



Insights into post-fledging dispersal of Bearded Vultures *Gypaetus barbatus* in southern Africa from GPS satellite telemetry

Sonja Krüger & Arjun Amar

To cite this article: Sonja Krüger & Arjun Amar (2017): Insights into post-fledging dispersal of Bearded Vultures *Gypaetus barbatus* in southern Africa from GPS satellite telemetry, *Bird Study*, DOI: [10.1080/00063657.2017.1295019](https://doi.org/10.1080/00063657.2017.1295019)

To link to this article: <http://dx.doi.org/10.1080/00063657.2017.1295019>



Published online: 31 Mar 2017.



Submit your article to this journal [↗](#)



Article views: 2





View related articles [↗](#)



View Crossmark data [↗](#)

Insights into post-fledging dispersal of Bearded Vultures *Gypaetus barbatus* in southern Africa from GPS satellite telemetry

Sonja Krüger ^{a,b} and Arjun Amar ^b

^aEzemvelo KwaZulu-Natal Wildlife, Cascades, South Africa; ^bPercy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

ABSTRACT

Capsule: Fledglings progressively increase their home range size and ranging behaviour as they age.

Aims: To examine the home range size and ranging behaviour of Bearded Vulture fledglings during the post-fledging dependence period and determine the onset of natal dispersal.

Methods: Post-fledging movements of three individuals were investigated in southern Africa using global positioning system (GPS) satellite telemetry which enabled home range sizes and distances travelled from the nest to be calculated.

Results: Fledglings increased their home range size from an average of 0.4–10 999 km² (100% Minimum Convex Polygons) and 9.13–11 466 km² (fixed 95% kernels) within the first six months post fledging. They also increased home range use as they aged with maximum daily distances travelled from the nest occurring between 98 and 136 days post fledging (when fledglings were aged between 222 and 262 days), after which time they dispersed from their natal area. Distances between fixes were highest during the dispersal period.

Conclusion: GPS satellite telemetry allows us to accurately demonstrate how fledglings progressively increase and use their home ranges as they age and undertake pre-dispersive exploratory flights. Results confirm the notion that juveniles disperse at the onset of the following breeding season and suggest that dispersal occurs earlier in the southern hemisphere.

ARTICLE HISTORY

Received 18 September 2016

Accepted 8 January 2017

Understanding how species use their environment in both space and time can play a critical role in designing effective conservation management strategies (Primack 2010). The post-fledging dependence period is one of the most critical periods in the life stages of birds (Weathers & Sullivan 1989) and can strongly influence population dynamics (Yackel Adams 2006, Smart *et al.* 2010, Sim *et al.* 2011). The risk of mortality is particularly high during this period as fledged birds learn to fly and become self-sufficient (Bustamante & Negro 1994, Soutullo *et al.* 2006, Delgado *et al.* 2009). Understanding the space use by birds during the post-fledging dependence period and the timing of dispersal is particularly important in the conservation of a species with delayed maturity, high parental investment and low fecundity (Ferrer 1993, Ferguson-Lees & Christie 2001, Amar *et al.* 2000, Margalida & Bertran 2000, Margalida *et al.* 2003, Penteriani & Delgado 2009, López-López *et al.* 2013).

The Bearded Vulture *Gypaetus barbatus* is a long-lived, large scavenging raptor that exhibits delayed breeding, nests on high mountain cliffs in Africa, Europe and Asia and forages extensively over the

surrounding mountains (Hiraldo *et al.* 1979, Brown 1997). The sub-species *Gypaetus barbatus meridionalis* is distributed south of the Tropic of Cancer, in sub-Saharan Africa (Hiraldo *et al.* 1984, Mundy *et al.* 1992). In southern Africa the sub-species is restricted to the Maloti-Drakensberg mountains of Lesotho and South Africa, where its range and population size have declined markedly in the last few decades and there are now no more than 110 occupied territories (Brown 1991, Krüger *et al.* 2014a). This population has recently been classified regionally as 'Critically Endangered' as a result of these declines and the ongoing threats faced by the population throughout its foraging range (Krüger 2015). These threats include the use of poisons and the construction of energy structures (power lines and wind turbines) with the associated risk of collisions (Brown 1991, Mundy *et al.* 1992, Rushworth & Krüger 2014, Reid *et al.* 2015). Fledglings are assumed to be particularly vulnerable to threats within the first few months of fledging because they are inexperienced flyers and are unfamiliar with their surroundings and potential threats within their home range.

The post-fledging dependence period of the southern African population has been described by Brown (1990) based on visual observations and the radio-tracking of one individual. However, the latest studies of this population, using more accurate global positioning system (GPS) satellite telemetry methods, do not include information on post-fledging movements (Urios *et al.* 2010, Krüger *et al.* 2014b). Studies conducted in the European Pyrenees also focussed on visual observations and radio-tracking (Sunyer 1991) and more recently used GPS satellite telemetry to examine fledgling movements (López-López *et al.* 2014, Margalida *et al.* 2016).

We studied the post-fledging movements of three Bearded Vultures in southern Africa between 2008 and 2010 using GPS satellite tags. These data on post-fledging dependence and natal dispersal will provide additional useful information to guide the implementation of conservation measures.

Methods

The study took place in the Maloti-Drakensberg region of Lesotho and South Africa which encompasses the entire distributional range of the Bearded Vulture population in southern Africa (Figure 1). The Maloti-Drakensberg mountains dominate the study area with a mean altitude of 2200 m above sea level (range 1280–3500 m) (Sycholt 2002). The remaining study area constitutes predominantly protected areas, commercial and communal farmland in South Africa and communal rangeland in Lesotho which is extensively grazed by livestock.

Three nestlings were fitted with 45 g solar-powered GPS-platform transmitter terminals (North Star Science and Technology, LLC, Virginia, USA), referred to from here on as tags, prior to fledging during November 2008 ($n=2$) and November 2010 ($n=1$). All three birds were identified as female through genetic sex determination performed by Molecular Diagnostic Services (MDS Pty Ltd., Westville, South Africa) using nucleic acid amplification procedures with blood taken from the brachial vein ($n=1$) or from the tip of the feather shaft of a breast feather ($n=2$).

Tags were attached using a pelvic harness attachment (Hegglin *et al.* 2004) constructed using a 2 mm silicon cord inserted into 6 mm tubular Teflon Ribbon® (Bally Ribbon Mills, Bally, Pennsylvania). The harnesses incorporated a weak link sewn with dental floss to allow birds to lose the harness after the end of the tag's life cycle (Fuller 1987), which was predicted to be between five and eight years. The tags recorded one

GPS position every three hours continuously, as well as movement speed, date and time.

Home range size

The home range or utilization distribution of each individual was estimated by means of a kernel density approach (Worton 1989, 1995, Kenward *et al.* 2001). Home range estimates were derived as described in Krüger *et al.* (2014b). Home range sizes were calculated in R (R Core Team 2013) using the package *adehabitatHR* v.0.4.10 (Calenge 2006) with the package *rgdal* v.0.8–16 (Bivand *et al.* 2013) to process the spatial data. We calculated the minimum convex polygon (MCP) and the fixed 95% and 50% kernel density contours over 15-day periods to allow for comparisons with other similar studies. The 100% MCP represents the maximum area of activity, the 95% kernel estimates the majority of the home range area and the 50% kernel estimates the core (intensive use) area (Worton 1989, Seaman & Powell 1996, Fieberg 2007). The cumulative size of the home range was also calculated over 15-day periods.

Dispersal distance

To quantify the extent of fledgling movements, each day we determined the maximum distance of each individual from the nest within their first year based on the straight-line distance between the nest and the furthest location fix obtained for that day, calculated using the software Geospatial Modelling Environment (GME) (Beyer 2012). The date of fledging was taken as the first day where a distance over 100 m from the nest was obtained.

The maximum daily distance of fledglings from the nest was used to calculate the dispersal date from the natal area. We used the method of Weston *et al.* (2013) to identify the timing of transition from dependence to independence from the natal locus. This was done as follows: The home range boundaries of six breeding adults (Krüger *et al.* 2014b) were used as a proxy for the area of potential parental influence. The maximum distance parents were recorded from their nest site was based on the radius of the average 90% kernel home range (5.5 km) whereas the core ranging distance was based on the radius of the average 50% kernel home range (2.1 km), the latter being more concentrated around the nest (Krüger *et al.* 2014b).

A 14-day period away from the natal home range was used as a proxy for independence. This period was considered the maximum time that a juvenile can survive without additional food from its parents (H. Frey and A. Llopis, pers. comm.). Using this method, an individual had to move the equivalent of the radius

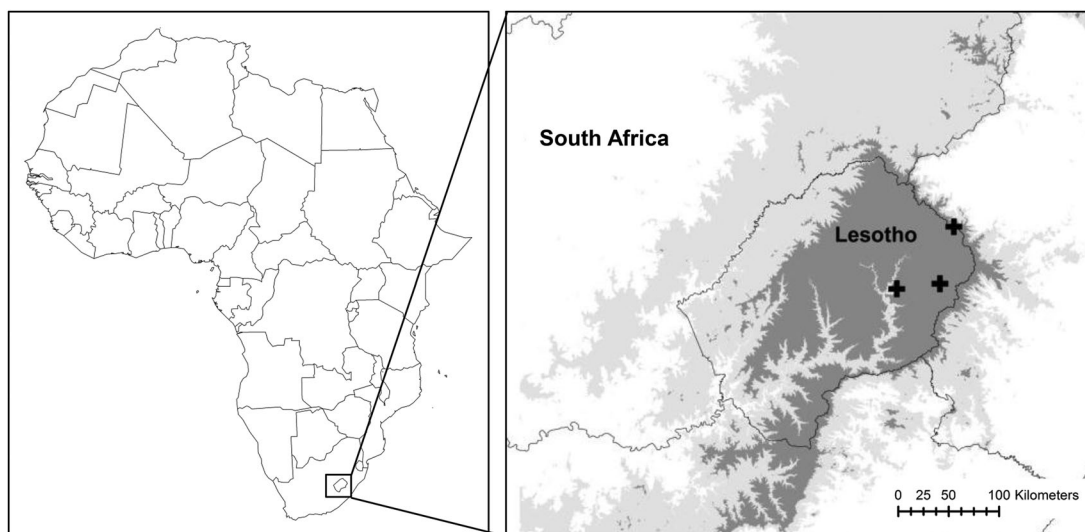


Figure 1. The Maloti-Drakensberg region in southern Africa depicted by the high lying areas (grey shading >2000 m above sea level) and indicating the sites where nestlings were tagged (+).

of the adult's mean maximum ranging area from the nest (90% kernel, 5.5 km radius) and not return to within the adult's mean core ranging area (50% kernel, 2.1 km radius) within the following 14 days, at which stage it was classified as having dispersed.

Statistical analysis

For all spatial analyses the GPS locations were projected to the Universal Transverse Mercator (UTM) coordinate system (World Geodetic System 1984 UTM Zone 35S) for use in R v. 3.0.1 (R Core Development Team 2013), ArcGIS v. 10.0 (ESRI, Redlands, USA) and the GME (Beyer 2012).

We explored changes in fledgling home range size (95% and 50% kernels and 100% MCPs), in each 15-day period since fledging for the first six months post fledging; these were the months for which data were available for all three individuals. For this we used a general linear model with 'period' as a continuous variable, and 'individual' as a fixed effect.

A preliminary analysis showed that there was no significant correlation between the number of location fixes used for the kernel analyses and home range size, using the 95% kernel ($\chi^2_{33} = 1.61$, $P = 0.20$) and the 50% kernel ($\chi^2_{33} = 1.47$, $P = 0.23$), which eliminated

possible bias in the estimation of space use due to individual variability (Kernohan *et al.* 2001). There was some correlation between the number of fixes and home range size using the MCP method of home range estimation ($\chi^2_{33} = 6.03$, $P < 0.01$).

We examined how movement patterns changed over time using generalized additive models. Within these models we fitted 'day' as a continuous fixed effect and 'individual' as a categorical fixed effect, and explored their relationship with the maximum daily distance from the nest.

Results

We obtained satellite tracking data from three fledglings for at least the first six months post-fledging (i.e. a combined total of 24 bird-months; 2528 GPS fixes in total) between November 2008 and September 2011 (Table 1). Individual and mean values of home range area exploration, and the maximum distance from the nest are reported in Table 2.

Home range use

Fledgling home range (95% kernel, 50% kernel and MCP, respectively) sizes did not differ between the

Table 1. Details of the tracking information for the three Bearded Vultures used in southern Africa between November 2008 and November 2011. Tracking of 87.1 terminated when the bird died, whereas termination date of the other two birds is the date they were classified as juveniles and no longer fledglings.

ID	Date tagged	Date fledged	Date tracking terminated	Dispersal date	Post fledging dependency period (days)	Months tracked
87.1	22 Nov 2008	1 Dec 2008	8 Jun 2009	15 Apr 2009	136	6
88	23 Nov 2008	6 Dec 2008	31 Aug 2009	6 Apr 2009	122	9
87.2	11 Nov 2010	7 Dec 2008	31 Aug 2011	14 Mar 2011	98	9

Table 2. The number of GPS fixes obtained in the study period, home range sizes measured in 50% fixed kernels, 90% fixed kernels and 100% MCP, and the maximum distance travelled in km from nest by three Bearded Vultures six months after fledging.

ID	No. of GPS fixes	Home range in km ²			Maximum daily distance
		50% kernel	95% kernel	MCP	
87.1	398	1363	11 644	10 813	194 ± 23
88	1270	2370	15 915	14 209	127 ± 28
87.2	860	1088	6840	7976	72 ± 22
Mean	843 ±	1067 ±	11 466 ±	10 999 ±	132 ± 52
±sd	436	675	4 540	3120	

three individuals ($\chi^2_2 = 0.77$, $P = 0.68$; $\chi^2_2 = 0.31$, $P = 0.86$; $\chi^2_2 = 1.97$, $P = 0.37$) but did differ between 15-day periods ($\chi^2_{33} = 11.27$, $P < 0.001$; $\chi^2_{33} = 12.49$, $P < 0.001$;

$\chi^2_{33} = 15.68$, $P < 0.001$; Figure 2a). Cumulative home range sizes increased from time since fledging from a mean of 6, 9 and 0.4 km² in the first 15 days to a cumulative home range of 1607, 11 466 and 10 999 km² at six months for the 50% and 95% kernels and MCP, respectively (Figure 2b).

Similarly, the maximum daily distances of each fledgling from the nest (natal point) increased significantly ($F_{7,8} = 103$, $P < 0.001$) over the first six months following fledging (Figure 3), with a dramatic increase in the maximum daily distance from the nest area during the onset of the next breeding season at between 120 days (23.14 ± 22.96 km from the nest) and 150 days (53.03 ± 53.95 km from the nest), which coincided with dispersal (98–136 days since fledging; Figure 4).

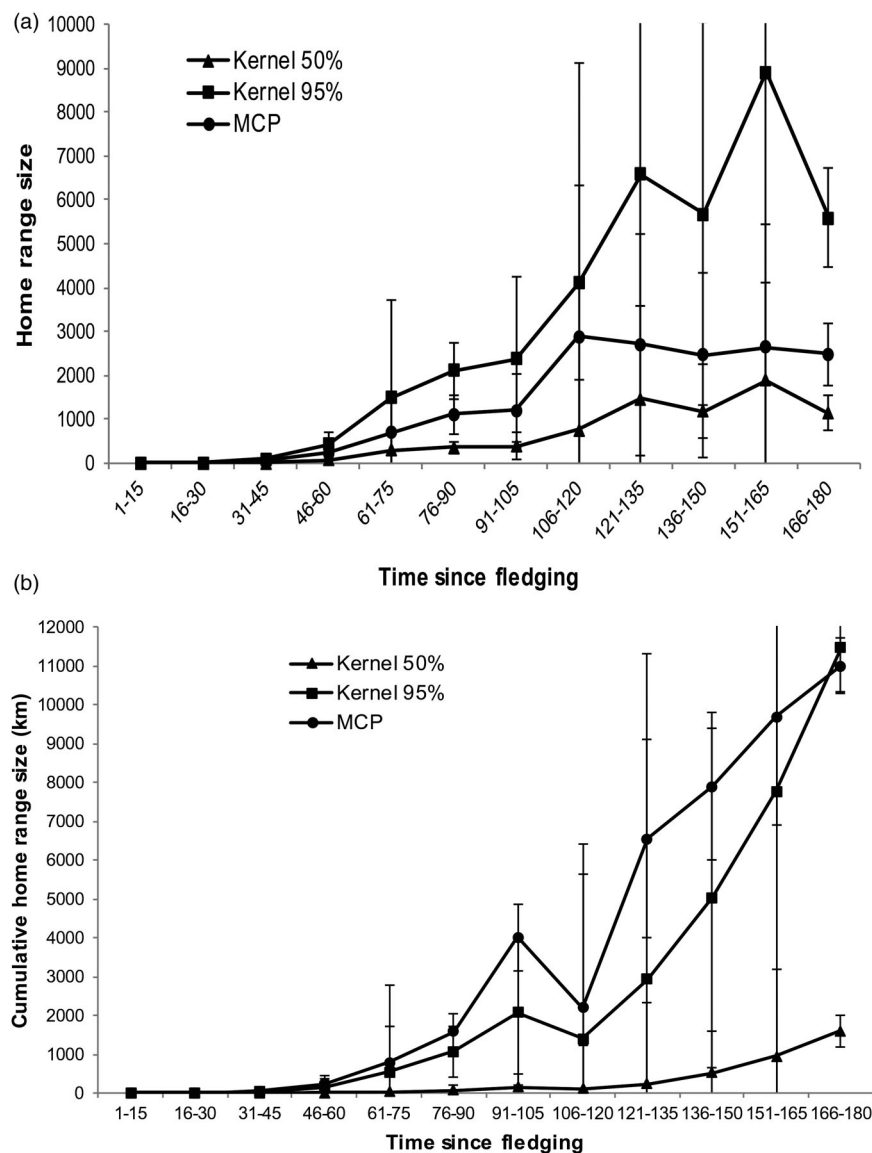


Figure 2. The mean (±standard deviation) size of the 50% kernel, 95% kernel and MCP (a) home range and (b) cumulative home range in km² of three fledgling Bearded Vultures depicted in 15-day intervals for the first six months post fledging, showing an increase in home range size with days since fledging. In (a) the standard deviation could not be calculated for the second time period (16–30 days) because the number of locations was insufficient (>5) for two individuals to determine home range size.

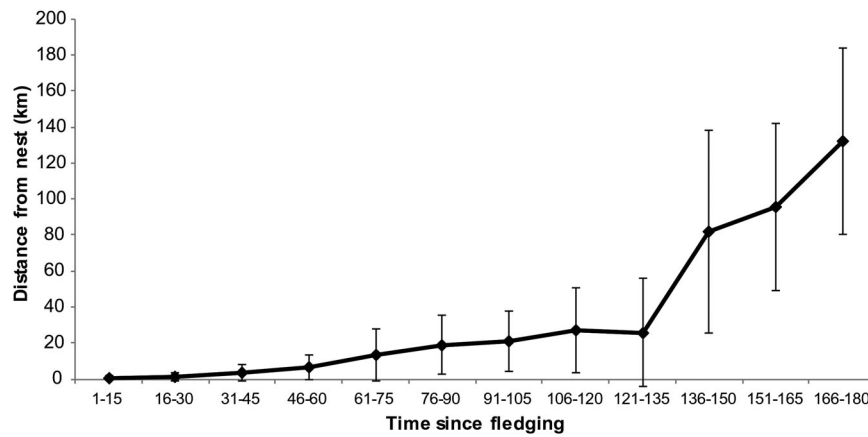


Figure 3. The mean (\pm standard deviation) maximum daily distance in km from the nest of three fledgling Bearded Vultures depicted in 15-day intervals for the first six months post fledging, showing an increase in maximum daily distance from the nest with days since fledging.

Dispersal ages were calculated as the age at which a fledgling had moved at least 5.5 km from the nest and had not returned to within 2.1 km for at least 14 days, with age at fledging taken as 126 ± 2 days (Brown 1990). Based on this we estimated the age of dispersal of the three individuals at between 222 and 226, 246 and 250 and 260 and 264 days old, and the post-fledging dependency period for each individual to be 98 (14 March), 122 (6 April) and 136 (15 April) days after fledging. The mean dispersal age was 245 days and the mean post-fledging dependency period was 119 days.

Discussion

This study provides important information on the spatial movements of fledged Bearded Vulture in southern Africa, which should aid conservation management planning for this species. Although the sample size is small, the use of more accurate technology in this study has allowed us to obtain more explicit information on

the length of the post-fledging dependence period and the timing of the onset of natal dispersal.

We recorded a progressive increase in home range size and distance from the nest during the post-fledging dependency period. Our movement results agree with those of Margalida *et al.* (2013), López-López *et al.* (2014) and Margalida *et al.* (2016) that fledglings progressively increase the distance from their natal area as they age and undertake pre-dispersive exploratory flights.

The sizes of the home range areas reported in this study for the first six months post fledging (ranging from 0.4 to 10 999 km², MCP) were considerably larger than those described for this species by others. For example, the birds in this study explored an MCP area of 2193 km² at four months post fledging compared with 78 and 65 km² calculated by Brown (1990) and Sunyer (1991), respectively, probably as a result of more accurate satellite telemetry technology (Cadahía *et al.* 2008, Krüger *et al.* 2014b). When compared to studies using similar technology, the total home range area explored by this sub-species at six months (10

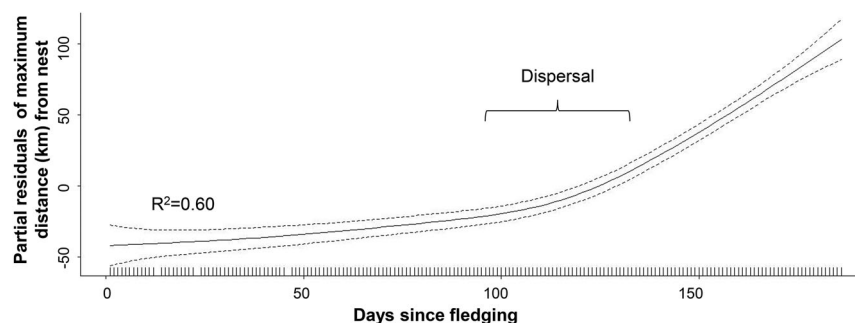


Figure 4. The partial residuals (---) with smoothing parameters estimated using the Generalized Cross Validation criterion, from a General Additive Model of the increase in the average maximum daily distance (km) travelled from the nest with days since fledging of three fledgling Bearded Vultures for the first six months post fledging, after controlling for individual. Fledglings showed an increase in the extent of their movements with time until dispersal at between 98 and 136 days after fledging.

999 km²) is still much larger than those recorded for the northern sub-species in three studies: 2852 km² (López-López *et al.* 2014), 978–4544 km² (Gil *et al.* 2014) and 1566 km² (Margalida *et al.* 2016).

Although fledglings remained in their natal area for the first few months, the size of their home range after 31–40 days (99 km²; 95% kernel) was larger than the average home range size of breeding adults (95 km²; 90% kernel) recorded by Krüger *et al.* (2014b).

Our results confirm those of previous studies that the young leave the natal area at the onset of the following breeding season (Brown 1990, Sunyer 1991, López-López *et al.* 2014) characterized by the start of sexual activity of the adults and an increase in the defence of their territory (Margalida *et al.* 2003). The time to dispersal calculated in this study (119 days after fledging when aged 245 days old) was similar to that determined by Brown (1990; 126 days after fledging) and within the range calculated by Sunyer (1991) for the species in the Spanish Pyrenees (individuals aged 206–364 days). Our calculations were, however, lower than the estimates of López-López *et al.* (2014; 193 days when aged 317 days) using similar methods, suggesting that birds in the southern hemisphere disperse earlier than those further north. Adult birds did not show aggression towards their young, but rather stopped food provisioning to encourage dispersal (personal observation). Earlier dispersal dates therefore suggest that food is not a limiting resource in the study area, which supports the findings of Krüger *et al.* (2015). These authors found human impacts to negatively affect this population with the abandonment of territories more likely where these had higher densities of power lines and human settlements, suggesting that habitat quality may be the main regulatory mechanism of space use in this population.

The species experiences a high risk of mortality during the post-fledging dependence period (Lack 1954), therefore, detailed knowledge of home range size, ranging behaviour and the timing of dispersal aids conservation planning for the species.

Acknowledgements

We are grateful to the capture team for their patience and tireless efforts, in particular Allan Howell, Daniel Hegglin and Rickert van der Westhuizen, and mountain climbers David Allan, Charl Brummer, Timothy and Steven O'Connor. Vulture handling and marking procedures were approved by the Animal Ethics Committee of the Science Faculty of the University of Cape Town (reference: 2001V14\SK), South African National Parks and Ezemvelo KwaZulu-Natal Wildlife (Research Project Registration number W/2057/01) and were carried out under the Endangered Wildlife Trust's Threatened or Protected Species registration certificate granted by the

Gauteng Provincial Department of Agriculture, Conservation and Environment, South Africa (permit: 07046).

Funding

Tags were funded by the Wildlands Conservation Trust. Field work was undertaken by Sonja Krüger whilst in the employ of Ezemvelo KwaZulu-Natal Wildlife, who covered operational expenses and provided a bursary.

ORCID

Sonja Krüger  <http://orcid.org/0000-0002-5761-0139>
Arjun Amar  <http://orcid.org/0000-0002-7405-1180>

References

- Amar, A., Arroyo, B.E. & Bretagnolle, V. 2000. Post-fledging dependence and dispersal in hacked and wild Montagu's Harriers *Circus pygargus*. *Ibis* **142**: 21–28.
- Beyer, H.L. 2012. *Geospatial Modelling Environment* (Version 0.7.2.0) (software) [online]. Available from: <http://www.spatialecology.com/gme> [Accessed 1 November 2015].
- Bivand, R., Keitt, T. & Rowlingson, B. 2013. *rgdal: bindings for the geospatial data abstraction library* [online]. R package version 0.8-10. Available from: <http://CRAN.R-project.org/package=rgdal> [Accessed 1 November 2015].
- Brown, C.J. 1990. Breeding biology of the Bearded Vulture in southern Africa, Part III: the post-nestling dependence period. *Ostrich* **61**: 43–49.
- Brown, C.J. 1991. An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol. Conserv.* **57**: 315–337.
- Brown, C.J. 1997. Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr. J. Ecol.* **35**: 53–63.
- Bustamante, J. & Negro, J.J. 1994. The post-fledging dependence period in the Lesser Kestrel *Falco naumanni*. *J. Raptor Res.* **28**: 158–163.
- Cadahía, L., López-López, P., Negro, J.J. & Urios, V. 2008. Estimating the onset of dispersal in endangered Bonelli's Eagle *Hieraetus fasciatus* tracked by satellite telemetry: a comparison among methods. *Ibis* **150**: 416–420.
- Calenge, C. 2006. The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**: 516–519.
- Delgado, M.M., Penteriani, V. & Nams, V.O. 2009. How fledglings explore surroundings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*. *Ardea* **97**: 7–15.
- Ferguson-Lees, J. & Christie, D.A. 2001. *Raptors of the World*. Houghton Mifflin Company, New York.
- Ferrer, M. 1993. Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* **135**: 132–138.
- Fieberg, J. 2007. Kernel density estimators of home-range: smoothing and the autocorrelation red herring. *Ecology* **88**: 1059–1066.
- Fuller, M.R. 1987. Application and considerations for wildlife telemetry. *J. Raptor Res.* **21**: 126–128.
- Gil, J.A., Báguena, G., Sánchez-Castilla, E., Antor, R.J., Alcantara, M. & López-López, P. 2014. Home ranges and movements of non-breeding Bearded Vultures tracked by satellite telemetry in the Pyrenees. *Ardeola* **61**: 379–387.

- Hegglin, D., Wehrle, M. & Aebischer, A. 2004. *Satellite Tracking of Bearded Vultures – The Project ‘Bearded Vultures on the Move’*, 52–55. Annual Report of the Foundation for the conservation of the Bearded Vulture.
- Hiraldo, F., Delibes, M. & Calderon, J. 1979. *El Quebrantahuesos: sistemática, taxonomía, biología, distribución y protección*. Monografías 22, ICONA, Madrid.
- Hiraldo, F., Delibes, M. & Calderón, J. 1984. Comments on the taxonomy of the Bearded Vulture *Gypaetus barbatus* (Linnaeus, 1758). *Bonn Zool. Beitr.* 35: 91–95.
- Kenward, R.E., Clarke, R.T., Hodder, K.H. & Walls, S.S. 2001. Density and linkage estimators of home-range: nearest-neighbor clustering defines multi-nuclear cores. *Ecology* 82: 1905–1920.
- Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. 2001. Analysis of animal space use and movements. In Millspaugh, J.J. & Marzluff, J.M. (eds) *Radio Tracking and Animal Populations*, 125–166. Academic Press, San Diego, CA.
- Krüger, S.C. 2015. Bearded Vulture *Gypaetus barbatus*. In Taylor, M.R., Peacock, F. & Wanless, R.W. (eds) *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland*, 55–57. BirdLife South Africa, Johannesburg.
- Krüger, S.C., Allan, D.G., Jenkins, A.R. & Amar, A. 2014a. Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv. Int.* 24: 162–177.
- Krüger, S.C., Reid, T. & Amar, A. 2014b. Differential range use and anthropogenic risk exposure between age classes of southern African Bearded Vultures *Gypaetus barbatus*. *PLoS ONE* 9: e114920. doi:10.1371/journal.pone.0114920.
- Krüger, S.C., Simmons, R.E. & Amar, A. 2015. Anthropogenic activities influence the abandonment of Bearded Vulture *Gypaetus barbatus* territories in southern Africa. *The Condor* 117: 94–107.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- López-López, P., Zuberogoitia, I., Alcántara, M. & Gil, J.A. 2013. Philopatry, natal dispersal, first settlement and age of first breeding of Bearded Vultures *Gypaetus barbatus* in central Pyrenees. *Bird Study* 60: 555–560.
- López-López, P., Gil, J.A. & Alcántara, M. 2014. Post-fledging dependence period and onset of natal dispersion in Bearded Vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. *J. Raptor Res.* 48: 173–181.
- Margalida, A. & Bertran, J. 2000. Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: minimal difference in parental activities. *Ibis* 142: 225–234.
- Margalida, A., García, D., Bertran, J. & Heredia, R. 2003. Breeding biology and success of the Bearded Vulture *Gypaetus barbatus* in eastern Pyrenees. *Ibis* 145: 244–252.
- Margalida, M., Carrete, M., Hegglin, D., Serrano, D., Arenas, R. & Donazar, J.A. 2013. Uneven large-scale movement patterns in wild and reintroduced pre-adult Bearded Vultures: conservation implications. *PLoS ONE* 8: e65857.
- Margalida, A., Pérez-García, J.M., Afonso, I. & Moreno-Opo, R. 2016. Spatial and temporal movements in Pyrenean Bearded Vultures (*Gypaetus barbatus*): Integrating movement ecology into conservation practice. *Sci. Rep.* 6, article no. 35746. doi:10.1038/srep35746
- Mundy, P., Butchart, D., Ledger, J. & Piper, S. 1992. *The Vultures of Africa*. Russel Friedman Books cc, Johannesburg.
- Penteriani, V. & Delgado, M.M. 2009. Thoughts on natal dispersal. *J. Raptor Res.* 43: 90–98.
- Primack, R.B. 2010. *Essentials of Conservation Biology*, 5th edn. Sinauer Associates, Sunderland, MA.
- R Core Team. 2013. *R: A Language and Environment for Statistical Computing* [online]. R Foundation for Statistical Computing, Vienna. Available from: <http://www.R-project.org> [Accessed 1 November 2015].
- Reid, T., Krüger, S., Whitfield, P. & Amar, A. 2015. Using spatial analyses of Bearded Vulture movements in southern Africa to inform wind turbine placement. *J. Appl. Ecol.* doi:10.1111/1365-2664.12468.
- Rushworth, I. & Krüger, S. 2014. Wind farms threaten southern Africa’s cliff-nesting vultures. *Ostrich* 85: 13–23.
- Seaman, D.E. & Powell, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075–2085.
- Sim, I.M.W., Rebecca, G.W., Ludwig, S.C., Grant, M.C. & Reid, J.M. 2011. Characterizing demographic variation and contributions to population growth rate in a declining population. *J. Anim. Ecol.* 80: 159–170.
- Smart, J., Amar, A., Sim, I.M.W., Etheridge, B., Cameron, D. & Christie, G. 2010. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – the red kite *Milvus milvus*. *Biol. Conserv.* 143: 1278–1286.
- Soutullo, A., Urios, V., Ferrer, M. & Peñarrubia, S.G. 2006. Dispersal of golden eagles *Aquila chrysaetos* during their first year of life. *Bird Study* 53: 258–264.
- Sunyer, C. 1991. El period de emancipación en el Quebrantahuesos: consideraciones sobre su conservación [The post-fledging period of the Bearded Vulture: implications for its conservation]. In Heredia, R. & Heredia, B. (eds) *El quebrantahuesos (Gypaetus barbatus) en los Pirineos. Características ecológicas y biología de la conservación. Colección Técnica*, 47–65. Instituto para la Conservación de la Naturaleza, Madrid (in Spanish).
- Sycholt, A. 2002. *A Guide to the Drakensberg*. Struik Publishers, Cape Town.
- Urios, V., López-López, P., Limiñana, R. & Godino, A. 2010. Ranging behaviour of a juvenile Bearded Vulture (*Gypaetus barbatus meridionalis*) in South Africa revealed by GPS satellite telemetry. *Ornis Fenn* 87: 1–5.
- Weathers, W.W. & Sullivan, K.A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.* 59: 223–246.
- Weston, E.D., Whitfield, D.P., Travis, J.M.J. & Lambin, X. 2013. When do young birds disperse? Tests from studies of golden eagles in Scotland. *BMC Ecology* 13: 42. Available from: <http://www.biomedcentral.com/1472-6785/13/42> [Accessed 12 April 2016].
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home-range estimators. *J. Wildl. Manage.* 59: 794–800.
- Yackel Adams, A.A. 2006. Post-fledging survival. *Bull. Ecol. Soc. Am.* 87: 20–24.