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Productivity of the declining Bearded Vulture *Gypaetus barbatus* population in southern Africa[§]

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Recent research has shown that anthropogenic influences are driving the abandonment of breeding territories in the declining southern African Bearded Vulture *Gypaetus barbatus meridionalis* population. Survival rates appear to be low (86% for adults) due to poisoning and collisions with powerlines, which are the primary causes of death from tracked birds. However, there is no information published on the population's current productivity levels, and whether this may be a contributing factor in the declines of this population. This information is vital for a more holistic approach to the conservation of the population. In this study we use data from breeding territory surveys between 2000 and 2016 to estimate productivity for this population. Only around 54% ± 74% (17–91%) of pairs attempted to breed each year, and although nesting success for pairs attempting to breed was relatively high (0.75 ± 0.22; 0.44–1.00), this resulted in low productivity of only 0.42 ± 0.65 (0.28–0.67) young per pair per year. These results contrast with previous surveys, suggesting the productivity may have declined over the last three decades, principally due to many pairs not attempting to breed in each year. Understanding the factors influencing productivity amongst pairs could be useful to guide conservation actions.

Productivité de la population en déclin de *Gypaetus barbatus* en Afrique du Sud

Des recherches récentes ont montré que les influences anthropiques entraînent l'abandon des territoires de reproduction de la population méridionale en déclin de *Gypaetus barbatus meridionalis* d'Afrique du Sud. Les taux de survie paraissent faibles (86% pour les adultes) en raison de l'empoisonnement et des collisions avec des lignes électriques, qui sont les principales causes de mortalité des oiseaux traqués. Cependant, aucune information n'a été publiée sur les niveaux actuels de productivité de la population et si cela peut contribuer au déclin de cette population. Cette information est vitale pour une approche plus holistique de la conservation de la population. Dans cette étude, nous utilisons les données des enquêtes sur le territoire de reproduction entre 2000 et 2016 pour estimer la productivité de cette population. Seul 54% ± 74% (17–91%) des couples ont tenté de se reproduire chaque année et, bien que le succès de la nidification pour les couples tentant de se reproduire soit relativement élevé (0.75 ± 0.22; 0.44–1.00), cela a entraîné une faible productivité de seulement 0,42 ± 0,65 (0.28–0.67) jeunes par couple par année. Ces résultats contrastent avec les enquêtes antérieures, ce qui suggère que la productivité a diminué au cours des trois dernières décennies, principalement au fait que de nombreux couples ne se sont pas reproduits chaque année. La compréhension des facteurs influençant la productivité, parmi les couples, pourrait être utile pour guider les actions de conservation.

Keywords: breeding rate, conservation, nesting success, population decline, productivity

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Introduction

Populations that are small and geographically isolated have a heightened extinction risk (Gaston 1994). Small populations are more vulnerable to demographic stochasticity, local catastrophes, slow rates of adaptation and inbreeding (Brown 1995; Lande 1999). In addition, species with low reproductive rates are less able to compensate for increased mortality with increased fecundity, making them

more vulnerable to population extinction (MacArthur and Wilson 1967; Saether and Bakke 2000).

Populations of large raptors in particular are sensitive to reductions in demographic rates, notably survival rates (Smart et al. 2010), particularly when their populations are small. Vultures are among the most endangered raptors, partly due to their extremely low reproductive rates (Newton

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1998; Ogada et al. 2012). The Bearded Vulture *Gypaetus barbatus meridionalis* population in southern Africa is a geographically isolated population restricted to the Maloti-Drakensberg Mountains in South Africa and Lesotho. The population has declined in distribution, density and territorial occupancy in the past few decades (Krüger et al. 2014). As a result, the species has been up-listed regionally to Critically Endangered (Krüger 2015), indicating that it faces an extremely high risk of extinction in the wild as a result of a reduction in population size and geographic range and the continuing threats to the species (IUCN 2001).

Krüger et al. (2014) suggested that anthropogenic influences were driving the abandonment of Bearded Vulture territories, particularly on the periphery of the breeding range. Krüger et al. (2015) investigated the mechanisms of territorial abandonment and found strong support for anthropogenic factors, particularly the density of power lines and settlements, driving the decline. Neither study, however, investigated the productivity of the population, although both recognised that lower recruitment could in theory be the mechanism driving these declines, with the population shrinking back to their core range with suboptimal territories being abandoned and less recruits being available to replace lost pairs. Understanding levels of productivity, particularly in relation to historic rates, could highlight how important this demographic parameter is to the overall population decline.

Historical breeding records of the southern African Bearded Vulture population indicate that several monitored pairs bred annually (Penzhorn 1969). Subsequent more comprehensive monitoring from the 1980s indicated that all monitored pairs attempted to breed annually and had a relatively high productivity (0.89 young pair⁻¹ y⁻¹) (Brown 1990). In other parts of their global range, however, pairs do not breed every year and have lower average productivity (between 0.16 and 0.55 young pair⁻¹ y⁻¹) (Brown 1977; Urban et al. 1982; Razin et al. 2004; Arroyo and Razin 2006; Xirouchakis and Tsiakiris 2009; Seguin et al. 2010; Margalida et al. 2014).

In this study, we assessed the breeding parameters of the southern African (South Africa and Lesotho) Bearded Vulture population. First, we determined whether the birds attempted to breed every year, and second, we determined the success of their breeding attempts. We determine whether productivity may be currently limiting population growth and discuss our findings in the context of other limiting factors to ensure a more holistic management approach for the species.

Methods

Study species and study area

The Bearded Vulture is a long-lived predominantly monogamous raptor that nests in potholes on large cliffs usually at high elevations, higher than 1 850 m in southern Africa (Brown 1990). Although predominantly monogamous, a number of cases of polyandrous trios have been observed throughout the species' range (Fasce et al. 1989; Carrete et al. 2006a; Heredia and Donázar 1990; Bertran and Margalida 2002, 2003; Krüger 2007). The Bearded Vulture has a prolonged breeding cycle and both sexes contribute

to breeding activities (Piper 2005). Generally, two eggs are laid during autumn–early winter (May–July), but only one chick ever survives to fledging (Brown 1990; Margalida et al. 2004). Fledging takes place in summer (December–January) at between 110 and 123 d (Piper 2005).

The study was carried out during 2000–2016 in the 28 125 km² breeding range of the species within the Maloti-Drakensberg mountains of southern Africa documented by Krüger et al. (2014) (Figure 1). The study area contains 109 occupied breeding territories where breeding has occurred at some stage during the study period. The emphasis was on detecting territorial pairs through aerial and foot surveys of breeding sites as per the method of Krüger et al. (2014).

Territories across the breeding range were surveyed at least once to determine breeding activity, or at least twice to determine breeding success. Monitoring was conducted during the breeding season (between the pre-laying to fledging period; May–December) through ground and aerial helicopter surveys by trained individuals following a standardised monitoring protocol. Ground surveys were undertaken primarily on foot, and by road, using 20–60× telescopes at distances between 200 and 1 000 m. Breeding territories were observed between first and last light for an average of 4 h or until the type of breeding activity was confirmed. Aerial helicopter surveys were undertaken at approximately 100–500 m from the cliff edge at an average flying speed of 70–80 km h⁻¹ with a minimum of two observers looking out of the port side of the aircraft.



Figure 1: Location of occupied breeding territories within the breeding range of the Bearded Vulture in southern Africa where darker shades indicate higher altitudes (dark grey = >2 800 m asl)

Productivity

We calculated the productivity of the population using data collected on breeding activity between 2000 and 2016. For this long-lived raptor that maintains the same territory throughout the year and does not necessarily breed every year, there can be a large difference between nesting success per territorial pair and nesting success per breeding pair. For this reason, our breeding productivity calculations took into account breeding rate and nesting success, which we defined as per Murgatroyd et al. (2016), where breeding rate is the proportion of monitored occupied territories that made a breeding attempt each year, nesting success is the proportion of breeding attempts that successfully reared a nestling, and productivity is the number of monitored pairs that successfully rear a nestling (Steenhof and Newton 2007), taking into account that no more than one nestling could be reared per breeding attempt (Margalida et al. 2004).

We defined an occupied territory as that where at least one adult was flushed off the cliff or seen flying or roosting in the area, entering a pothole or overhang on the cliff; or if a chick or fledgling was seen, or if there was fresh whitewash and plant material (sticks) on the nest indicating recent use attributed to this species based on the location of the whitewash and the type of nest structure. Territories where no activity had been recorded for more than five consecutive years ($n = 5$) were considered abandoned and were not included in the calculation of breeding rate and nesting success described below. Year-to-year fluctuations in nesting success and productivity are common in raptors (Steenhof and Newton 2007), therefore in order to reduce 'measurement error' (the misclassification of the status of a particular pair or breeding territory as a result of differences in survey effort, field situation, weather or observer inexperience), we used only occupied territories that had been surveyed at least nine times during the 17 survey years (i.e. >50%, $n = 36$) in our calculation of breeding rate. All territories included in the analyses were established territories known to the authors and the authors were not aware of any new territories established within the study period.

Breeding activity or attempt (which could not be confirmed in the majority of cases from actually seeing a clutch) was attributed to an occupied territory if it contained two birds that appeared to be paired or one or more adults engaged in territorial defence, nest affinity or other reproductive-related activity. To calculate nesting success we only used data from occupied territories that were attributed to having breeding activity that were visited more than once during the breeding season ($n = 36$). The aim of this strict criterion was to avoid the danger of biasing any conclusions by using incomplete records. In addition, for nests to be included in our final analysis, nest checks had to be during the pre-laying or incubation stage as well as at the late-nestling or fledging stage. The pairs monitored for nesting success were not necessarily the same pairs monitored for breeding rate since pairs monitored for less than nine breeding seasons in 17 years (the criterion chosen to reduce measurement error for breeding rate calculations) could still be assessed for nesting success.

Statistical analyses

We tested whether there was a change in (1) breeding rate, (2) nesting success and (3) productivity over the 17, 15 and 17 years monitored, respectively, using R 3.2.2 (R Core Team 2015). For these analyses, ideally we would have liked to have been able to fit nest site as a random term within a generalised linear mixed model (GLMM), but this was not possible because the models failed to converge. Instead we used a more conservative approach fitting a generalised linear model (GLM) with a binomial error structure and a logit link function, and nest site as a categorical fixed explanatory term together with year as a continuous explanatory variable. Thus, we explicitly controlled for differences in territory quality before examining for the effect of year. In addition, we used the GLM to generate annual means and 95% confidence intervals for the figures, by fitting year as a single categorical fixed-effect term in the models. Means are presented as mean \pm standard deviation and the ranges of the means per annum are presented in parentheses.

Results

During 2000–2016, 485 visits were undertaken to 36 individual territories (Supplementary Table S1), representing one-third of the territories in the breeding range. The breeding rate was 0.54 ± 0.74 (0.17–0.91) and, after controlling for the significant effect of nest site ($\chi^2 = 94.6$, $df = 35$, $P < 0.001$), did not change significantly over time ($\chi^2 = 0.006$, $df = 1$, $P = 0.93$) (Figure 2a). This rate therefore suggests that, on average, birds only breed every second year.

Data from 106 breeding attempts of 36 breeding pairs (Supplementary Table S1) were used to determine nesting success. The overall nesting success of breeding birds recorded in this study was 0.75 ± 0.22 (0.44–1.00) and, after controlling for the significant effect of nest site ($\chi^2 = 55.7$, $df = 35$, $P = 0.014$), declined significantly over time ($\chi^2 = 7.2$, $df = 1$, $P = 0.007$) (Figure 2b). We had little information on the causes of failure, but of the three nesting attempts where the cause was known, breeding failures were attributed to mate loss in two cases and the effects of fire in the other case.

The productivity of the population, calculated from 513 visits to 51 territories (Supplementary Table S1) was 0.42 ± 0.65 (0.28–0.67) young pair⁻¹ y⁻¹ and, after controlling for the significant effect of nest site ($\chi^2 = 108.8$, $df = 50$, $P < 0.001$), did not change significantly over time ($\chi^2 = 0.42$, $df = 1$, $P = 0.51$) (Figure 2c).

The range in each of the breeding parameters we measured (Figure 3) is an indication that territory quality varied across the study area, which was controlled for in our models as described above.

The current productivity of the southern African population is similar to the average (0.43; range 0.16–0.66) of the most recent productivity values recorded in studies elsewhere in the species' range (Figure 4).

Discussion

Our findings suggest that the productivity of the southern African Bearded Vulture population is much lower than

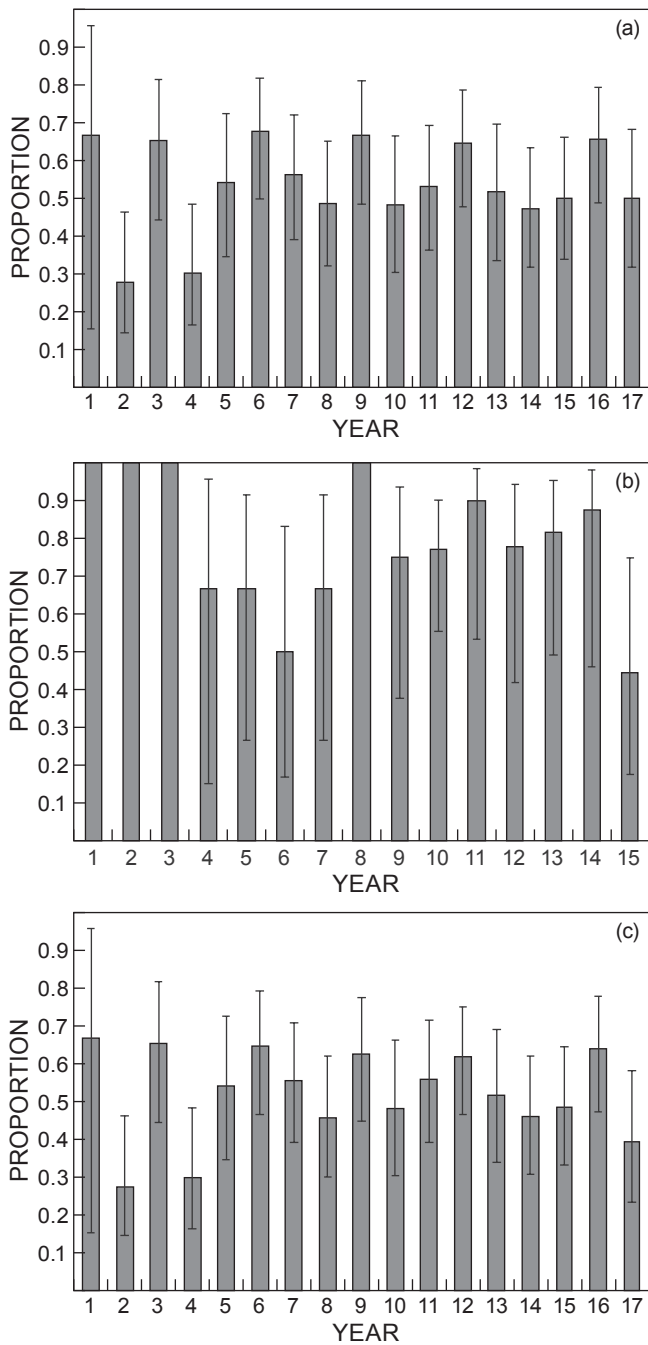


Figure 2: (a) Proportion, with 95% confidence limits from the binomial model, of monitored occupied territories of Bearded Vulture in southern Africa that made a breeding attempt each year during the 17-year study period (2000–2016). (b) Proportion, with 95% confidence limits from the binomial model, of breeding attempts of Bearded Vulture in southern Africa that successfully reared a nestling during the 15-year study period (2002–2016). (c) Proportion, with 95% confidence limits from the binomial model, of monitored pairs of Bearded Vulture in southern Africa that successfully reared a nestling during the 17-year study period (2000–2016)

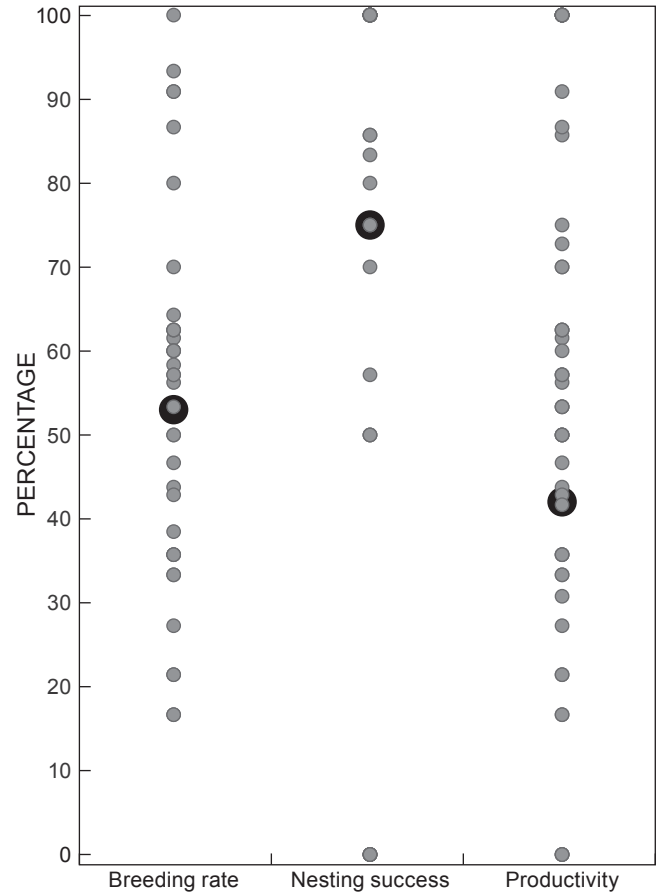


Figure 3: The mean (●) breeding rate, breeding success and productivity of the Bearded Vulture in southern Africa and the average value of these breeding parameters (expressed as a percentage) over the years monitored for each territory, indicating the range in territory quality across the study area

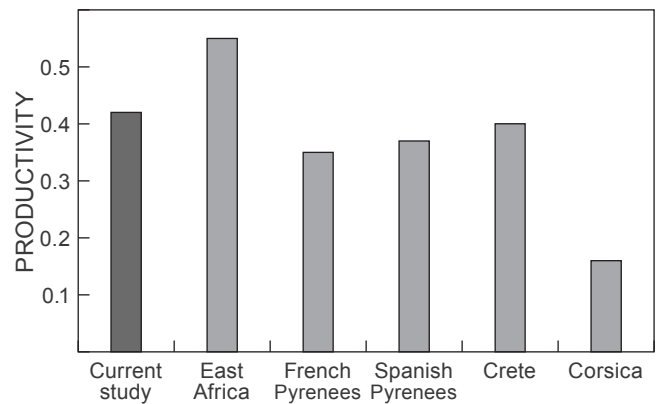


Figure 4: Current breeding productivity, the number of young per pair per year, of the Bearded Vulture at various study sites within the entire species' range. 'Current study' represents this study, East Africa (Brown 1977), French Pyrenees (Razin et al. 2004; Arroyo and Razin 2006), Spanish Pyrenees (Margalida et al. 2014), Crete (Xirouchakis and Tsiakiris 2009) and Corsica (Seguin et al. 2010)

previously recorded (Brown 1990) and appears to have declined since the early 1980s. However, we recognise that these previous records were based on a small sample of breeding pairs and that these may have been the more productive pairs, which would have biased breeding productivity upwards. However, in contrast to the findings of Brown (1990), who found that pairs generally bred each year, we found the average breeding rate to be only around 50%. This difference seems to represent a clear change over time and this reduction in productivity may be an additional contributing factor to the decline documented for this population by Krüger et al. (2014).

For Bearded Vulture in southern Africa that do attempt to breed, their nesting success is relatively high (0.75), although our results show that the success rate has declined over time. In addition, the birds do not attempt to breed (breeding rate of 0.54) as frequently as recorded in the past, thereby lowering the overall productivity of the population. The productivity recorded for the southern African population (0.42 young pair⁻¹ y⁻¹) is lower than that recorded in the past for the species in East Africa (Brown 1977) and Ethiopia (Urban et al. 1982) (0.55 young pair⁻¹ y⁻¹), in the French Pyrenees (Terasse 1991) (0.66 young pair⁻¹ y⁻¹) and in the Spanish Pyrenees (Heredia 1991) (0.65 young pair⁻¹ y⁻¹). More recent records on the productivity of the species in Europe are more comparable with our results; for example, 0.43 young pair⁻¹ y⁻¹ (Margalida et al. 2003) and 0.37 young pair⁻¹ y⁻¹ (Carrete et al. 2006b; Margalida et al. 2014) in the Spanish Pyrenees, 0.35 young pair⁻¹ y⁻¹ in the French Pyrenees (Arroyo and Razin 2006), 0.40 young pair⁻¹ y⁻¹ in Crete (Xirouchakis and Tsiakiris 2009) and 0.16 young pair⁻¹ y⁻¹ in Corsica (Seguin et al. 2010). Although nesting success declined over time, our population did not show a decline in productivity over the past 17 years, whereas Margalida et al. (2014) showed a decline from 0.37 to 0.29 young pair⁻¹ y⁻¹ over the same time period and Carrete et al. (2006b) showed a decline from 0.80 to 0.37 young pair⁻¹ y⁻¹ over a 25-year period. The latter two studies represent a density-dependent scenario in a dense population where the average productivity decreases as the population increases because progressively poorer territories are used. This is not the case in the small and declining southern African population where nesting density has decreased over the past few decades, with no corresponding increase in productivity being observed (Krüger et al. 2014). Our breeding rates are also comparable with those of other large raptors (e.g. Brown and Hopcroft 1973; Gargett 1977; Mundy 1982; Vernon et al. 1983; Tarboton and Allan 1984; Watson 1990; Murgatroyd et al. 2016).

We are unsure why the population breeding rates have declined so substantially compared with those recorded by Brown (1990). For other species, variation in breeding rate (i.e. annually or biennially) has been attributed to variation in food supply levels (Amar et al. 2004; Murgatroyd et al. 2016). This could either be directly by influencing the condition of the female (Amar and Redpath 2002) or indirectly by influencing the length of the post-fledgling dependency period (PFDP). The PFDP in our population is currently around 119 d (Krüger and Amar 2017), which is comparable (if slightly lower) to that found previously for

this population by Brown (1990), and is actually slightly lower than that found for other Bearded Vulture populations in Europe (Sunyer 1991; López-López et al. 2014). Thus, the hypothesis that prolonged PFDP has given rise to this reduction in breeding rates seems unlikely.



Food limitation, meaning that females are often unable to get into breeding condition, is a possible explanation for the low breeding rate witnessed in our population, although previous research examining factors associated with territorial abandonment did not find strong evidence to support the idea that food limitation was important (Krüger et al. 2015). Experimental provisioning of food to pairs during the pre-laying period could be used to test this explanation (Amar and Redpath 2002).

An alternative explanation for the low breeding rate currently experienced is that it is linked to elevated mortality rates due to human poisoning, which is the main threat to this population (Krüger et al. 2015), as it is elsewhere in the species range (Margalida et al. 2008). Losses of territorial birds would mean a high turnover of individuals within pairs, and this is known to have an influence on the breeding performance of vultures (Margalida et al. 2012). It may also mean that in some years lack of breeding activity could have been due to the site not being actively occupied or being occupied by only one bird if the partner had died. This has been documented in at least two cases from GPS-tracked birds (SCK unpublished data). If this is indeed the explanation for the low breeding rates, any conservation action aimed at reducing poisoning or other forms of adult mortality may also indirectly benefit the productivity of the population.

This study has provided better information on the productivity of the population, but further research is required on the factors influencing breeding rate and nesting success in order to improve the success of conservation strategies aimed at addressing the population decline.

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