How does urbanisation affect the breeding performance of African Crowned Eagles (*Stephanoaetus coronatus*)?

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Abstract

Birds face many challenges from the process of urbanisation. Those species that are able to occupy urban areas offer opportunities to understand processes of acclimatisation to urban life and may help in the development of urban spaces for the benefit of wildlife. In many bird species, individuals that occupy territories in more urban areas show lower productivity and lower body condition of nestlings, which is thought to be mediated by food availability. Most of the studies exploring this issue were done on passerines and carried out in the global north, with very few studies exploring this topic on non-passerines, and even fewer in Africa. Studies addressing urban productivity in apex predators with slow life histories that are often of conservation concern are largely missing. Here, we explore the breeding performance of the African Crowned Eagles (*Stephanoaetus coronatus*) across an urbanisation gradient in KwaZulu-Natal, South Africa. Specifically, we explored the hypothesis that living in an urban environment allows this species, which is typically a biennial breeder, to breed annually more often (i.e. increased breeding rate), and whether this might increase the productivity of this species. We also explore whether there may be any hidden costs of such a breeding strategy by examining the condition of chicks for pairs which had successfully bred in the previous year. We found that Crowned Eagles breeding in more urban areas attempted to breed more often (i.e., higher breeding rate), but that these birds also suffered from lower breeding success. These two contrasting responses counteracted each other and meant that overall productivity (number of young produced per occupied territory) was not influenced by urbanisation. Breeding annually did not appear to have a negative cost on the chick condition, as offspring in the year following a successful breeding attempt did not have lowered body condition. This species appears to be well adjusted to breeding in an urban environment. Crowned Eagles are currently considered vulnerable in South Africa, and ensuring that an urban population of this species is able to persist can help secure the conservation status of this charismatic species

Keywords: apex predator; urban green space; Africa; breeding frequency; breeding success; body condition; urban conservation

Introduction

Urbanisation is one of the greatest threats facing biodiversity conservation. It is a rapid and globally occurring process whereby natural environments are being transformed into novel urban systems. Usually, these new systems are characterised by highly fragmented and disturbed landscapes with an increase in the amount of unproductive sealed surface area (McDonnell & Pickett, 1990) and a decrease in biological richness and diversity (Chace & Walsh, 2006). The spatial growth of cities is accelerating and the irreversible loss of habitats due to land transformation is recognised as a leading threat to biodiversity (McKinney, 2006; Seto et al., 2012).

It has been predicted that demand for land and subsequent urban growth is expected to triple in the next 30 years, resulting in the transformation of 1.2 million km^2 (Seto et al., 2012). These novel habitats are characterised by well-known abiotic changes that can affect biodiversity such as the urban heat island effect (e.g. McCarthy, Best & Betts, 2010), light (e.g. Dominoni, Quetting & Partecke, 2013) and noise pollution (e.g. Francis, Ortega & Cruz, 2009), as well as air and soil contamination with anthropogenic chemicals (Alberti et al., 2003). Interestingly, contemporary urbanisation differs substantially from historical urban growth. Unlike historical urban development, contemporary cities have expanded rapidly and are increasingly dynamic and complex landscapes. They are characterised by an urban sprawl developing in fractal patterns (Ramalho & Hobbs, 2012). This new type of urban growth has implications for the ecology of cities and offers opportunities for biodiversity conservation within these landscapes.

In avian communities, species richness changes across the gradient of increasing urbanisation (Marzluff, 2001; Shochat, 2004; Faeth et al., 2005; Clergeau et al., 2006; McKinney, 2006) with peaks of richness in areas of intermediate urbanisation (Blair, 1996, 1999; Crooks, Suarez & Bolger, 2004). Factors which affect a species ability to integrate into urban areas include the presence and size of remnant natural vegetation patches, competition with exotic species, non-native predators and supplementary feeding by humans (Chace & Walsh, 2006). Although there are many ways to group species responses to urbanisation, urban ecologists have suggested three different categories based on species tolerance to urban disturbance (Blair, 1999; McKinney, 2002): ‘urban avoiders’, ‘urban adapters’ and ‘urban exploiters’.

Due to the increasing influence of urban landscapes on avian communities, it is important to understand the responses of birds in regards to their life history strategies. A review of the studies that have compared demographic parameters between urban and non-urban populations, suggested that urban passerine populations show patterns of earlier lay dates, smaller clutch size, lower nestling weight and lower productivity per nesting attempt (Chamberlain et al., 2009). One key driver of these demographic parameters is food availability. Human-supplied food may improve adult condition resulting in earlier laying and, for some species, higher survival rates and breeding densities (Chamberlain et al., 2009). However, it is possible that the scarcity of natural food during chick rearing may result in lower chick condition and lower productivity per nesting attempt (Chamberlain et al., 2009). Additionally, the number of species exhibiting a multi-brood strategy increased with urbanisation, indicating that some species are also able to increase their breeding rate in more urban areas (Reale & Blair, 2005).

Raptor species are often considered to be highly sensitive to environmental changes, because of their higher trophic position and because they are K-strategists. Raptors are perhaps not the most obvious group to acclimate to and persist in urban habitats. However, across the globe there are many species of urban adapting raptors (Kettel et al., 2018). It is important to understand how certain species within this group are able to persist in these urbanised habitats that are now present in much of their range. Urban raptors populations include for instance Peregrine falcons (*Falco peregrinus*; Cade, Martell & Redig, 1996; Altwegg, Jenkins & Abadi, 2014), Eurasian kestrels (*Falco tinnunculus* ; Kübler, Kupko & Zeller, 2005; Sumasgutner et al., 2014a), Cooper’s hawks (*Accipiter cooperii*; Boal & Mannan, 1999, 2000) , Northern goshawks (*Accipiter gentilis*; Rutz, 2008) and Black sparrowhawks (*Accipiter melanoleucus*; Martin et al., 2014; Suri et al., 2016; Rose et al., 2017). Urban raptors are usually medium sized (Chace & Walsh, 2006) and it is thought that their success is due to lower direct persecution, increased availability of nesting sites (Rutz, 2008; Sumasgutner et al., 2014b) and food supplies (Kettel et al., 2018). Large eagles are largely missing from urban areas. This is most likely due to the more profound effects of habitat fragmentation or overall habitat reduction on raptors with large home range requirements (Newton, 1979; Chace & Walsh, 2006).

Kettel et al.'s (2018) review of urban raptors suggested that prey availability was one of the main drivers for the success of any raptor species in an urban environments (Kettel et al., 2018). Specialised avian hunters in particular, are thought to be able to profit from the high biomass of small birds in cities (Suri et al., 2017), whereas species relying on small mammals are more often negatively affected by urbanisation (Kettel et al., 2018; Sumasgutner et al., 2014a). This review suggested that in general, raptors had larger brood sizes and bred earlier in urban areas. However, some species were less productive (fledged fewer young) mainly due to reduced prey availability and sometimes by increased human disturbance (Kettel et al., 2018). Thus, there is potentially an 'ecological trap' developing for some large raptor species (e.g. Mannan & Boal 2008; Sumasgutner et al., 2014a).

One pattern that is clear from all reviews of urban avian ecology including urban raptors, is the distributional bias of the studies in this field that may distort our understanding of these trends. Most urban raptor studies have been conducted in the Northern Hemisphere. Southern Africa alone has over 60 diurnal raptor species (Ferguson-Less & Christie, 2005), and yet there is little published knowledge regarding large urban raptors and their populations (Chamberlain et al., 2017; Amar et al., 2018).

Many large raptor species exhibit a biennial breeding strategy (i.e. breeding every other year) and produce a maximum of 1 chick per breeding attempt (Newton, 1979). In general, breeding rate in eagles is thought to be strongly influenced by food supply (Murgatroyd et al., 2016), and that more abundant or more consistent food supplies can improve long term productivity of some species (Brown, 1970), although this aspect has not been well explored. If urbanised habitats provide a food rich habitat this could lead to annual breeding in large eagles which breed there, and therefore potentially higher productivity rates in urban areas. Indeed, for other large eagle species, that are not restricted to biennial breeding, the rate at which they breed (i.e. the number of years with breeding attempts) can have a profound influence on their overall productivity (e.g. Murgatroyd et al., 2016).

African Crowned Eagles (hereafter: Crowned Eagle; *Stephanoaetus coronatus*) are one of three species of large raptors that have been reported as residents in South African cities (McPherson, 2015). They exhibit characteristics that are typical of K-strategists: a long lifespan, long maturation period and low reproductive rate (Swartridge, 2009; McPherson, Brown & Downs, 2016). This species also has a long post-fledgling dependency period of up to 14 months (Skorupa, 1989; Shultz, 2002). They are apex predators in forest habitats throughout sub-Saharan Africa with a range that extends from West African forests across the tropical belt to the Kenyan coastline and south along the eastern coastline to South Africa (Brown, Urban & Newman, 1982; Boshoff, 1997b; McPherson, 2015). Globally, the Crowned Eagle was up-listed from Least Concern to Near Threatened at the 2012 revision of the IUCN Red List of Threatened Species (BirdLife International, 2018). In South Africa the species was recently up listed to Vulnerable (Taylor, Peacock & Wanless, 2015). The biggest threats throughout their range are losses of habitat and prey availability due to deforestation and competition with the bush meat trade for prey (BirdLife International, 2018).

Crowned Eagles have been able to adjust to the urban mosaic of major cities in KwaZulu-Natal, in south eastern South Africa, and are also know from other urban sites elsewhere in Africa (e.g. Kenya; Wachira, 2017). In general birds of prey face threats that can lead to serious injuries or death such as collisions with traffic, windows and power lines (Mannan & Boal, 2004; Donázar et al., 2016). In particular, Crowned Eagles are prone to direct persecution due to the human-wildlife conflicts that arise from their occasional predation on pet animals in urban settings (McPherson, 2015). Despite the challenges posed by living in an urban mosaic, this species is seemingly thriving within the major metropolitan areas around Durban and Pietermaritzburg, with up to 120 breeding territories identified in southern KwaZulu-Natal between 2012-2017. A contributing factor to this is the ecosystem services that were identified in Durban, and which consequently led authorities to develop a planning strategy that incorporates the Durban Metropolitan Open Space System, known as D'MOSS (McPherson, 2015). Unlike cities in Europe and North America, the residential areas in tropical cities like Durban have certain features which could make them more suitable for a diverse range of species to become urban adapters. For example, low density community conservancies and eco-estates are common in the greater Durban area.

Within this urban Crowned Eagle population, it is suspected that there has been a shift away from biennial breeding, which is more typical elsewhere in their range (Vernon, 1984; Malan, 2005; Oatley, 2008), toward more occurrences of annual breeding (McPherson, 2015). It has been suggested that this shift may be due to high juvenile mortality (McPherson, 2015), or may be due to the high availability of smaller prey items (e.g. Rock Hyraxes *Procavia capensis* or nestling Hadeda Ibis *Bostrychia hagedash*; McPherson, Brown & Downs, 2016a) resulting in juveniles dispersing quicker compared with other populations where they must learn to prey on more challenging larger prey (such as antelope or monkeys; Vernon, 1984; Skorupa, 1989; Swartridge et al., 2014). In both cases, this means that adults are not restricted by the need to provide the extended post-fledging care that is a characteristic of this species and so are freed up to make another breeding attempt the following year (Pickford, Pickford & Tarboton, 1989).

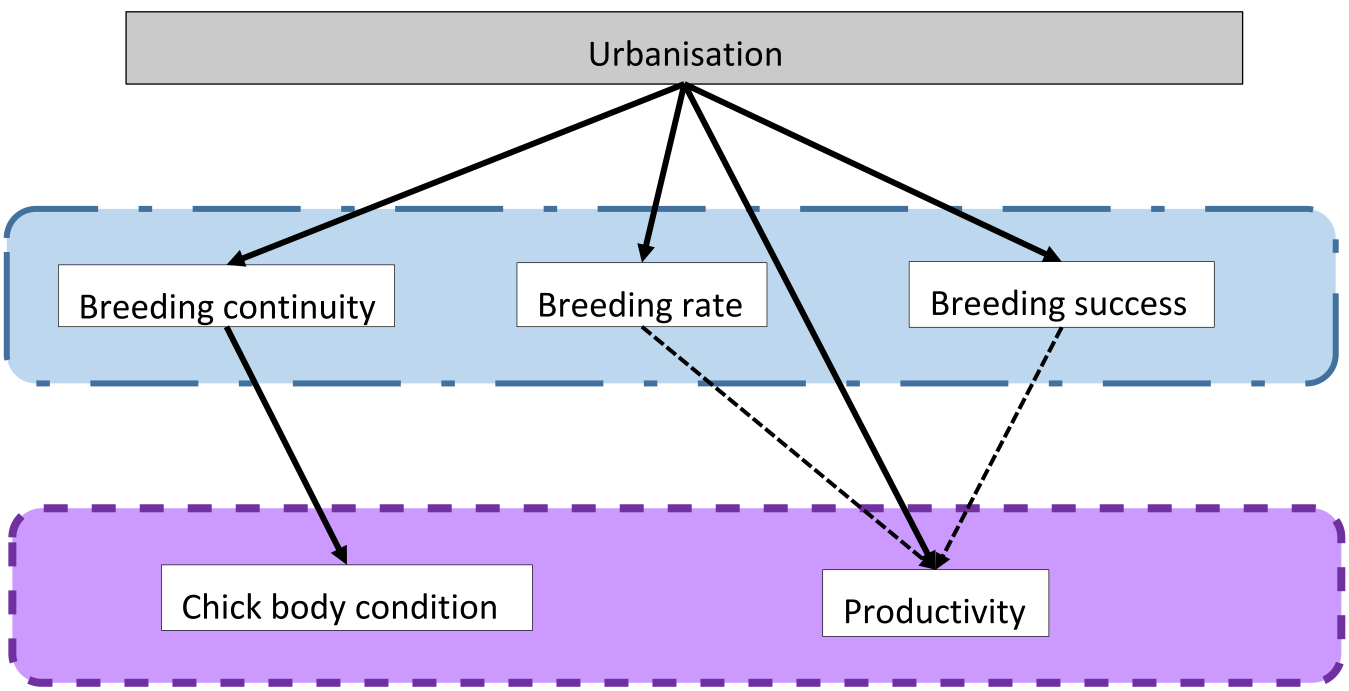

Figure 1: *A diagram of the flow of reasoning that informs this study. The external environmental pressure is indicated in grey (urbanisation), demographic mechanisms are represented in the blue box and fitness measures in the pale purple box. Urbanisation may affect productivity and*

this might occur either through changes in i) breeding rates or ii) breeding success. We hypothesise that breeding rates may increase because urbanisation alters the breeding strategy, shifting birds away from a biennial strategy toward a more continuous annual strategy (continuity measure). However, if birds breed more regularly (i.e. annually) there may be hidden costs associated with reduced chick body condition which may ultimately influence individual fitness of the chicks and thus ultimately the reproductive fitness of birds nesting in urban environments.

This study aims to investigate whether urbanisation effects either breeding rates (through an increase in annual breeding) or breeding success, and whether urbanisation effects the productivity of this species across an urbanisation gradient in Kwa-Zulu Natal, South Africa. Lastly, we explore whether more frequent annual breeding may affect chick condition, this might occur if adults are compromised in their provided parental care when they are breeding more frequently given the long post-fledging dependency period. Thus, they may be trading chick quantity with chick quality. Our prediction is that chicks that are fledged in year following a successful breeding attempt, are in lower condition, which could indicate a hidden cost of urban living.

Methods

Ethics statement:

All data were obtained with techniques approved and permits obtained from Ezemvelo KZN Wildlife (OP3731/2018), SAFRING (ID number Petra Sumasgutner – 17600, and Shane McPherson – 1619) and the University of Cape Town Animal Ethics Committee (2018/v21/AA).

Study species:

Crowned Eagles are large raptors, weighing up to 5kg. Their powerful feet and talons allow them to take prey much heavier than their own body mass (Fowler, Freedman & Scannella, 2009). Crowned Eagles are successful ambush predators and hunt in densely forested areas. In contrast to their secretive behaviour, they are known to put on lively aerial displays during courtship and for territorial rituals (Brown & Amadon, 1989).

Study area:

The study area covers approximately 20,000km^2 in southern KwaZulu-Natal, centred on the metropoles of Durban and Pietermaritzburg, extending to several coastal towns both North and South of Durban (Figure 2). Within this area there are four biomes, the Indian Ocean Coastal Belt, which lies within ca. 20km of the coastline, the Sub-escarpment Savannah found between 20 and 60km from the coast, the Sub-escarpment Grassland 60 km inland and lastly, patches of zonal forest that were dispersed throughout these areas (McPherson, 2015).

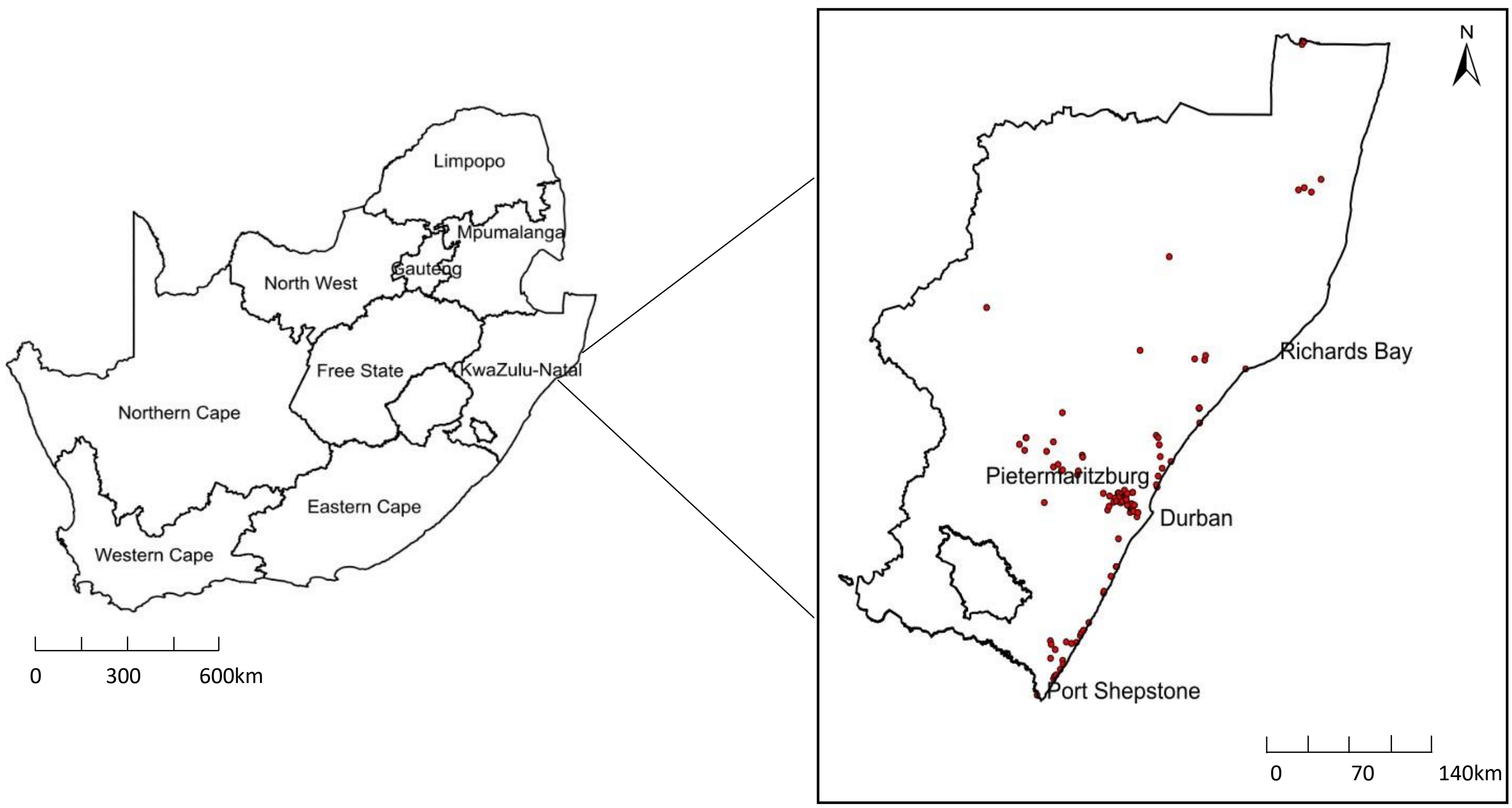

Figure 2: *A map of South Africa, with the study area Kwa-Zulu Natal enlarged and major cities labelled. All known Crowned Eagle nest sites from 2012-2017 are indicated by red circles. Scale bars are provided.*

Data collection:

All data used for the analyses in this study were collected by Shane McPherson from the University of KwaZulu-Natal between April 2012 and January 2017. For more details on how the nests were initially selected see (McPherson, Brown & Downs, 2016b).

Most of the monitoring effort was conducted between August and December over the peak breeding period. Territories were visited regularly, at least twice in the first month of the monitoring period, in order to monitor the progress of each nest through the season (e.g. nest building, incubation or brooding). A nest was classified as active if nest building or fresh green leaves were seen on the nest or if the adults were present in the first two nest site visits. A nest was classified as attempting to breed if incubation or brooding behaviour was seen in the early part of the breeding season. Breeding attempts were monitored until conclusion to provide information on breeding success. A successful breeding attempt was classified as the chick surviving until ringing age (70 ± 5 days old) after which failure to fledge for this species and most large raptors is very low. Nests were observed from vantage points, generally 50-200m away from the nest.

Chicks were ringed when their estimated age was 65-75 days, which was based on size and plumage development compared to reference material gathered from nest cameras and footage of pullis of known age (McPherson, Brown & Downs, 2017). Each nestling was fitted with a G-ring and an alpha-numeric colour ring. During ringing, chicks were weighed (with an electronic hanging scale to the nearest 5g) and the total length and unfurled length of the 8^{th} primary feather taken (with a straight rule to the nearest 1mm). All measurements were done in accordance with the SAFRING user manual (de Beer et al., 2001).

Urbanisation score for each nest:

All analyses presented in this study were carried out by me, Rebecca Muller. In order to establish the percentage of urbanisation around each nest site, I used the LandCover 2014 raster (GEOTERRAIMAGE, 2015), which classifies land use into 72 different land cover classes. The raster was clipped to the study area and analysed in R in order to determine the percentage of each of the 72 land cover classes in a buffer surrounding each nest site. This buffer was set at 10km^2 (radius = 1784.1m) based on Mcpherson, Brown & Downs (2019) covering the average home range size during breeding season, known from 4 GPS tagged adult eagles. Once I had calculated the the percentage of each land class around each nest site, the values for all land classes containing sealed surface (see Rose et al., 2017) were used to calculate an urban score (%) for each nest. In territories where there was more than one nest, the average urban score was taken to represent the territory.

Breeding parameters:

Breeding rate was defined as the number of breeding attempts (i.e. incubation) out of the total number of years a nest had been monitored. Breeding success was defined as the number of successful breeding attempts (chick reaching 70±5 days) out of the total number of active years. Our breeding continuity measure was the number of consecutive breeding attempts out of the total number of years monitored. Finally, productivity was defined as the number of young fledged out of the total number of years monitored. In order to derive a chick body condition score, we regressed the weight of the chick at ringing against the total length of the 8th primary feather and extracted the residuals, which were used as our measure of condition (see for example Suri et al., 2017).

Statistical analyses:

All analyses were conducted in R version 3.5.1 (R Core Team, 2018). The following packages were used: 'lme4'(Bates et al., 2015), 'car' (Fox & Weisberg, 2011), and 'effects' (Fox, 2003). I fitted generalised Linear Models (GLMs) as well as Linear Mixed Models (LMMs), details of the models are explained in Table 2 and Table 3 respectively. An initial model selection considered both the linear or quadratic relationship between urbanisation and our response variables, as a quadratic relationship could reveal changed breeding demography at intermediate levels of urbanisation. In all cases, the linear relationship had the best model fit (lowest AIC) and thus only linear relationships were considered in further analyses. Results are presented as estimates (± SE) of the correlation coefficients of urbanisation from the models. Several two vector response variables was used to investigate the effect of urbanisation. The response variable included either i) the no. attempts and no. non-attempts for the total number years a territory was monitored – for breeding rate, ii) the no. success and no. failures for all the years which the territory was active – for breeding success, or iii) the no. continuous attempts and the no. non-continuous attempts for the total number of years monitored – for breeding continuity. The models used the cbind function and a binomial distribution to fit the response variable; this approach automatically accounts for different sample sizes of years monitored/active years by weighting each sample according to the total number of years monitored (models i and iii) or total number of active years (model ii). A GLM was used to investigate productivity where the response was the total count of the number of young fledged for each territory fitted with a Poisson distribution, with an offset specified as the log (number of years monitored). An LMM was used to investigate the influence of a breeding attempt or a breeding success in the previous year in relation to chick body condition. The response variable was the condition of each chick, and the explanatory variable was either (t-1) attempt, where 0= No attempt previous year, and 1= Attempt the previous year; or (t-1) success, where 0= No successful chick produced in the previous year, and 1=Chick successfully produced in the previous year. I included Year and Territory ID as random terms to account for the repeated measures from the same territory and from different territories in the same year.

Table 1: *Description of GLM's model structure. The database consisted of an entry for each Crowned Eagle territory within the study area, KwaZulu-Natal, that was monitored yearly for more than 3 years during the period 2012-2017 (n=57).*

Analysis	Response variable	Distribution (link)	Explanatory variable	Offset
1	Breeding rate (attempt/no. attempt)	Binomial (logit)	Urbanisation	-
2	Breeding success (success, failure)	Binomial (logit)	Urbanisation	-
3	Breeding continuity	Binomial (logit)	Urbanisation	-
4	Productivity (no young fledged)	Poisson (log)	Urbanisation	log(number years monitored)

Table 2: *Description of LMM model structure. The database consisted of an individual entry per Crowned Eagle chick recorded (n=72) and the associated information on the previous year's breeding attempt for each territory (n=57) within KwaZulu-Natal, monitored for between 4 to 7 years during the period 2012-2017.*

Analysis	Response variable	Random terms	Fixed terms
1	Chick condition	Year, Territory ID	(t-1) attempt
2	Chick condition	Year, Territory ID	(t-1) success

Results

It was found that Crowned Eagles in more urban areas were breeding at a higher rate than those in less urban areas (Table 3, Figure 3a). This higher breeding rate was driven by an increase in breeding continuity (the frequency of consecutive breeding attempts) which increased with increasing urbanisation (Table 3, Figure 4). In contrast, breeding success decreased with increasing urbanisation (Table 3, Figure 3b). A higher percentage of completely annual breeders compared to completely biennial breeders were seen in Crowned Eagle pairs breeding in territories above 50% urbanisation. Amongst pairs breeding in more natural areas (below 50% urbanisation), a slightly higher percentage of territories showed completely biennial breeding rather than completely annual breeding.

Overall Crowned Eagles in urban areas were attempting to breed more often and had more consecutive breeding attempts, but these attempts were less successful. As a result, overall productivity was found to be similar across the urban gradient (Table 3, Figure 5).

There appeared to be no hidden cost to this higher breeding frequency, with no relationship found between chick condition and a breeding attempt the previous year (attempt (t-1)), or between chick condition and whether the attempt the previous year was successful (success (t1)) (Table 3, Figure 6).

Table 3: *Results of the GLMs and LMM showing the relationships between demographic parameters (breeding rate, breeding success, breeding continuity), productivity, and fitness costs (chick condition) of Crowned Eagles to the urban gradient in KwaZulu-Natal during the period 2012-2017. Quantitative variables were scaled.*

Model	Error structure	Estimate	SE	X^2	P-value
Breeding rate	Binomial				
Urbanisation		0.014	0.005	7.628	0.006
Intercept		0.323	0.203		0.112
Breeding success	Binomial				
Urbanisation		-0.014	0.006	5.641	0.019
Intercept		1.315	0.289		<0.001
Breeding continuity	Binomial				
Urbanisation		0.015	0.005	9.256	0.002
Intercept		-0.699	0.223		0.001
Productivity	Poisson				
Urbanisation		-0.0001	0.003	0.962	0.962
Intercept		-0.756	0.142		<0.001
Chick body condition	Gaussian				
Attempt (t-1)		0.144	0.124	1.356	0.244
Intercept		-0.055	0.260	0.045	0.832
Success (t-1)		0.089	0.126	0.498	0.480
Intercept		-0.046	0.249	0.034	0.853

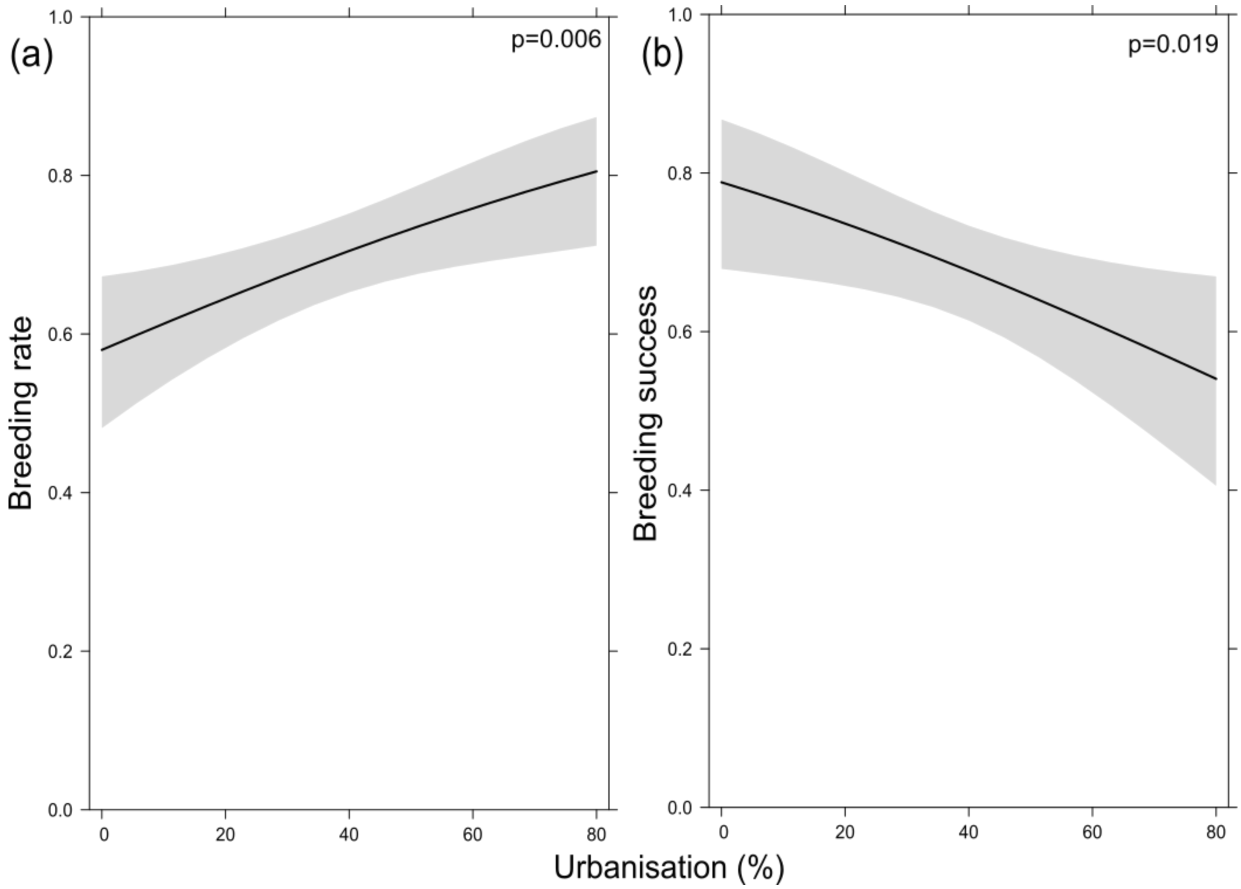

Figure 3: *The relationship between (a) breeding rate and (b) breeding success and urbanisation (%) for Crowned Eagles in KwaZulu-Natal during 2012-2017, based on the predicted values of the GLM, with 95% CIs in shaded grey. Model details in Table 4.*

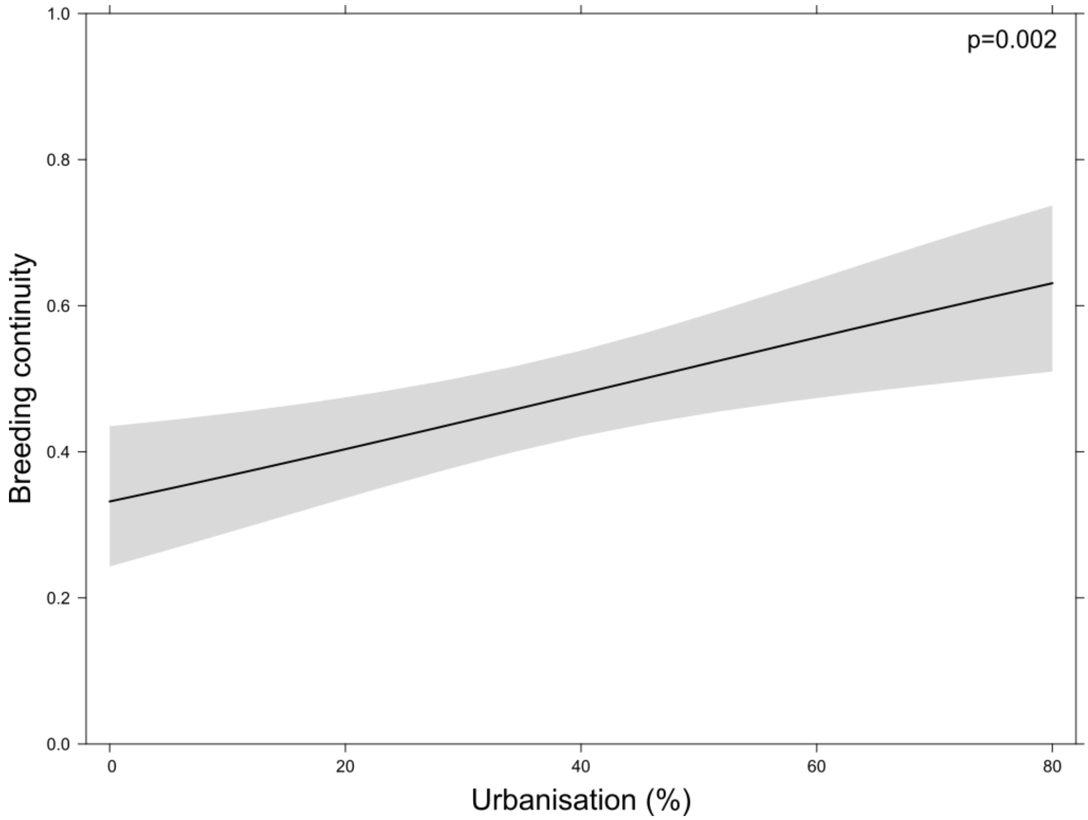

Figure 4: *The relationship between breeding continuity and urbanisation (%) for Crowned Eagles in KwaZulu-Natal during the period 2012-2017, based on the predicted values of the GLM, with 95% CIs in shaded grey. Model details in Table 4.*

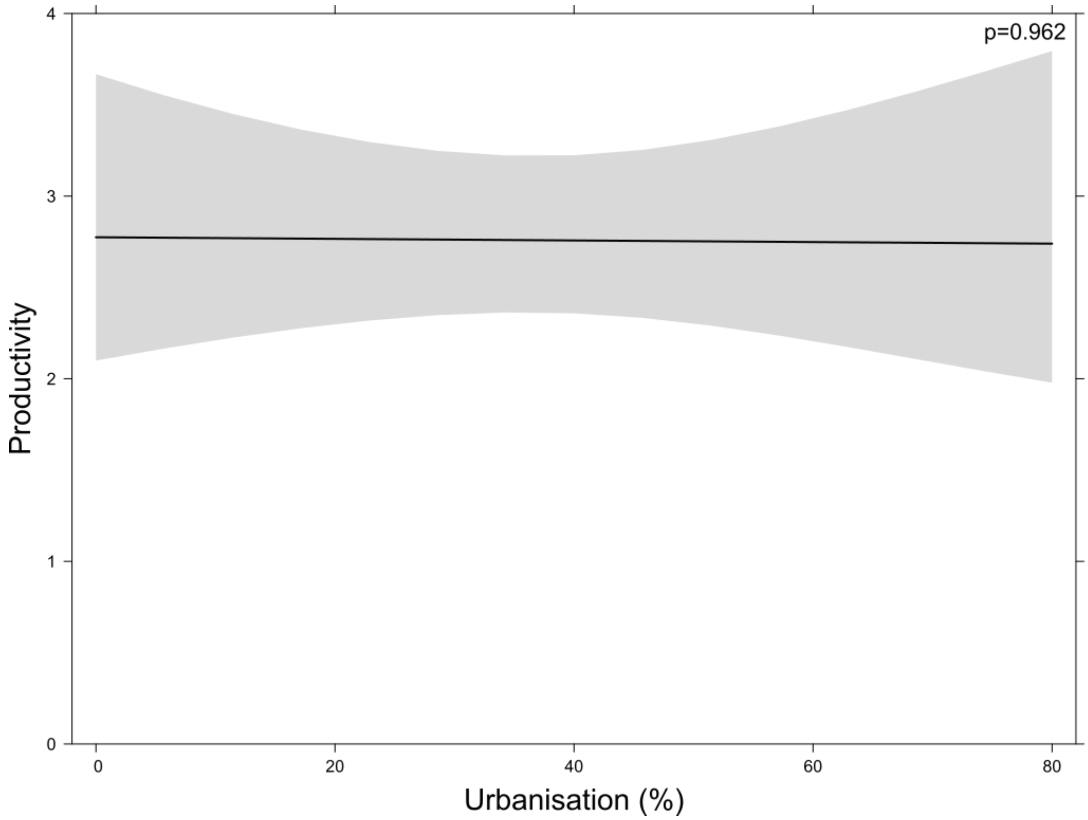

Figure 5: *The relationship between overall productivity and urbanisation (%) for Crowned Eagles in KwaZulu-Natal during the period 2012-2017, based on the predicted values of the GLM, with 95% CIs in shaded grey. Model details in Table 4.*

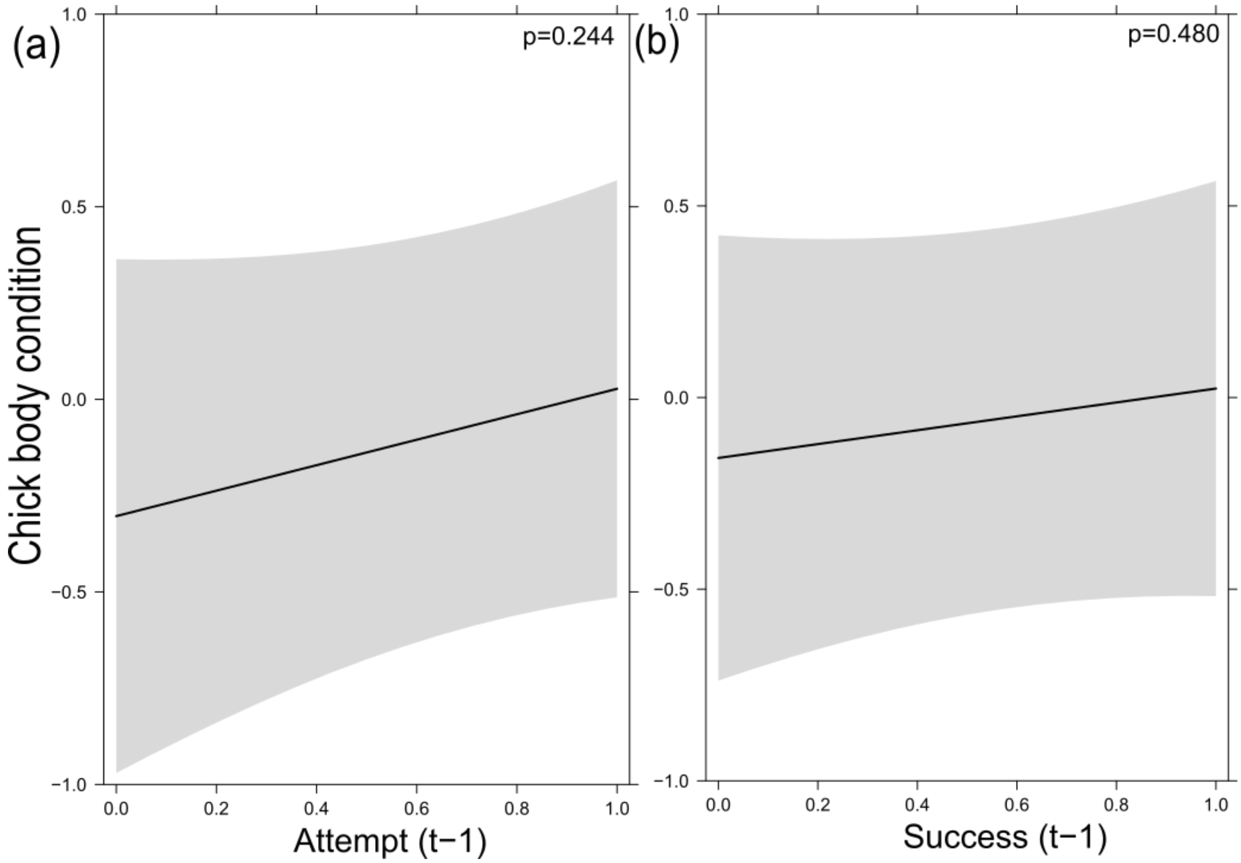

Figure 6: *The relationship between chick body condition and (a) attempt the previous year (attempt (t-1)) and (b) success of a breeding attempt the previous year (success (t-1)) for Crowned Eagles in KwaZulu-Natal during 2012-2017, based on the predicted values of the LMM, with 95% CIs in shaded grey. Model details in Table 4.*

Discussion

The findings of this study suggested that urban nesting Crowned Eagle pairs were able to breed more often than pairs nesting in less urbanised habitats, and that this was achieved via a shift toward a more annualized breeding strategy. However, whilst urbanisation appeared to be beneficial for one breeding parameter, I also found negative effects of urbanisation on breeding success, with a higher failure rate of those that attempted to breed in more urbanised areas.

The contrasting effect of urbanisation on breeding rate and breeding success resulted in similar overall productivity across the urban gradient.

Furthermore, the study found no hidden costs of the tendency for more consecutive breeding in relation to the condition of the chicks that were fledged. The study found that chick condition did not vary in relation to whether an attempt was made in previous year or whether the previous attempt was successful. This suggests that there is no obvious trade-off between the number of young produced and the quality of those young at this stage of the nestling phase.

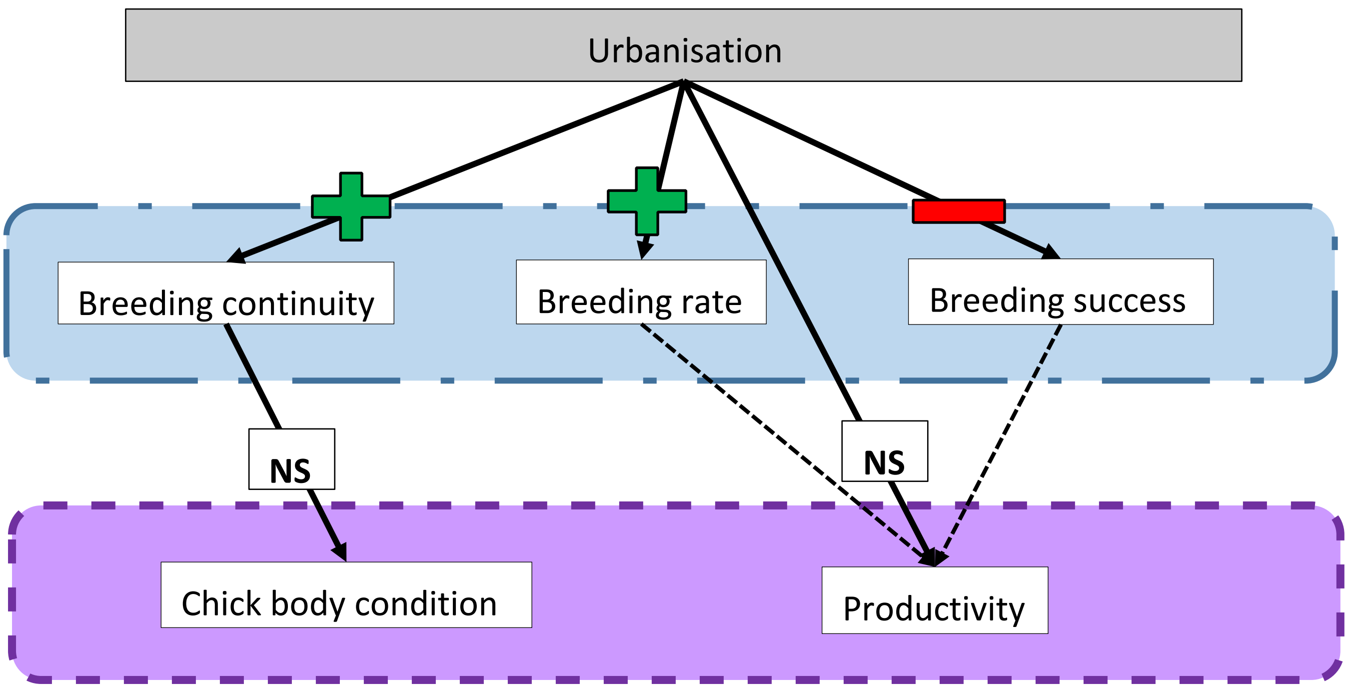

Figure 7: *A diagram illustrating the findings of this study. The positive effect of urbanisation on breeding rate and the negative effect on breeding success, leading to no effect on overall productivity. Urbanisation had a positive effect on breeding continuity, which shows a possible shift to more annualised breeding. But this increase in breeding continuity apparently had no impact on chick condition. This was true for both nests that attempted in the previous year, and nests that successfully reared a chick in the previous year.*

The similar productivity, despite higher breeding rates, across the urban gradient found in this study may have implications for other studies examining the breeding productivity of raptors in relation to urbanisation. Few studies, which examine the impacts of urbanisation on avian productivity, have attempted to tease apart the influences of breeding rate and breeding success (Kettel et al., 2018). Although this is perhaps not surprising given that only large eagles and vultures are known to regularly use a biennial breeding strategy (Hustler & Howells, 1987; Kruger & Amar, 2017). Importantly, the year to year variation of productivity in raptors makes it difficult to extract obvious patterns from the data. Although several of the nests in this study had been studied for 7 years, some only had 4 years of data due to logistical constraints. This reinforces the importance of studies on lifetime reproductive success, which is difficult to achieve for long lived species such as large raptors, as well as the importance of data on large raptors in urban environments.

Importantly, although an increase in frequency of breeding attempts has only recently been noted in large raptors, birds that breed annually have been noted as increasing their frequency of breeding attempts by double brooding in urban environments. For example, Black Sparrowhawks nesting in urban areas in South Africa have been shown to occasionally double brood (Curtis et al., 2004), which might indicate another raptor species breeding more frequently in urban areas. Multiple brooding can also be found in raptors who capitalise on periods of prolonged food abundance when they occur (e.g. Blackshouldered Kite; Mendelsohn, 1981).

Prey availability may be a key mechanism by which Crowned Eagles were able to increase their breeding rate to breed more continuously in urban settings. For raptors, urban areas are viewed as having greater prey availability than natural areas, but only for avian prey specialists as opposed to those specialised on small mammals (Kettel et al., 2018). However, in tropical areas such as KwaZulu-Natal, cities may show an entirely different composition of animal species compared to more temperate areas where many of the studies have been done. This difference in species composition may benefit small mammal and generalist species in addition to specialists. For example, in Durban, many colonies of Rock Hyrax have established within cities, proliferating in stone walls and culverts (Malan et al., 2016), Hadeda Ibis are very common in urban areas (Singh & Downs, 2016), and Vervet Monkey (*Chlorocebus pygerythrus*) populations occur at high densities (Smithers, 2012). In addition, fenced luxury housing estates and eco-estates often stock duiker (*Cephalophinae*) and other small antelope - a favoured prey item of Crowned Eagles (Malan et al., 2016). It is also suggested that in areas with plenty of easier prey items, such as Rock Hyrax, juvenile Crowned Eagles might have a shorter post fledgling dependency period, which would allow parents to regain their breeding condition and potentially breed the very next year as they no longer have to provision for a juvenile (Pickford, Pickford & Tarboton, 1989; Skorupa, 1989). This assumption of post-fledging dependency duration varying depending on the commonest prey types in the territory remains untested and would be an interesting topic to explore for future research.

Another possible explanation of increased breeding rate in urban areas, and the observed shift toward annual breeding attempts, may be linked to the decreased breeding success. More failed attempts in urban areas could mean a reduced investment in a particular year, which could allow breeding adults to recover quicker and breed again the next year. In Martial Eagles living in a protected area, a failed attempt in one year was more often followed by a breeding attempt the following year than after a successful attempt (Hustler & Howells, 1987). This shows that in large raptors a failed breeding attempt one year might be a trigger for attempting again the very next year and not taking a sabbatical year as a true biennial breeder might. A failed breeding attempt in the previous year releases the pair from the demands of a dependent offspring in the area. Future research should look into the timing and causes of nest failure in the urban population of Crowned Eagles. From the data used in this study, of the known nest failures (n=73), approximately half occurred during incubation, and half during chick rearing. If these causes were identified and mitigated, then there might be a benefit to overall productivity within urban areas.

There are at least two possible explanations for the lower success of urban Crowned Eagle nests. Firstly, it could be linked to greater exposure of nest sites in more urban areas. Nests in urban areas are most often found in exotic blue gum trees (*Eucalyptus saligna*; McPherson, Brown & Downs, 2016b), which are subject to ring barking by local government. Ring barking kills the leaves and branches of the trees, increasing the exposure of the nest, which may be problematic during extreme weather events such as very hot days, or heavy rainfall, which are both common during the breeding season. Alternatively, increased failure rates might be linked to higher levels of nest site disturbance. Disturbances can be frequent and prolonged in urban areas, and are often human development activities (e.g. clearing alien vegetation, laying new pipelines and cabling). Sustained disturbances might result in nest desertion and failure.

Apex predators are important in healthy ecosystems as they are able to shape species assemblages and behaviours (Amar et al., 2018). The loss of large raptors from urban areas in Africa has been linked to an increase in species that are considered nuisances by humans (e.g. Eygptian Geese (*Alopochen aegyptiaca*); Atkins et al., 2017). On the other hand, experimentally reintroducing raptors into urban systems has resulted in decreased number of individuals and increased vigilance of nuisance species (Atkins et al., 2017). This has been observed in Durban where the presence of Crowned Eagles appears to result in Vervet Monkeys being more vigilant and spending less time bothering residents (personal observation). However, this is based on anecdotal observations and research to test this perceived pattern would be useful to clarify the ecosystem services provided by large predators in an urban context. Within Europe another large eagle, the White-tailed Eagle (*Haliaeetus albicilla*) is shown to reduce the spread on a non-native invasion predator, the American Mink (*Neovison vison*; Salo et al., 2008), and there is the potential for African Crowned Eagles to exert the same influence on locally invasive or unwanted species in the urban settings of KwaZulu-Natal. In the context of conservation and landscape planning strategies, raptors are important as they are often indicators of urban ecosystem health (Chace & Walsh, 2006; Symes & Kruger, 2012). Durban provides a perfect example of the value of natural/conserved areas within urban centres, for providing ecosystem services for people as well as enabling an apex predator to persist and maintain important trophic relationships in an urban area.

The presence of Crowned Eagles in Durban and surrounds, will contribute to ecosystem function and health, and may be a valuable population of conservation significance. However, it is not yet known what threshold of prey abundance, habitat quality or human disturbance may dictate the overall population viability in this region. Future research should aim to investigate the mechanisms for the observed decreased breeding success in urban areas. Mitigating these, would hopefully result in the continued presence of Crowned Eagles in urban areas, despite the increasing pressure from habitat fragmentation. Understanding the requirements of a top apex predator, integrated within the urban environment, provides a unique opportunity to understand what can be done to achieve similar outcomes in other urban areas that will be developed in future years, within African and globally.

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