derived from a 30 m-resolution Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) using the ‘raster’ package (Hijmans et al. 2015) for geographic data analysis and modelling in R Version 3.1.2 (R Core Team 2015). Meteorological variables (wind direction (°), wind speed (m s^{-1}), temperature (C°)) were derived from the South African Weather Services (SAWS) data at hourly intervals. For eagles tracked in the Cederberg we used meteorological data recorded at Clanwilliam (32.1760S, 18.8880E) and for eagles tracked in the Sandveld we used data recorded at Lambert’s Bay (32.0350S, 18.3320E), which are *c.* 30 km from the nest sites of the tracked eagles. Although altitude differences between the location of the meteorological stations and the study areas could influence the accuracy of weather data, this was the most accurate available data for the region.

The angle of incidence (°) between the topographic aspect and wind direction was calculated to account for the expected relationship between these variables on windward and leeward slopes. Values can range from zero to 180°, whereby low values correspond with the wind directly hitting the slope (e.g. a south facing slope and wind coming from the south). Angle of incidence equal to 90° would be equivalent to wind perpendicular to the topographic aspect (e.g. a south facing slope and wind coming from either the east or the west). Highest values correspond with the lowest potential to generate orographic lift, where the wind is coming from directly behind a slope (e.g. a south facing slope and wind coming from the north).

Statistical analysis of flight behaviour

A median filter was applied to the behavioural classification to smooth the data by matching dissimilar single data points with the wider behaviour bout, within windows of five locations (15−30 sec). Following this, all points where eagles were classified as perched were excluded, to focus only on flight behaviour. GPS locations classified as ‘gliding’ were included in the response variable, but owing to the fact that gliding occurs largely independently of the underlying topography and is dependent on altitude gained in prior soaring flights and could be assisted by occasional wing beating (Pennycuick 2008), gliding probabilities could not be tested in the same fashion as soaring. The relationships between soaring flight behaviours (thermal and orographic soaring) and the meteorological and topographical variables were explored using two generalized linear models (GLM) with binomial response variables (i.e. Model T: 1 = thermal soaring; 0 = other flying points; Model O: 1 = orographic soaring; 0 = other flying points) and logit link functions. For the purpose of these models, both aspect and wind direction were classified into one of four cardinal directions. Elevation and slope were additionally included in the models as quadratic variables to account for potential non-linear relationships between uplift behaviours and topography. To examine which variables best explained thermal and orographic soaring a model selection approach was implemented using Akaike’s Information

Criterion with correction for finite sample size (AIC_c). Models were ranked according to their AIC_c score using the ‘MuMIn’ package (Barton 2014) and the most parsimonious model was selected to describe variables associated with the two soaring flight behaviours. Overall model accuracy was assessed using the Area Under the Curve (AUC) value of a Receiver Operating Characteristic (ROC) plot for the most parsimonious model for each soaring flight behaviour (Swets 1988, Robin et al. 2011).

To facilitate interpretation of the model coefficients and their relative influence on predicting soaring flight, the most parsimonious GLM for both soaring flight behaviours was refitted using standardised variables. Variables were standardised by centring (subtracting the sample mean) and scaling (diving by the sample standard deviation) (Schielzeth 2010, Katzenberger et al. 2015). The categorical variables (aspect and wind direction) could not be interpreted in the same way. Therefore, although they were included in the GLM using standardised variables they were excluded from the interpretation of the correlation coefficients. Selection for wind direction and topographic aspect were assessed separately by least squares means with pairwise comparisons (Lenth 2014).

Predicting flight behaviours

A territory was defined as a 3 km buffer around known nest sites, based on previous home range estimates (Chapter 4), which provided a territory area of 28.17 km^2. All known monitored active territories in the core study area (Chapter 2) were included, except for one in the Sandveld (where there was more than 50 % overlap of the territory buffer with the sea) (Cederberg n=19; Sandveld n=18). Topographical data were extracted from the 30 m-SRTM DEM for all grid squares within each territory. The availability of lift is expected to change through the day and through the year with seasonal changes in weather patterns (Duerr et al. 2015). Therefore we investigated lift availability on a territory level each month of the year using meteorological variables recorded at hourly intervals from 07:00−19:00 SAST between 2011−2014, which is inclusive of the tracking period. These meteorological data were derived from SAWS weather stations located at Clanwilliam (for Cederberg territories) and Lambert’s Bay (for Sandveld territories). Monthly averages for each area were calculated for wind speed and temperature. Wind direction was converted to cardinal directions and the most frequently occurring direction was selected for each area each month. Cardinal directions were converted back to degrees (N=0°, E=90°, S=180°, W=225°) for the purpose of calculating the angle of incidence between wind and topography.

Using the inverse logit probability of parameter estimates (β) for the variables in the most parsimonious GLMs, the availability of thermal and orographic lift was predicted in eagle territories (with resolution taken from the original 30 m DEM) for each month of the year. To assess the effects of seasonal changes on overall lift availability, the predicted availability of thermal and orographic lift were combined to get an estimate of the total lift availability. T-tests were used to test for significant differences in the predicted lift availability between the study areas on a monthly basis.

Profitability and strength of lift

To investigate if thermal or orographic soaring was more profitable we investigated parameters of soaring bouts. A bout represented the duration of one type of consecutive flight (thermal soaring or orographic soaring) in the smoothed data. Bouts with less than four fixes were excluded from this analysis. This threshold was *ad hoc* but based on the fact that single data points could not be used in this analysis and we wanted to focus on extended bouts of each soaring behaviour. Lift profitability was reflected by the height gain (m) of soaring bouts and lift strength was reflected by the speed of height gain ($m\ s^{-1}$). T-tests were implemented to test for differences in behaviour parameters between thermalling and orographic soaring.

Results

More than 160 000 GPS locations collected over 130 days from three eagles were reliably classified as one of four behaviours. The overall ‘out of bag’ error rate of the classification tree was 9 %. The class with the highest classification error was orographic soaring (42 %), followed by gliding (19 %) and thermal soaring (18 %), and perching (<1 %) had the lowest classification error, most likely because a large proportion of the training set consisted of that behaviour (Appendix 2). Following temporal subsetting and exclusion of perched points, 43 017 GPS location were classified as flying and used in further analysis (Table 1).

The most parsimonious model for thermal soaring included all variables (Appendix 3). The AUC value for this model was 0.625. Thermal soaring showed a significant quadratic correlation with elevation (Figure 2, Table 2). Below *c*. 750 m variations in elevation had little effect on the probability of thermal soaring, above this height the likelihood decreased. There was a significant quadratic relationship between thermal soaring and slope (Figure 2, Table 2). Probability of thermal soaring was highest in flat areas and decreased as the angle of the slope increased, although steep slopes were also selected for this behaviour. There was a positive correlation between temperature and thermal soaring, although the effect of this was small (Figure 2, Table 2). Thermal soaring showed a negative correlation with wind speed (Figure 2, Table 2). Thermal soaring favoured wind coming from the south. North and west facing aspects were preferred for thermalling (Figure 3 (a)). However, the particular use of slopes will depend on the interaction between wind direction and aspect and this was evident in the positive correlation between thermal soaring and the angle of incidence between these variables (v) (Table 2). Thus, thermal soaring occurs most often on flat ground when it was hot and still and on leeward sides of slopes.

Table 1. Summary of Verreaux's eagle GPS data reliably classified into flight categories (g, gliding: o, orographic soaring; t, thermal soaring) and used in further analysis. *n* unique days is the number of different days per eagle which contributed data.

Eagle id	Area	Date range	*n* unique days	*n* fixes g	o	t
721	Cederberg	08/04/2012−14/04/2012	3	710	639	333
722	Cederberg	09/10/2012−20/03/2013	121	15778	10942	10976
723	Sandveld	26/08/2012−11/09/2012	6	1311	997	1331

The most parsimonious model for orographic soaring included all variables except for the quadratic term for slope (Appendix 4). The AUC value for this model was 0.634. Orographic soaring showed a quadratic correlation with elevation (Figure 2, Table 3), where there was little effect of elevation on orographic soaring below *c.* 750 m and the probability of orographic soaring increased with elevation thereafter. Orographic soaring also showed a positive correlation with slope (Figure 2, Table 3) and wind speed (Figure 2, Table 3) and a negative correlation with temperature, although the effect of this was small (Figure 2, Table 3). Similar to thermal soaring, north and west facing slopes were favoured for orographic soaring, however, wind coming from the north or east direction which is expected to favour the formation of orographic lift (Figure 3b) and this was reflected in the negative relationship with ‘v’ (Table 3). Thus, orographic soaring occurs most often on steep sided slopes at high elevations, and in windy conditions, which produces strong orographic lift.

Elevation and slope had highest greatest influence for predicting both orographic and thermal soaring (Figure 4). The next most important variable determining both flight behaviours was wind speed. High wind speed favours orographic soaring and low wind speed favours thermal soaring. The effect size of temperature and angle of incidence between topography aspect and wind direction were relatively small.

Table 2. Slope coefficients (β) from most parsimonious model predicting the likelihood of thermal soaring by Verreaux's eagles in the Cederberg and the Sandveld, South Africa. Model parameters abbreviations: elev, elevation; elev^2, quadratic term; slope, topographic slope; slope^2, quadratic term; aspect, topographic aspect, four categories; temp, temperature; w.dir, wind direction, four categories; w.speed, wind speed; v, angle of incidence between aspect and w.dir (calculated in degrees).

					Confidence Intervals	
	β	SE	z value	p value	2.5 %	97.5 %
(Intercept)	-0.454	0.091	-5.003	5.64E-07	-0.632	-0.276
elev	0.001	1.16E-04	5.602	2.12E-08	4.24E-04	0.001
elev^2	-7.19E-07	5.76E-08	-12.495	< 2E-16	-8.32E-07	-6.07E-07
slope	-0.039	0.003	-13.903	< 2E-16	-0.044	-0.033
slope^2	0.001	5.07E-05	10.182	< 2E-16	4.17E-04	0.001
w.speed	-0.138	0.011	-13.021	< 2E-16	-0.159	-0.117
aspect N	0.084	0.040	2.093	0.036	0.005	0.162
aspect S	-0.018	0.031	-0.568	0.570	-0.078	0.043
aspect W	0.125	0.033	3.766	1.66E-04	0.060	0.190
w.dir N	-0.020	0.039	-0.521	0.603	-0.097	0.057
w.dir S	0.136	0.033	4.109	3.98E-05	0.071	0.201
w.dir W	0.119	0.037	3.231	0.001	0.047	0.191
temp	0.017	0.002	7.475	7.70E-14	0.013	0.022
v	0.001	2.24E-04	3.991	6.57E-05	4.55E-04	0.001

Table 3. Slope coefficients (β) from most parsimonious model predicting the likelihood of orographic soaring by Verreaux's eagles in the Cederberg and the Sandveld, South Africa. Model parameters abbreviations: elev, elevation; elev^2, quadratic term; slope, topographic slope; aspect, topographic aspect, four categories; temp, temperature; w.dir, wind direction, four categories; w.speed, wind speed; v, angle of incidence between aspect and w.dir (calculated in degrees).

					Confidence Intervals	
	β	SE	z value	p value	2.5 %	97.5 %
(Intercept)	-1.112	0.092	-12.087	< 2E-16	-1.292	-0.932
elev	-0.001	1.14E-04	-8.044	8.70E-16	-1.14E-03	-0.001
elev^2	4.56E-07	5.48E-08	8.313	< 2E-16	3.48E-07	5.63E-07
slope	0.031	0.0009	33.825	< 2E-16	0.029	0.032
w.speed	0.116	0.010	11.627	< 2E-16	0.097	0.136
aspect N	0.095	0.042	2.233	0.03	0.011	0.177
aspect S	-0.022	0.032	-0.684	0.49	-0.084	0.041
aspect W	0.066	0.034	1.934	0.05	-8.16E-04	0.133
w.dir N	0.165	0.038	4.340	1.43E-05	0.090	0.239
w.dir S	-0.150	0.033	-4.546	5.45E-06	-0.215	-0.085
w.dir W	-0.125	0.036	-3.453	5.53E-04	-0.195	-0.054
temp	-0.008	0.002	-3.443	5.76E-04	-0.012	-0.003
v	-0.002	2.28E-04	-6.936	4.04E-12	-0.002	-0.001

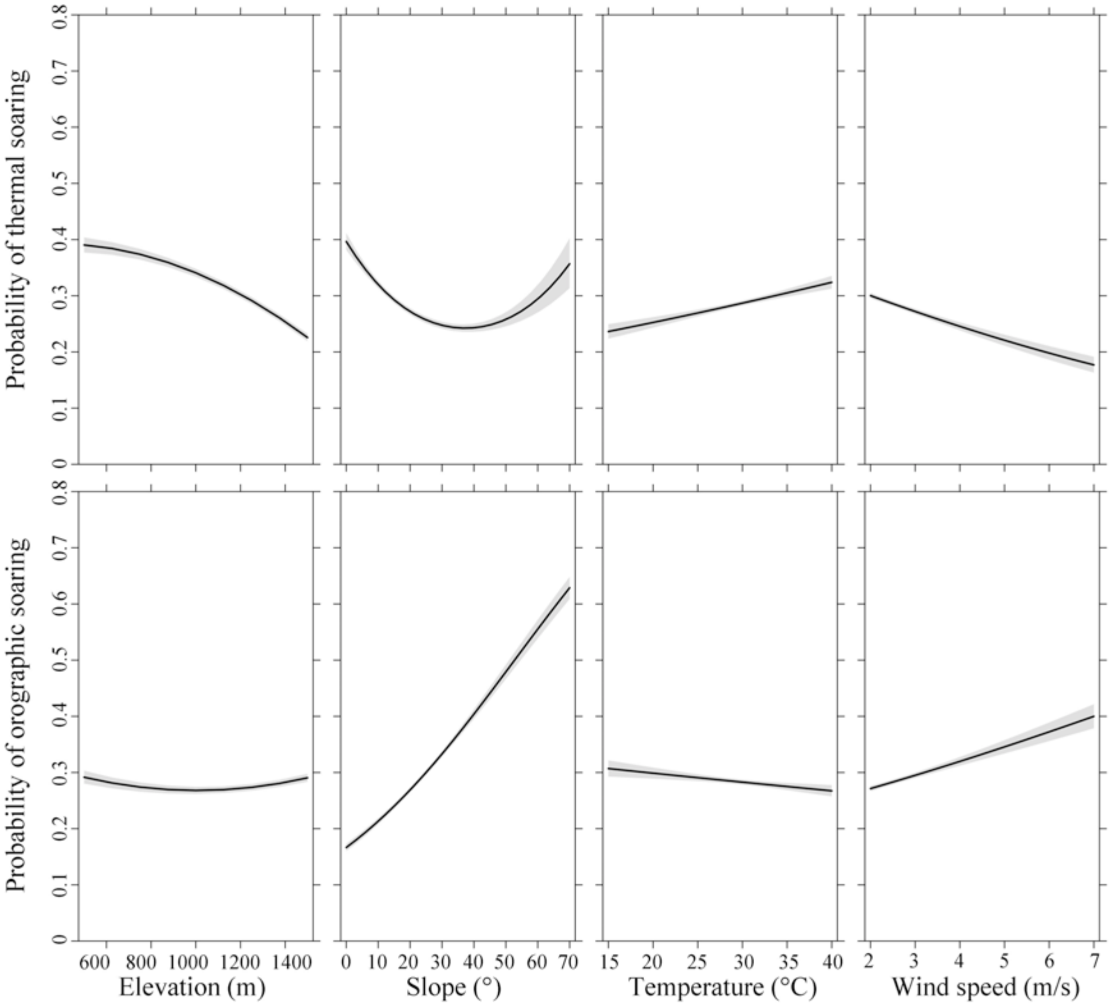


Figure 2. The effects of topographic (elevation and slope) and meteorological (temperature and wind speed) variables on soaring probability (thermal and orographic soaring) by Verreaux's eagles. Where quadratic variables were significant, these have been displayed instead of linear relationships (i.e.: elevation and slope). Grey shading shows 95 % confidence limits.

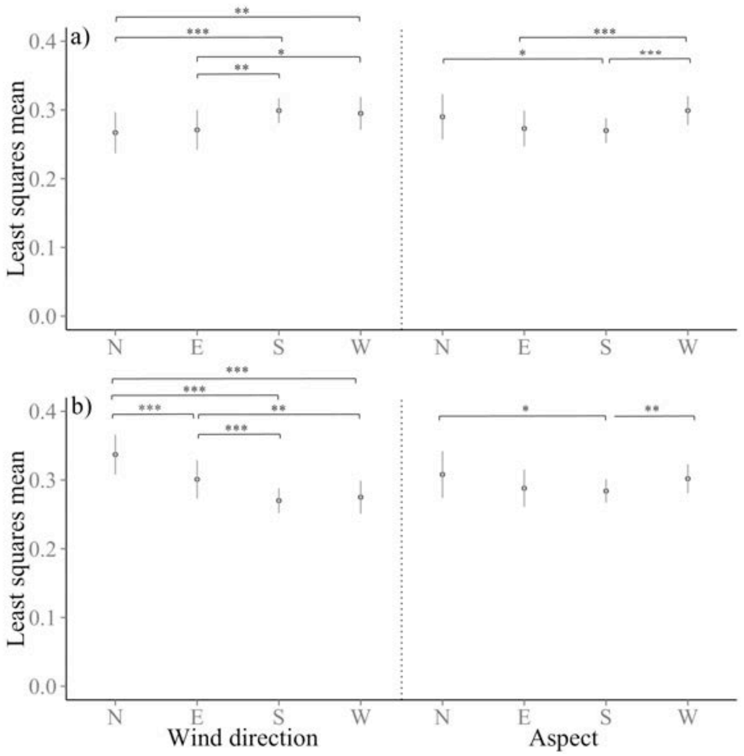


Figure 3: Least squares means showing relative use of wind direction and topographic aspect for a) thermal soaring and b) orographic soaring by Verreaux’s eagles.

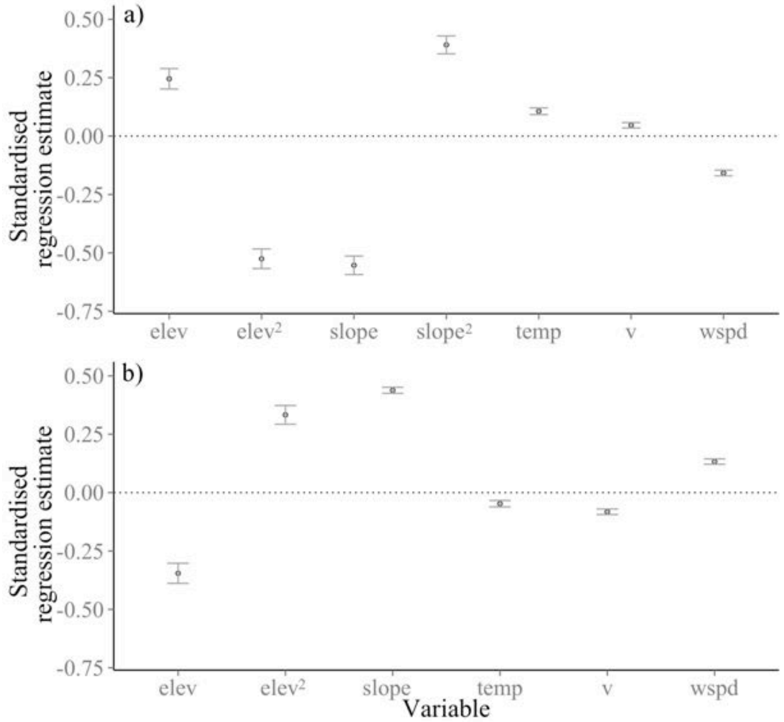


Figure 4. Standardised regression estimates from GLMs fitted on standardised data to determine the correlates of a) thermal soaring and b) orographic soaring in Verreaux’s eagles. Bars show standard error. Terms with the highest deviance from 0 (dotted line) in either direction have the largest influence in predicting soaring flight behaviours. Variable abbreviations: Elevation (elev); quadratic term (elev^2); slope; quadratic term (slope^2); temperature (temp)’ angle of incidence between topography aspect and wind direction (s); wind speed (wspd).

Soaring lift availability was predicted in territories in the Cederberg and the Sandveld. The predicted availability of lift varied through the year (Figure 5). Predicted thermal lift availability was generally highest outside of the breeding season (during summer months). Predicted orographic lift availability was highest during the breeding season (winter months). These differences were largely driven by change in the prevailing wind speed and direction.

The predicted availability of thermal lift was significantly higher during all months for territories in the Sandveld compared to the Cederberg (Figure 5, Appendix 6). The predicted availability of orographic lift was higher in territories in the Cederberg than the Sandveld from February to April and during September. Owing to northerly wind direction (favoured for orographic soaring) in the Sandveld (Appendix 5) and a reduction in wind speed in the Cederberg (Appendix 5); predicted orographic lift availability was higher in territories in the Sandveld than the Cederberg from May to August (Figure 5, Appendix 6).

The total predicted lift availability was significantly greater in territories in the Sandveld than the Cederberg throughout the year (Figure 5, Appendix 6). Between-territory variations in soaring opportunities were greater in the Cederberg than the Sandveld, evident in the larger error bars (Figure 5).

The differences in lift opportunities were illustrated for all study nests in the Cederberg and the Sandveld during one month (May) (Figure 3). It is evident that the flatter terrain, which is more prevalent in the Sandveld is favourable for thermal soaring and steep slopes are favourable for orographic soaring.

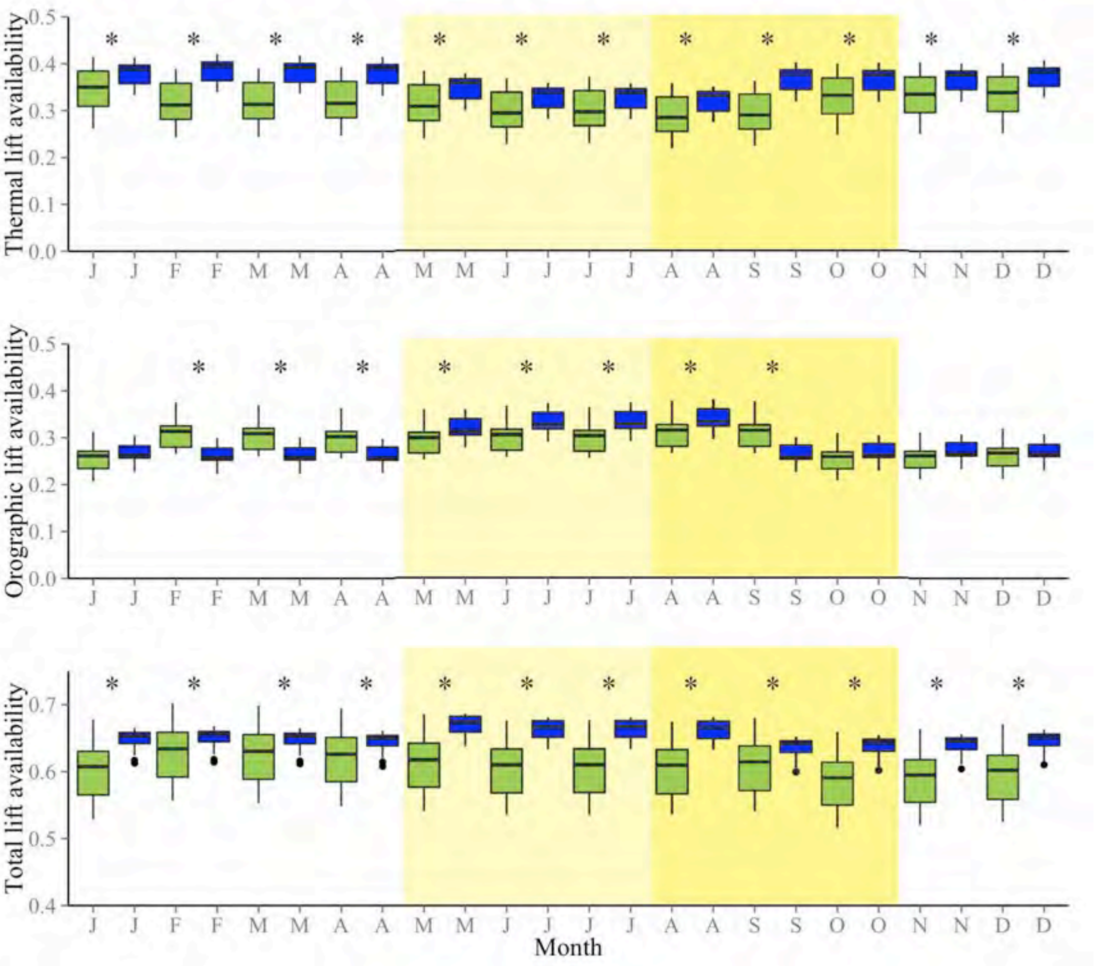


Figure 5: Predicted thermal, orographic and total lift availability in Verreaux's eagle territories in the Cederberg (Green, *n*=19) and the Sandveld (Blue, *n*=18) through the year. Approximate breeding period indicated by yellow shading: pale yellow=incubation, dark yellow=nestling phase. *Indicates significant differences on a monthly basis between the study areas. The upper and lower whiskers extend from the box to the highest and lowest territory values that are within 1.5 times the interquartile range. Values outside of this range are considered outliers and are represented by black dots.

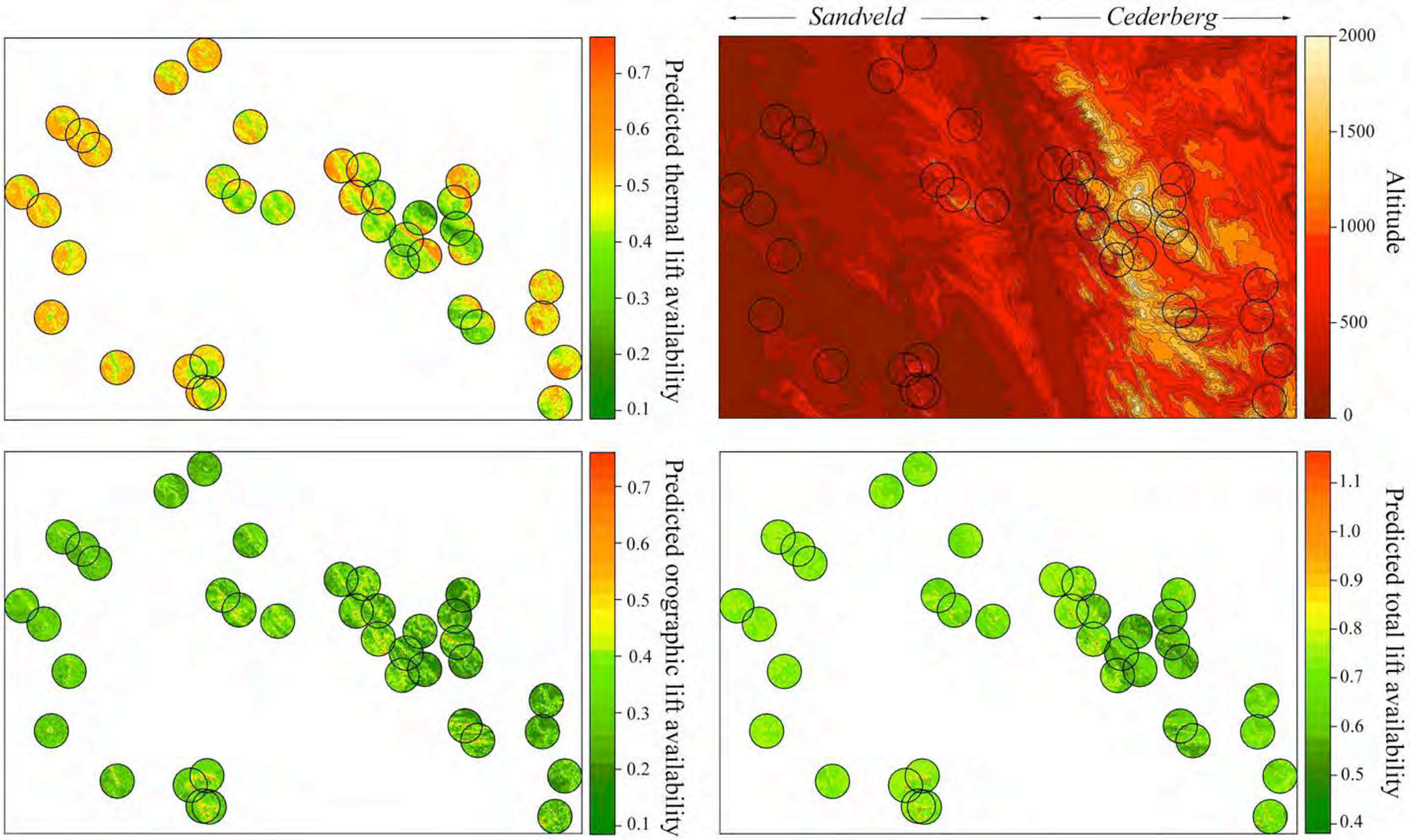


Figure 6. Maps showing predicted thermal, orographic and total lift availability on Verreaux's eagle territories (3 km radius circular buffers around known nest sites) in the Cederberg (n=19) and the Sandveld (n=18). Digital elevation model demonstrates topographic differences between the study areas.

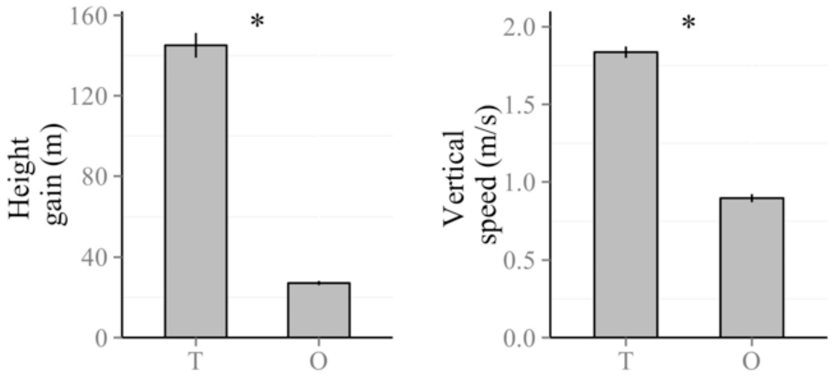


Figure 7. Descriptions of flight behaviour bouts by Verreaux's eagles (*n*=3) with standard error bars. T= Thermal Soaring (*n*=639), O= Orographic soaring (*n*=1130). Significant differences (*) tested by t-test.

A total of 1769 bouts of soaring flight behaviour were identified (Figure 7, Appendix 7). Height gained and vertical speed of thermal soaring bouts (145.1 ±6.1 m; 1.8 ±0.04 ms^{-1}) were significantly greater than that of orographic soaring bouts (27.1 ±1.1 m; 0.9 ±0.03 ms^{-1}) (height gained: t= 3.57, df= 207.60, p <0.001; speed: t= 11.20, df= 272.19, p <0.001).

Discussion

High-resolution GPS tracking data from Verreaux's eagles allowed the differentiation of fine scale responses to the spatially and temporally variable environment in which flight occurs. We found that the use of lift by eagles follows patterns that can be explained by an understanding of the formation of thermal and orographic lift (Brandes and Ombalski 2004, Bohrer et al. 2012, Katzner et al. 2015). The sample size of eagles that are predictions are based on remains small, however, this study illustrates the potential use of the methods developed here.

Topographic variables and meteorological variables contributed to determining the method of soaring. In line with our prediction (i), thermal soaring usually occurred over flat topography at lower elevations. There was additional evidence that eagles also use steep slopes to some extent for thermal soaring opportunities. Rocky mountain slopes facing the sun have the ability to heat up faster than flatter surfaces below, and this can result in the formation of good thermal lift (Shamoun-Baranes et al. 2003). High wind speed causes turbulence which tends to break down or inhibit the formation of thermals (Bohrer et al. 2012, Shepard and Lambertucci 2013) and this was evident in the selection for low wind speed and leeward locations for thermal soaring. In contrast to thermal soaring, eagles tend to use orographic soaring on the windward rather than the leeward side of a cliff or slope (Bohrer et al. 2012). Our results supported this, where winds coming from a northerly direction and north-facing slope were preferred for their low angle of incidence between terrain aspect and wind direction, which drives air movements over topographic features to create orographic lift. The slope angle and wind speed also had a positive correlation with orographic soaring, which are known to contribute to increased orographic lift availability or strength (Bohrer et al. 2012). Overall these results were in agreement with our second prediction (ii) that orographic soaring favoured windward slopes at higher elevations, and times of increased wind speed.

Using these correlates of soaring flight it was possible to predict the spatiotemporal likelihood of soaring and this reflected the predicted availability of thermal and orographic lift across the wider landscape. Although the monthly weather scenarios represent average, not actual dynamically changing conditions in the territories, our results are a reflection of the contrasting environments during the period when breeding data were collected (Chapter 2) and the same methods could be applied to measure differences in lift availability for any given meteorological scenario. Nevertheless, in accordance with prediction (iii), the predicted availability of thermal lift was higher in eagle territories in the Sandveld than the Cederberg. This was consistent for every month of the year and was driven by the flatter topography in the Sandveld compared to the Cederberg, which has a large effect on generating lift. To some extent the predicted availability of orographic lift was greater in territories in the Cederberg than the Sandveld. However, contrary to prediction (iv), from May to August which inclusive of a large proportion of the breeding season, predicted orographic lift availability was actually higher in the Sandveld than the Cederberg.

This was driven by a change in prevailing wind direction in the Sandveld, which favoured orographic soaring.

The availability of both lift types was subject to seasonal fluctuations. Warm temperature and low wind speed induces the formation and strength of thermals (Bohrer et al. 2012) and this was evident in the increase in predicted thermal lift availability during austral summer months, outside of the breeding season. A greater use of thermal soaring in the summer season, compared to the winter, has been recorded in other large raptors (Nathan et al. 2012). During the breeding season, the availability of orographic lift tended to increase, largely caused by changes in wind.

Despite the greater predicted availability of orographic lift in the Cederberg than the Sandveld territories during some months, the consistently higher predicted thermal lift availability in the Sandveld than the Cederberg meant that the relatively flat Sandveld has greater total predicted lift availability. This demonstrates that contrary to usual expectations, the flatter Sandveld area might actually present preferable flight habitat with more widespread lift availability compared to the mountainous Cederberg area. The large inter-territory variations in predicted lift availability in the Cederberg might be interpreted as the difference between good and bad quality territories for eagles.

Further information on the relative energy requirements of eagles in each area would benefit our understanding of the relative costs incurred by eagles inhabiting contrasting environments. Migration of golden eagle is faster and more energetically efficient when thermal soaring combined with gliding is used compared to orographic soaring (Duerr et al. 2012), and migratory flight has been positively correlated with weather conditions promoting thermal lift, suggesting eagles preferentially travel when conditions favour thermal soaring over orographic soaring (Duerr et al. 2015). However whether these advantages would apply equally to resident eagles ranging within their own territories is debatable. Terrain ruggedness has been identified as an important determinate of increased heart rate in turkey vultures *Cathartes aura* due to its presumed effect on decreasing the spatiotemporal predictability of uplift (Mandel et al. 2008), potentially representing the cost associated with soaring in highly variable mountainous conditions. Therefore eagles living in conditions suited to orographic soaring could incur greater energetic costs of flight.

The relative strength of lift is important for determining the potential energy gain or lift profitability. The vertical velocity of soaring birds is expected to increase with the strength of the lift source being exploited (Shannon et al. 2002). As a proxy for lift profitability, the altitude gained during bouts of soaring flights was examined. This analysis is based on a small sample of eagles and the effects of meteorological conditions during the time of data collection have not been accounted for. Accepting these limitations, differences between lift sources were found. The altitude gained while thermal soaring was greater than that gained while orographic soaring and the vertical speed of thermal soaring was significantly faster than orographic soaring. This demonstrates the greater capacity for potential energy gain from thermal lift than orographic lift. However, this is only one measure of usefulness and an important aspect of interpreting these results is the behavior with which each lift form is associated. Thermal lift might be beneficial for cross-country flying, but less useful for foraging, where eagles will need to maintain visibility of the ground (Shepard et al. 2011). Therefore the relative usefulness of lift forms in day-to-day behaviour should be further investigated.

Overall, these results indicate that the Sandveld is characterized by better lift availability in comparison to the Cederberg and the predominant lift form (thermal) is likely to be more energetically profitable than the predominant lift form (orographic) in the Cederberg Mountains. If thermal soaring is more energetically beneficial than orographic soaring and there is better availability of lift in the Sandveld, these differences could contribute to the significantly higher breeding productivity of eagles in the Sandveld than the Cederberg (Chapter 2). The large variability in lift availability between territories in the Cederberg might relate to the large discrepancies in the productivity of specific territories in the area (pers. obs). Higher energetic costs will require greater prey availability and food intakes for them to be energetically plausible (Wilson et al. 2011), otherwise a negative effect on population demography and individual fitness would be expected (Weimerskirch et al. 2012).

The AUC values for both models were low (Thermal soaring= 0.625, Orographic soaring=0.634) suggesting poor model fit. This could in part be due to the small sample size of eagles used in the analysis and the disproportionately large contribution of data from one eagle alone. Further tacking studies would alleviate this problem and therefore strength the ecological inferences of the results. In checking the behavioural classification rates, some behavioural states were particularly prone to error. In particular discerning orographic soaring from gliding was difficult. Improvement of the behavioural classification might benefit the model fit and might be achieved by other methods such as Hidden Markov Methods (Michelot et al. 2016).

Other limitations that we were unable to address in the study also persist. For example, the use of other variables which have been associated with good soaring conditions, including atmospheric boundary layer height, surface sensible heat flux and cloud cover were explored (Spaar et al. 2000, Shamoun-Baranes et al. 2006, Bohrer et al. 2012, Vansteelant et al. 2014b). However, the coarse temporal and spatial resolution of the data available (*c.* 80 km, 6 hourly intervals (ECMWF 2015)) did not sufficiently represent the fine scale responses of birds, particularly when considering localized lift availability, and so these variables could not be incorporated into the analyses. Further to this, the spatiotemporal variation of irrigation in the Sandveld could not be accounted for. Greater evapotranspiration occurs when fields are irrigated and this will affect the atmospheric boundary layer and reduce the potential for thermals to form (Miller 1984, Bohrer et al. 2012, Cammalleri et al. 2014). Spatiotemporal records of irrigation would help assess this factor in the future and this will be relevant to investigating if irrigation contributed to the avoidance of areas with no natural vegetation (Chapter 4). In the same manner, vegetation cover or habitat type contributes to the capacity for the absorption of solar energy and this affects the formation of thermal lift (Miller 1984).

The quadratic relationship between elevation and soaring flights could be a regional effect caused by the lack of an overlap in the elevation range of the study areas. This was investigated in an ad hoc way by running the same models for both soaring flight behaviours separately for each study area. The results corresponded with the initial findings with a general decline in the probability of thermal soaring at higher elevations and a positive correlation between orographic soaring and elevation (Appendix Figure 2). Interestingly, in the Cederberg the quadratic relationship showed an increase in the probability of thermal soaring at very high elevations, which could be due to the ability of high elevation mountain slopes to heat up and generate thermals.

In order to address the limitation of the absence of information on the internal state of the eagles in each behavioural mode we would require further technical or methodological advances (Nathan et al. 2008), such as heart rate monitors (Mandel et al. 2008, Duriez et al. 2014) to estimate energetic efficiencies or the relative costs of flight behaviours. Accelerometers are useful in assessing energy expenditure in terrestrial animals by calculating factors such as the overall dynamic body acceleration (ODBA) (Halsey et al. 2008, 2009) and can also be used to distinguish between flight modes in birds (Halsey et al. 2011, Williams et al. 2015). However ODBA is likely to be affected by air turbulence making it difficult to make similar assessments of energy expenditure for different flight modes (Gleiss et al. 2011). The use of accelerometers could also allow additional information such as flapping flight (Williams et al. 2015), prey strikes (Harper et al. 1991, Volpov et al. 2015) or feeding behaviour (Kays et al. 2011, Nathan et al. 2012) to be captured, which would help elucidate the ultimate purpose of movements. Flight behaviour can determine the ability to find and capture prey, travel long distances or make a visible presence within a territory. Therefore, movement behaviour can be indicative of the purpose of flights (Nathan et al. 2008). For example, Montagu’s harrier *Circus pygargus* use intricate sky-dancing display flights to demonstrate fitness or quality during the pre-lay period (Arroyo et al. 2013) and hovering is commonly used by small raptors to maintain a static position while foraging (Brown 1976). Although our tags included accelerometer devices, the temporal resolution of the accelerometer data collected was low and in this scenario we were able to infer more behavioural information from the high-resolution GPS data than the sparse accelerometer data.

This study develops novel methods to predict flight behaviour and lift availability using high resolution GPS data and widely available topographic data and meteorological information. This is made possible largely by the association of such behaviours with topographic features, which drive uplift and the potential for energy-saving flight techniques. These methods could be applied to any soaring species for which high resolution GPS data has been collected. Improved knowledge of flight behaviours can be used for modelling potential anthropogenic risks, in particular the effects of wind turbines and associated energy infrastructure (McLeod et al. 2002, Reid et al. 2015). Thus, it will be important to extend this research to model and mitigate future risk, particularly in light of the proliferating wind energy industry globally (Reid et al. 2015).

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Appendices

Appendix 1. Summary of Verreaux's eagle GPS tacking data collected in the Cederberg and the Sandveld, South Africa from 2012−2013, used for behavioural classification. *n* unique days is the number of different days per eagle which data was collected on.

Eagle id	Area	*n* unique days	*n* fixes
721	Cederberg	4	9890
722	Cederberg	165	347330
723	Sandveld	7	15669
726	Sandveld	1	1329
727	Sandveld	1	1519

Appendix 2. Confusion matrix of behavioural classifications of Verreaux's eagle tracking data, with class error. Abbreviations: t, thermal soaring; g, gliding; o, orographic soaring; p, perched.

		Predicted				
		t	g	o	p	Class error
Observed	t	1499	49	275	7	0.181
	g	30	1922	288	155	0.198
	o	275	340	1000	110	0.420
	p	0	62	24	11845	0.007

Appendix 3. Results from the top three models ranked by AICc value, comparing model fit for thermal soaring probability by Verreaux's eagles. Model parameters abbreviations: elev, elevation; elev^2, quadratic term; slope, topographic slope; slope^2, quadratic term; aspect, topographic aspect, four categories; temp, temperature; w.dir, wind direction, four categories; w.speed, wind speed; v, angle of incidence between aspect and w.dir (calculated in degrees). Other column abbreviations: df, degrees of freedom; logLik, log likelihood; ΔAICc, change in AICc relative to the highest ranked model; w_i, AICc weight. The most parsimonious model is shown in bold.

Model	df	logLik	AICcΔ	w_i
elev+elev^2+aspect+slope+slope^2+temp+w.dir+w.speed+v	**14**	**-25174.67**	**0**	**0.999**
elev+elev^2+aspect+slope+slope^2+temp+w.dir+w.speed	13	-25182.65	13.95	0.001
elev+elev^2+aspect+slope+slope^2+temp+w.speed+v	11	-25189.74	24.12	0

Appendix 4. Results from the top three models ranked by AICc value, comparing model fit for orographic soaring probability by Verreaux's eagles. Model parameters abbreviations: elev, elevation; elev^2, quadratic term; slope, topographic slope; slope^2, quadratic term; aspect, topographic aspect, four categories; temp, temperature; w.dir, wind direction, four categories; w.speed, wind speed; v, angle of incidence between aspect and w.dir (calculated in degrees). Other column abbreviations: df, degrees of freedom; logLik, log likelihood; ΔAICc, change in AICc relative to the highest ranked model; w_i, AICc weight. The most parsimonious model is shown in bold.

Model	df	logLik	AICcΔ	w_i
elev+elev^2+aspect+slope+temp+w.dir+w.speed+v	**13**	**-25027.91**	**0**	**0.517**
elev+elev^2+aspect+slope+slope^2+temp+w.dir+w.speed+v	14	-25027	0.19	0.47
elev+elev^2+aspect+slope+slope^2+w.dir+w.speed+v	13	-25032.58	9.35	0.005

Appendix 5. Monthly average weather variables in derived from the South African Weather Services (SAWS) data at hourly intervals between 7:00−19:00 SAST from 2011−2014, recorded at Clanwilliam (32.1760S, 18.8880E) for the Cederberg and Lambert's Bay (32.0350S, 18.3320E) for the Sandveld.

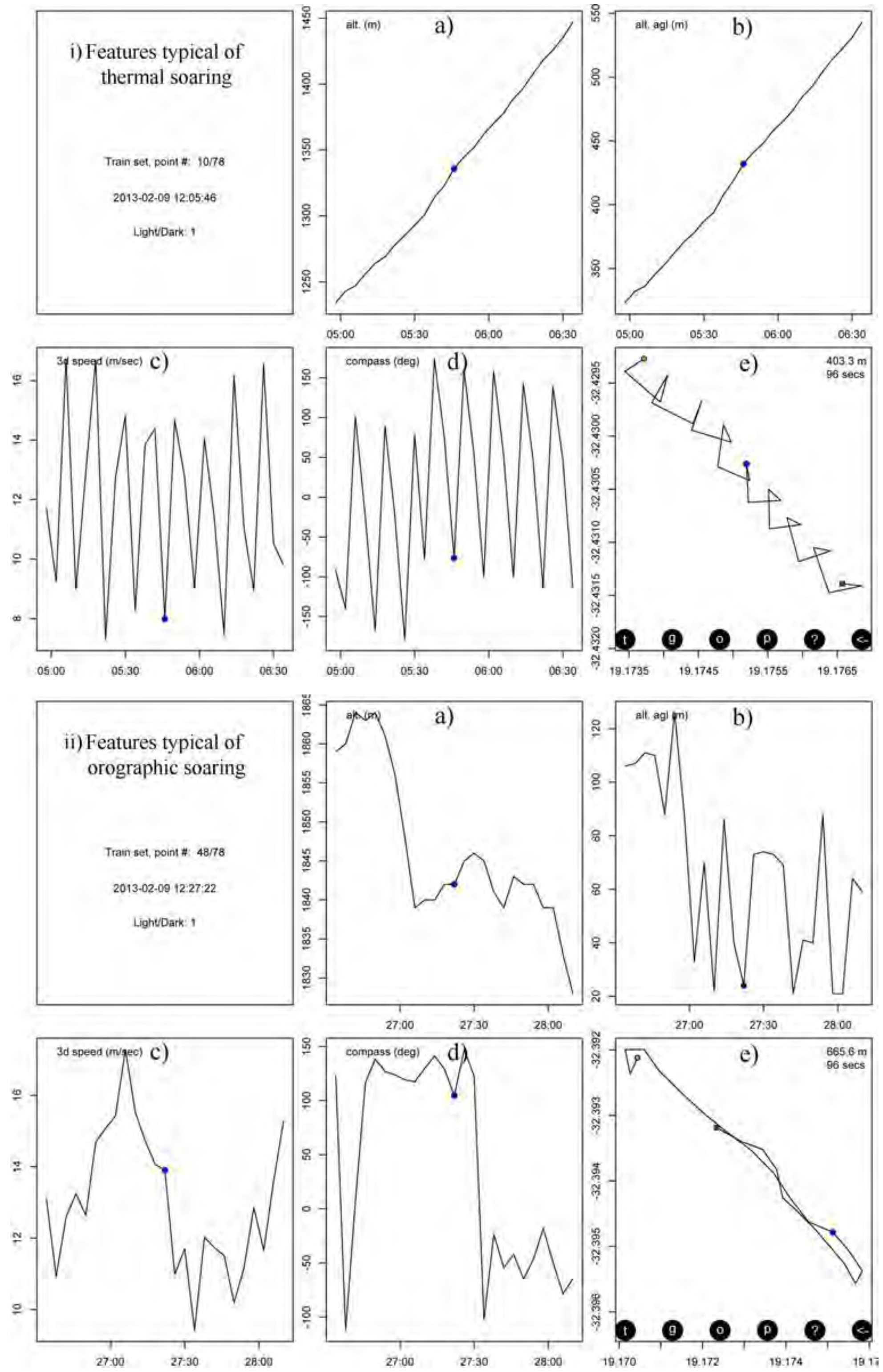
	Cederberg			Sandveld		
Month	Temp (°C)	Wind speed m s^{-1}	Wind direction	Temp (°C)	Wind speed m s^{-1}	Wind direction
Jan	30.3	2.6	W	22.0	3.6	W
Feb	30.0	2.5	N	21.9	3.3	W
Mar	27.4	2.1	N	20.6	3.3	W
Apr	24.1	1.6	N	20.4	3.4	S
May	19.2	1.2	N	16.5	2.7	N
Jun	15.3	1.2	N	14.6	3.1	N
Jul	15.3	1.1	N	14.9	3.2	N
Aug	15.9	1.6	N	14.8	3.4	N
Sep	18.8	1.8	N	16.4	3.3	S
Oct	23.1	2.4	S	18.4	3.6	S
Nov	25.7	2.6	S	20.0	3.8	S
Dec	28.4	2.8	W	21.2	3.6	W

Appendix 6. Monthly average (±SD) predicted (thermal, orographic and total) soaring availability in Verreaux’s eagle territories in the Cederberg (*n*=19) and the Sandveld (*n*=18) and the results from t-tests to identify significant differences in lift opportunities per month between the study areas. Significant differences ($p<0.05$) are in bold).

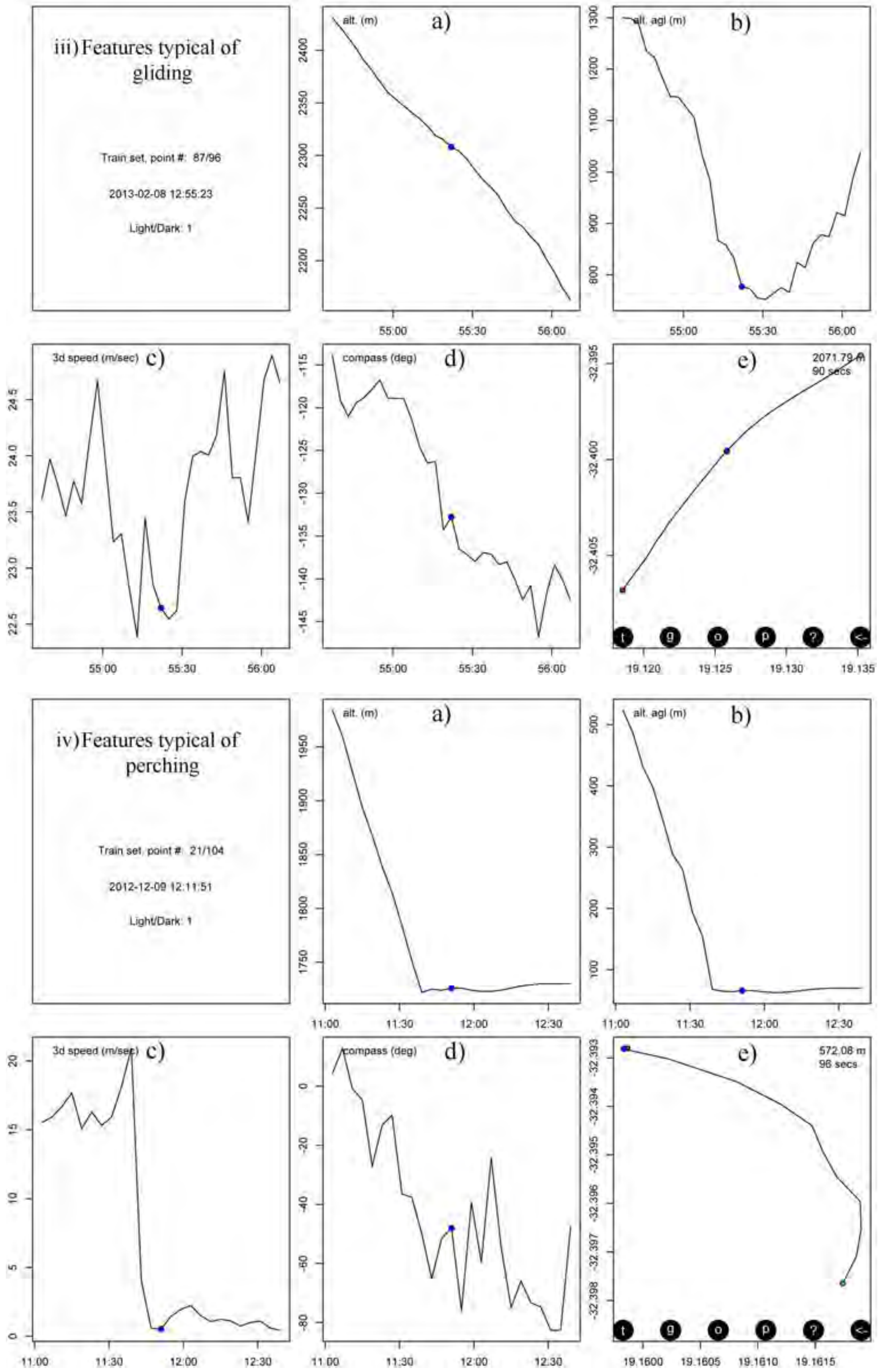
	Cederberg	Sandveld	t	df	p
Thermal Soaring					
Jan	0.34 ±0.05	0.38 ±0.03	-2.82	27.93	**0.009**
Feb	0.32 ±0.04	0.39 ±0.03	-5.79	28.95	**2.87E-06**
Mar	0.32 ±0.04	0.38 ±0.03	-5.40	28.84	**8.56E-06**
Apr	0.32 ±0.05	0.38 ±0.03	-5.04	28.80	**2.32E-05**
May	0.31 ±0.04	0.35 ±0.03	-2.96	28.79	**0.006**
Jun	0.30 ±0.04	0.33 ±0.02	-2.59	28.74	**0.015**
Jul	0.30 ±0.04	0.33 ±0.02	-2.28	28.62	**0.030**
Aug	0.29 ±0.04	0.32 ±0.02	-2.85	28.86	**0.008**
Sep	0.29 ±0.04	0.37 ±0.03	-6.41	29.37	**4.96E-07**
Oct	0.33 ±0.05	0.37 ±0.03	-3.13	27.95	**4.10E-03**
Nov	0.33 ±0.05	0.37 ±0.03	-2.89	27.88	**0.007**
Dec	0.33 ±0.05	0.37 ±0.03	-3.34	28.11	**2.35E-03**
Orographic Soaring					
Jan	0.26 ±0.03	0.27 ±0.02	-1.60	31.87	0.119
Feb	0.31 ±0.03	0.26 ±0.02	5.40	31.49	**6.59E-06**
Mar	0.31 ±0.03	0.26 ±0.02	4.79	31.65	**3.75E-05**
Apr	0.30 ±0.03	0.26 ±0.02	4.25	31.34	**1.79E-04**
May	0.30 ±0.03	0.32 ±0.02	-2.76	33.57	**0.009**
Jun	0.30 ±0.03	0.33 ±0.02	-3.51	33.64	**1.31E-03**
Jul	0.30 ±0.03	0.34 ±0.02	-3.91	33.70	**4.27E-04**
Aug	0.31 ±0.03	0.34 ±0.02	-3.17	33.53	**3.26E-03**
Sep	0.31 ±0.03	0.27 ±0.02	5.41	31.06	**6.56E-06**
Oct	0.25 ±0.03	0.27 ±0.02	-1.91	32.53	0.065
Nov	0.26 ±0.03	0.27 ±0.02	-2.01	32.54	0.052
Dec	0.26 ±0.03	0.27 ±0.02	-1.26	31.73	0.218
Total Soaring					
Jan	0.60 ±0.05	0.65 ±0.02	-4.30	22.49	**2.78E-04**
Feb	0.63 ±0.05	0.65 ±0.02	-2.08	22.67	**0.049**
Mar	0.62 ±0.05	0.65 ±0.02	-2.15	22.64	**0.043**
Apr	0.62 ±0.05	0.64 ±0.02	-2.25	22.50	**0.035**
May	0.61 ±0.05	0.67 ±0.02	-5.37	22.41	**2.05E-05**
Jun	0.60 ±0.04	0.66 ±0.02	-5.63	22.43	**1.10E-05**
Jul	0.60 ±0.04	0.66 ±0.02	-5.61	22.41	**1.15E-05**
Aug	0.60 ±0.04	0.66 ±0.02	-5.66	22.49	**9.96E-06**
Sep	0.61 ±0.04	0.63 ±0.02	-2.59	22.64	**0.017**
Oct	0.58 ±0.04	0.64 ±0.02	-4.91	22.54	**6.10E-05**
Nov	0.59 ±0.04	0.64 ±0.02	-4.72	22.50	**9.78E-05**
Dec	0.59 ±0.05	0.64 ±0.02	-4.62	22.55	**1.25E-04**

Appendix 7. Parameters (±standard error) of bouts of consecutive flight behaviour by Verreaux’s eagles (*n*=3) in the Cederberg and the Sandveld, as determined by high-resolution GPS tracking.

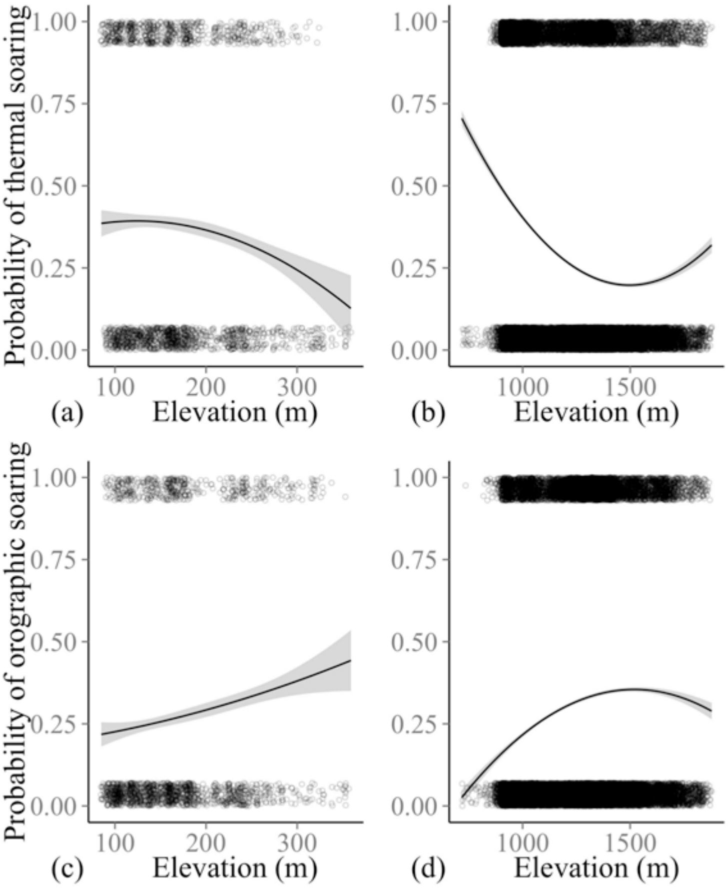
Flight behaviour	n	Height gain (m)	Vertical speed (ms^{-1})
Thermal soar	639	145.1 ±6.1	1.8 ±0.04
Orographic soar	1130	27.1 ±1.1	0.9 ±0.03
	1769		



Appendix Figure 1 (part 1). Track segment examples derived from high-resolution Verreaux's eagle GPS data. These segments illustrate the features that are typical of the following behaviours: i) thermal soaring; ii) orographic soaring; iii) gliding and iv) perching. Movement features which are extracted from Verreaux's eagle tracking data to identify each behaviour include: a) the change in altitude above sea level; b) the change in altitude above ground level within the segment; c) three-dimensional instantaneous speed; d) the series of compass bearings within the segment and e) latitude and longitude of track segment, including duration and spatial extent of the segment (top right corner).



Appendix Figure 1 (part 2). Track segment examples derived from high-resolution Verreaux’s eagle GPS data. These segments illustrate the features that are typical of the following behaviours: i) thermal soaring; ii) orographic soaring; iii) gliding and iv) perching. Movement features which are extracted from Verreaux’s eagle tracking data to identify each behaviour include: a) the change in altitude above sea level; b) the change in altitude above ground level within the segment; c) three-dimensional instantaneous speed; d) the series of compass bearings within the segment and e) latitude and longitude of track segment, including duration and spatial extent of the segment (top right corner).



Appendix Figure 2. The effects of elevation on soaring probability thermal soaring by Verreaux's eagles in the Sandveld (a) and the Cederberg (b) and the effects of elevation on orographic soaring in the Sandveld (c) and the Cederberg (d).

Chapter 6

Synthesis and conclusions

Synthesis

There is growing evidence that not all raptors respond to land use change in the same way. Some raptors appear to benefit from land use change and even increase in reproductive output, or distribution (Balbontín et al. 2008, Cardador et al. 2011) while others experience detrimental consequences including reduced breeding output, poorer offspring condition and delayed egg-laying (Byholm et al. 2007, Butet et al. 2010, Costantini et al. 2014, Almasi et al. 2015). Owing to this, there is speculation over the usefulness of using raptors in general as indicators of the health of the ecosystem (Cabeza et al. 2007, Rodríguez-Estrella et al. 2008). Species and area specific responses to land use change need greater attention to address conservation requirements in the rapidly changing world, where land use change is currently responsible for the greatest losses of biodiversity (Newbold et al. 2015).

In this thesis I have evaluated the effects of agricultural transformation in the Sandveld on breeding performance, diet and movement of Verreaux's eagle in order to better understand the pressures faced by this species in a changing environment. In the absence of any historical data on Verreaux's eagle breeding in the study region, the first aim was to establish baseline information on breeding performance and population trends in two study areas with contrasting land use. Primarily, Verreaux's eagles nesting in the agriculturally transformed Sandveld regions were found to be 2.7 times more productive than eagles nesting the Cederberg (Chapter 2). This was contrary to my predictions and the causative reasons for this finding were therefore the focus of the subsequent chapters. Although the reason for the poor breeding rate in the Cederberg remains unclear, heavy rainfall in this region largely contributes to poor nesting success. When incorporated into a population viability model, the discrepancies in breeding productivity between the study areas led to contrasting outlooks for the two populations. The low breeding productivity in the Cederberg is unlikely to be able to sustain the local population in isolation. The high breeding productivity in the Sandveld eagles highlighted this as an important population for conservation due to the potential role it plays as a source population to other areas. However, I did not have any information on the survival of adults or juvenile birds in these two areas. For the purpose of the models I therefore assumed equal survival for the two regions. If however, adult survival is very high for the Cederberg, but is very low for the Sandveld these conclusions may be erroneous (Ferrer and Penteriani 2005). Higher than average mortality rates of young raptors are often associated with human pressures, including electrocution or collision with power lines, persecution and starvation (Harmata et al. 1999, McIntyre et al. 1999, Millsap et al, 2004, Stoychev et al. 2014). Further to this, some nestlings can have higher stress levels and poorer body condition in agricultural compared to natural areas (Almasi et al, 2015), and this might have a negative effect on their post-fledging survival.

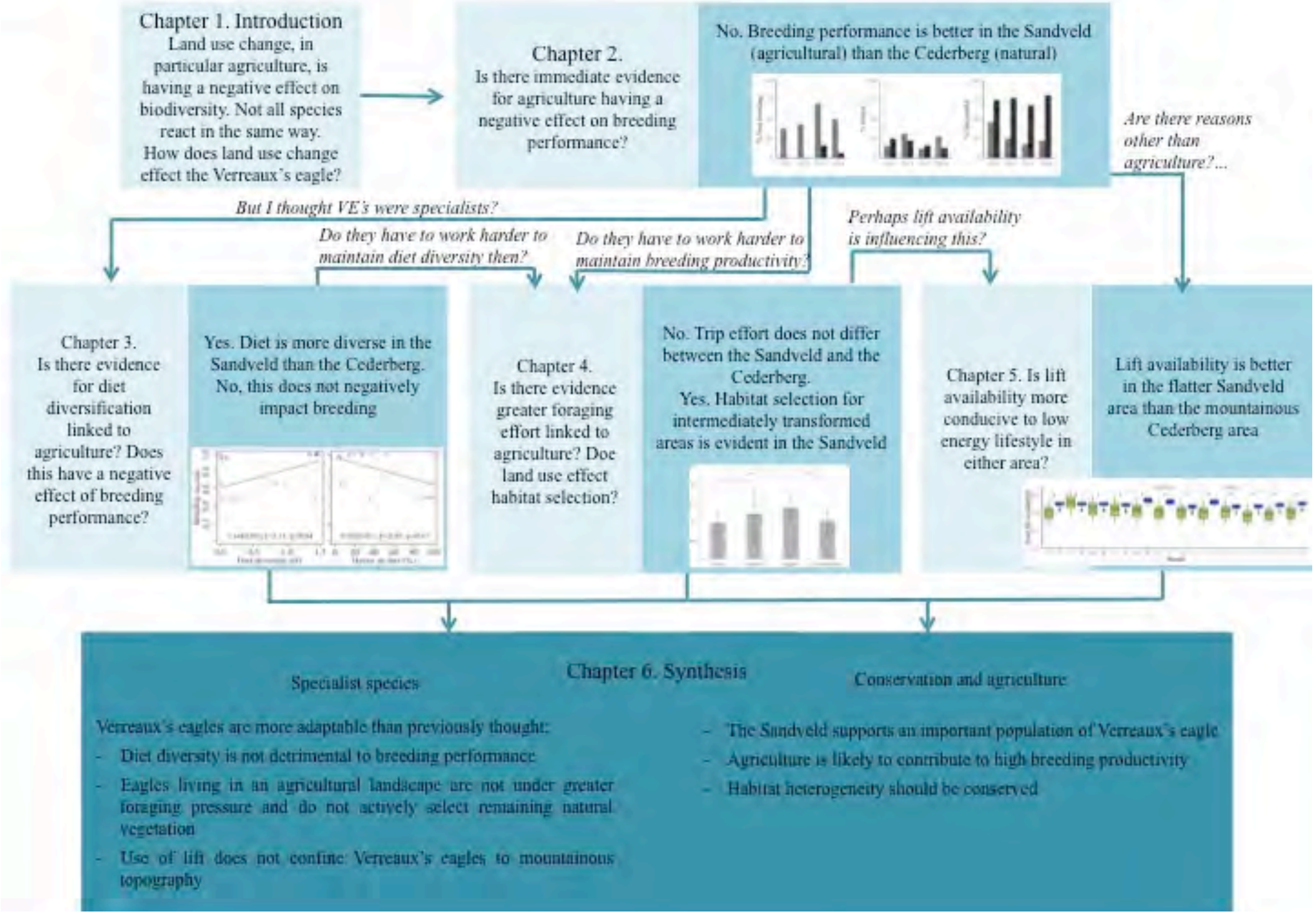
Rainfall regimes are expected to change in southern Africa in response to climate change. In particular, warmer mean seasonal temperatures, decreased total rainfall and increased occurrence of severe weather anomalies could impact the reproductive performance and long term persistence of eagles (Wichmann et al. 2003, Simmons et al. 2004, Coetzee et al. 2009). Although reduced rainfall during the chick rearing stage could be beneficial to the nesting success of Verreaux's eagles, predicted weather anomalies, including storm events, are likely to be detrimental to nesting success. Climate change might also impact the distribution and availability of prey resources (Erasmus et al. 2002).

As a result of the findings in Chapter 2, I went on to investigate causative reasons for the dissimilar reproductive outputs. Prey availability is a common limiting factor for breeding productivity in raptors, particularly specialist species (Korpimaki and Wiehn 1998, Millon et al. 2008, Terraube et al. 2011). Although I was unable to accurately measure prey abundance in the study area, largely owing to the complex terrain and evidence for consumption of multiple cryptic species in the diet, a good understanding of the variety of prey species taken was obtained via dietary studies (Chapter 3). The principal finding of Chapter 3 was that diet composition of eagles in the Sandveld is far more diverse compared to eagles in the Cederberg. Without baseline data it is impossible to assess if the use of a wide variety of prey species in the Sandveld region is an adaptation to change or a characteristic that existed in this area prior to land use change. However, the proportion of transformed land within eagle territories was related to the contribution of the three predominant prey species in the diet and the diet diversity increased with increasing land use cover diversity, thereby suggesting that habitat transformation might have driven changes in diet composition in this region. Further to this, the relationship between diet diversity and breeding performance was investigated both locally and in comparison to previous studies. There was no evidence to support the idea that diet diversification is detrimental to the breeding productivity of Verreaux’s eagle, which is contrary to expectations of a specialist species. In fact there was some evidence to suggest that a more diverse diet improved breeding performance for this species (Chapter 3).

In Chapter 4 preferential use of partially developed land by eagles in the Sandveld was identified. The use of ‘near natural’ and ‘degraded’ areas is likely to be indicative of enhanced prey availability or accessibility in these areas compared to ‘natural’ and completely transformed (‘no natural’) areas. Vegetation structure can have a strong impact on foraging habitat selection (Rodriguez et al. 2014). Open areas can facilitate prey capture and this can be more important than prey abundance in driving habitat selection (Wakeley 1978, Preston 1990). However, the avoidance of land which has been fully transformed for agriculture is likely to be an important indicator of the inability of such areas to adequately support prey species (Marzluff et al. 1997, Tella et al. 1998, Ursua et al. 2005). This also links with the quadratic relationship found in Chapter 3 between the proportion of agriculturally developed land within territories and diet diversity. The positive relationship between the area of agricultural land and diet diversity is not infinitely sustainable and upon reaching the threshold, diet diversity plateaued and would potentially decrease with further conversion, although this has not yet been observed. Chapter 4 also found that there were no significant differences between the study areas in the duration or distance travelled during trips away from the nests. This suggests that eagles are not under greater foraging effort caused by limited prey availability in either area (Petersen et al. 2006). However, from these data it was difficult to separate if between-area differences in the cost of transport are entailed due to contrasting topography driving dissimilar lift availability (Shepard et al. 2013). Therefore, these effects were investigated further in Chapter 5. As expected, the predicted availability of thermal lift was greatest in the Sandveld territories. The predicted availability of orographic lift was subject to seasonal fluctuations and was greatest in territories in the Cederberg Mountains from February to March and during September. However, for much of the breeding season the predicted availability of orographic lift was actually higher in the Sandveld, driven by a change in prevailing wind direction. Owing to the consistency in thermal lift availability in the Sandveld, the overall availability of lift was greater in this area than the Cederberg throughout the year. Furthermore, thermal flight appears to be more conducive to profitable, low energy consuming flying than orographic lift. Some limitations could not be accounted for, including the use of irrigation in the Sandveld, which can influence the formation of lift by causing spatiotemporal changes in evapotranspiration. This might also contribute to the avoidance of agricultural land seen in Chapter 3. Similarly vegetation structure and land use may contribute to thermal lift capacity. Although this has not been assessed here there is scope for further research on this topic, which would be relevant to risk mitigation in planning of wind turbines in agricultural landscapes.

Specialist species

Verreaux's eagles have been traditionally thought of as dietary and habitat specialists. Many of the hypotheses formed at the outset of this research predicted detrimental effects of land use change on Verreaux's eagles owing to the general view that specialists are unable to adapt well to changes in the environment, compared to generalists. This was contrary to my findings throughout this thesis, demonstrating the potential adaptability of Verreaux's eagles and questioning the previously presumed specialist nature of this species. Raptors such as the Verreaux's eagle might be perceived as specialists because they are subject to disturbance and/or persecution, which forces them to occupy non-disturbed and potentially marginal habitats with apparently specialised lifestyles. However, in the absence of such limiting factors, individual adaptation might in fact allow some raptors to occupy a wide range of habitats. For example, following population declines due to extensive human persecution in Europe in the early 20th century and organochlorine pesticide use in agriculture during the 1960s, the red kite *Milvus milvus* has successfully recolonized much of the UK, expanding its range and habitat use, since an initial reintroduction plan began in 1989 (Wotton et al. 2002). The recent phenomenon of urban raptors, such as goshawks *Accipiter gentilis* L. and peregrine falcons *Falco peregrinus*, which can be found breeding successfully in major cities also demonstrates the ability for some species to inhabit a wide range of habitats (Rejt 2001, Rutz 2008).



Chapter 1. Introduction
Land use change, in particular agriculture, is having a negative effect on biodiversity. Not all species react in the same way.
How does land use change effect the Verreaux's eagle?

Chapter 2.
Is there immediate evidence for agriculture having a negative effect on breeding performance?

No. Breeding performance is better in the Sandveld (agricultural) than the Cederberg (natural)

Are there reasons other than agriculture?...

But I thought VE's were specialists?

Do they have to work harder to maintain diet diversity then?

Do they have to work harder to maintain breeding productivity?

Perhaps lift availability is influencing this?

Chapter 3.
Is there evidence for diet diversification linked to agriculture? Does this have a negative effect of breeding performance?

Yes. Diet is more diverse in the Sandveld than the Cederberg.
No, this does not negatively impact breeding

Chapter 4.
Is there evidence greater foraging effort linked to agriculture? Doe land use effect habitat selection?

No. Trip effort does not differ between the Sandveld and the Cederberg.
Yes. Habitat selection for intermediately transformed areas is evident in the Sandveld

Chapter 5. Is lift availability more conducive to low energy lifestyle in either area?

Lift availability is better in the flatter Sandveld area than the mountainous Cederberg area

Chapter 6. Synthesis

Specialist species

Verreaux's eagles are more adaptable than previously thought:

- Diet diversity is not detrimental to breeding performance
- Eagles living in an agricultural landscape are not under greater foraging pressure and do not actively select remaining natural vegetation
- Use of lift does not confine Verreaux's eagles to mountainous topography

Conservation and agriculture

- The Sandveld supports an important population of Verreaux's eagle
- Agriculture is likely to contribute to high breeding productivity
- Habitat heterogeneity should be conserved

Figure 1. Infographic of the principle finding of each chapter investigating the ecology of Verreaux's eagles in natural and agriculturally transformed environments and how they relate to each other to from the conclusions of this study

Study limitations and future research

Breeding data were collected over four years. This was sufficient to enable between-area differences to be examined but not long enough to examine for long-term trends. The sample size of eagles that were GPS tracked was also small, and in particular study area was confounded by sex of eagles tracked during the pre-breeding season. These limitations can be assessed with further monitoring of breeding eagles and GPS tracking of eagles. Longer term monitoring of breeding productivity will be important to assess if changes in breeding productivity occur with progressive transformation of the Sandveld or with climatic changes.

Survival rates used in the population viability analysis (PVA) were derived from Vernon's (1972) calculation of life expectancy of Verreaux’s eagle in a stable population. No adequate long-term study has established actual survival rates of Verreaux’s eagle. To understand if the PVA predictions are robust and improve their overall accuracy it will be important to assess survival rates, which may even contrast between populations. For breeding raptors this is most easily achieved, by DNA analysis of moulted feathers collected at or near the nest site, which can provide individual identification of resident eagles for population monitoring (Rudnick et al. 2005). Alternatively, to understand survival rates of sub-adult birds a robust sample size of re-sightings of marked individuals would be required with a robust sample size, by recording re-sightings of marked individuals (Evans et al. 2009, Monadjem et al 2013). Marking nestlings prior to fledging with patagial tags would be the simplest and most cost effective method, since colour ring re-sightings would be too rare. However, there is also limited understanding of movements during natal dispersal in Verreaux’s eagles. Although patagial tagging could help us to understand this to some extent, for a detailed understanding of pre-adult movements, habitat use, causes of mortality and conservation requirements, GPS tracking of dispersing birds is also necessary (Soutullo et al. 2006, Sandgren et al. 2014, Stoychev et al. 2014).

To further our understanding of the relationships we have seen here between agricultural land-use in the Sandveld and the diet composition, the prey abundance in different habitats should be assessed. This will help to evaluate the relative usefulness of contrasting habitat types for conservation planning (Preston 1990, Butet et al. 2010). However, this is particularly challenging owing to the large variety of species consumed by Verreaux's eagles in this area. An assessment of provisioning rates to nestlings in the contrasting habitats would be more easily achieved and would also contribute to understanding the cost or benefit of the availability of different prey types and could provide evidence for prey shortages, greater foraging effort or diversion from optimal foraging strategies (Amar et al. 2003, Hinam and St Clair 2008, Cardador et al. 2012).

The findings in this thesis related to the positive effects of agriculture on the ecology of eagles have been derived from an agricultural area where habitat and land use cover heterogeneity is currently maintained. Further research should be aimed at investigating the same aspects (breeding productivity, diet and ranging behaviour) in more intensively transformed areas to find the threshold, which is predicted in this thesis (Chapter 3 and 4), where intensive agriculture is no longer beneficial to eagles. This will be important to making management decisions to maintain biodiversity in agricultural areas.

Conservation and agriculture

Various concepts have been proposed to maintain or increase crop yields and conserve biodiversity. Foremost, land sharing and land sparing have been considered as options by conservation biologists to balance land use for food production with conservation requirements (Chapter 1). Threats posed by agriculture to biodiversity (e.g. habitat loss, over use of pesticides, pollution from agrochemicals and fertilisers, introduced species, persecution of predators) are seemingly incompatible with species conservation. This perception has frequently led to the complete separation of areas designated for agriculture and conservation (Scherr and McNeely 2008) and supports land sparing concepts (Balmford et al. 2005, Green et al. 2005, Phalan et al. 2011b). However, a main argument against land sparing is that it can lead to the creation of nature reserves separated by inhospitable matrix creating island effects. Furthermore, evidence suggests that agricultural intensification rarely results in land sparing for biodiversity (Scherr and McNeely 2008). Consequently, recognising the capacity for farmland to retain some biodiversity and act as a functional habitat is important in making management decisions and this is promoted by land sharing advocates (Norris 2008). However, a recent review of the sharing-sparing dichotomy refers to this as a “choice between two undesirable options” (Kremen 2015). Land sparing can lead to isolated nature reserves within inhospitable matrix and land sharing often fails to support rare, endemic, specialised or area-demanding species (Kremen 2015).

In the Sandveld, the current land use configuration lies somewhere between the two strategies. It is not strictly land sparing, as this entails the formal protection of contiguous extents of habitat (Phalan et al. 2011a), and it is not land sharing owing to the high inputs of pesticides, herbicides and fungicides in potato production (Franke et al. 2011). A ‘both-and’ approach advocates large protected areas as well as wildlife-friendly agriculture, essentially incorporating land sharing and sparing (Kremen 2015). The current mosaic of land use in the Sandveld, which ranges from intensively farmed to patches of natural vegetation, provides areas that are important for biodiversity. The configuration appears to maintain landscape connectivity, even supporting small numbers of leopard *Panthera pardus* (Maree & Vromans, 2010; pers. obs.), which are estimated to require large conservation areas of >10 000 ha (Cowling et al. 1999). This configuration lends itself to maintaining biologically diverse flora and fauna. However, I recommend that in order for this area to continue to support such biodiversity, a series of guidelines should be implemented. Including:

i) Renewed efforts should be aimed at providing legislative protection and incentives for the conservation of remaining natural vegetation to maintain habitat heterogeneity and habitat corridors.

ii) Regulation of irrigation and reduction of chemical inputs.

The dependency on groundwater for irrigation in the Sandveld has resulted in lowering ground water levels and this has previously been highlighted as a conservation concern in the region (Franke et al. 2011). Irrigation can further cause the leaching of agrochemicals into ground water with negative effects on the environment. Therefore, increasing water use efficiency and decreasing the input of agrochemicals is essential. As top predators, eagles have the potential to bioaccumulate agrochemical components (Sergio et al. 2005, 2006; Murgatroyd

2008). Testing the levels of pollutants in feather allows non-invasive monitoring of contaminants in the environment and could be pursued (Lodenius and Solonen 2013, Gómez-Ramírez et al. 2014).

iii) Mitigation of current and future causes of unnatural mortality for eagles. Primarily these include persecution events, collisions with wind turbines and electrocution and collision with energy distribution infrastructure.

Verreaux's eagles have the potential to be beneficial to small live stock farming as losses attributed to eagle predation are usually outweighed by the average annual intake of hyrax which would otherwise reduce forage for livestock (Davies 1999). Although I did not attempt to calculate the trade-offs in the Sandveld between livestock and hyrax consumption, the relatively low contribution of livestock to the diet of eagles in this region (Chapter 3; 2.4 % livestock) and the importance of potato farming over livestock farming in the Sandveld (Franke et al. 2011) would likely mean that the presence of eagles is beneficial rather than detrimental to farmers. However, one occurrence of the sudden disappearance of a pair of eagles nesting in the Sandveld (pers. obs.) is a cause for concern and dissemination of information regarding the positive role of eagles may be further required in this region.

Wind turbines are a pervasive threat to raptors (de Lucas et al. 2008, Dahl et al. 2012, Marques et al. 2014, Rushworth and Krüger 2014). Recent deaths of Verreaux's eagles caused by turbines in South Africa have highlighted the urgent need for further research into the mitigation of collisions for this species (Smallie 2015). By expanding on the methodology developed in Chapter 5 it would be possible to develop predictive mapping models to plan turbine layout with minimum risk according to eagle flight techniques (Reid et al. 2015).

Conclusions

Agriculture is a major driver of biodiversity loss, however, it can also make important contributions to the conservation of species. Some raptors can readily adapt to human-modified habitats. Here, I have documented this in the Sandveld where there is a diverse availability of food resources, favourable breeding conditions and favourable flying conditions which all lead to a low energy lifestyle and a high breeding productivity of Verreaux’s eagle. In light of the conservation value of some agricultural areas, the ecological benefits of biodiversity on farmland and the global extent of agriculturally transformed land, greater effort should be made to integrate conservation and agriculture worldwide.

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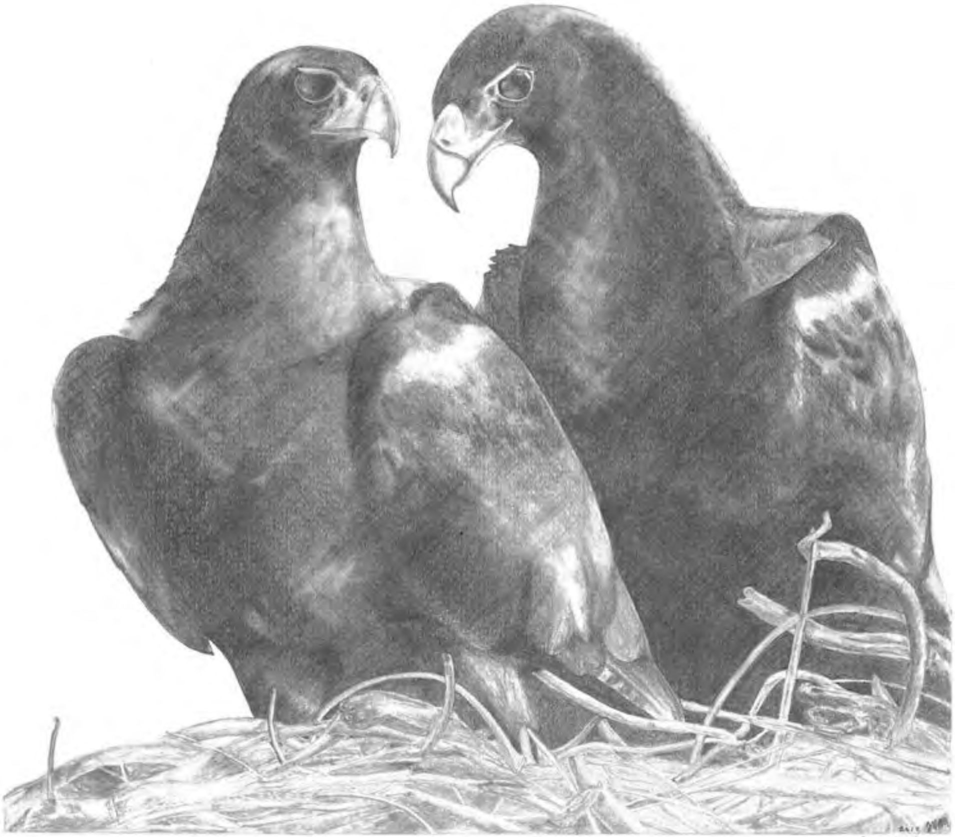

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