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HOME RANGES AND MOVEMENTS OF NON-BREEDING BEARDED VULTURES TRACKED BY SATELLITE TELEMETRY IN THE PYRENEES

ÁREAS DE CAMPEO Y MOVIMIENTOS DE QUEBRANTAHUESOS NO REPRODUCTORES SEGUIDOS MEDIANTE TELEMETRÍA SATELITAL EN LOS PIRINEOS

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Summary.—We present data on home range sizes and spatial parameters of six non-breeding bearded vultures *Gypaetus barbatus* (one adult, four subadults and one juvenile) using Argos satellite telemetry in the Pyrenees (Spain-France) between 1999 and 2006. None of the birds left the Pyrenees during the tracking period and all individuals included supplementary feeding stations (SFS) in their home ranges. Home range areas reported here were smaller than those previously reported in South Africa and slightly larger than those reported in the Pyrenees and the Alps. Overlap between home ranges and SFS shows the importance of predictable sources of food, especially for inexperienced juvenile birds. Satellite telemetry facilitates improved insight into the bearded vulture's spatial ecology and behaviour, which is key for the conservation of this threatened species.

Resumen.—Mostramos los resultados del tamaño del área de campeo y parámetros espaciales de seis quebrantahuesos *Gypaetus barbatus* no reproductores (un adulto, cuatro subadultos y un juvenil) seguidos mediante telemetría satelital vía Argos en los Pirineos (España-Francia) entre 1999 y 2006. Ningún ejemplar abandonó los Pirineos durante el período de seguimiento y todos los ejemplares incluyeron puntos de alimentación suplementaria (PAS) en sus áreas de campeo. El tamaño de las áreas de campeo fue inferior a lo descrito previamente en Sudáfrica y ligeramente superior a lo descrito en los Pirineos y los Alpes. El solapamiento entre las áreas de campeo y los PAS demuestra la importancia de las fuentes de alimento predecible, especialmente para los inexperimentados juveniles. La telemetría satelital permite comprender mejor la ecología espacial y el comportamiento del quebrantahuesos, lo cual es clave para la conservación de esta especie amenazada.

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Satellite tracking technology provides robust, spatially explicit information about animal movements and habitat use, which are essential for conservation (Rutz and Hays, 2009). In particular, accurate telemetry data is of utmost importance in identifying strategic locations where life-history events occur (i.e. dispersal, first breeding attempt, first successful bree-ding), as well as potential threats such as mortality hotspots.

The bearded vulture *Gypaetus barbatus* is a long-lived, cliff-nesting, obligate scavenger currently listed as a 'priority species' by the European Union (Annex I of the European Birds Directive) and listed as endangered in Spain (Antor *et al*., 2005). Bearded vultures are highly mobile during their extensive juvenile dispersal period. However, our knowledge about their spatial ecology, particularly post-fledging and dispersal movements, remains poorly understood (Brown, 1990; Margalida *et al.,* 2013; López-López *et al*., 2014a). Previous studies were mainly based on visual re-sightings of marked individuals and very high frequency (VHF) radio-telemetry (Brown, 1990; Heredia, 1991; Gil *et al*., 2010; López-López *et al*., 2013a). More recently, satellite tracking programmes are providing quantitative assessments of home range and movements throughout the distributional range, including the Caucasus (Gavashelishvili and MacGrady, 2007), South Africa (Urios *et al*., 2010), the Alps, Pyrenees and southern Spain (Margalida *et al*., 2013); and the Pyrenees (López-López *et al*., 2014a).

Here we show the results of a bearded vulture satellite tracking programme started in 1999 in Spain aimed at: (i) quantifying home range size and movement patterns in the Pyrenees; and (ii) determining the degree of overlap between home ranges and the location of Supplementary Feeding Stations (SFS). To this end, nine bearded vultures were captured and tracked by Argos satellite telemetry in the Pyrenees (Aragón, Spain) from 1999 to 2006 (table 1). Individuals were non-breeders according to fieldwork, i.e. they provided no observations of copulations, nest building, chick rearing or territorial behaviour. Nestlings were handled when *c*. 90-100 days old. The remaining birds were captured by cannon-netting at SFS. Bearded vultures were aged according to plumage characteristics (Sesé, 2011) and sexed by morphometric measurements and genetic analyses (García *et al*., 2009; López-López *et al*., 2011). Birds were ringed, marked with vinyl wing-tags and fitted with a satellite transmitter (PTT) affixed to the back by a Teflon harness (Kenward, 2001). Two different types of PTTs were used: three battery-powered 95 g PTT-100s supplied by Microwave Telemetry (Columbia, Maryland, USA); and six solar-powered 55-65 g Solar Bird-Borne PTTs supplied by North-Star (King George, Virginia, USA). PTTs were set to an 8-h on / 80-h off duty cycle. Small VHF radio-transmitters (Biotrack TW-5, weight 21 g, 150 MHz) were glued to each PTT to enable the location of an injured animal or its carcass in the event of an accident or death. PTTs weighed less than 3% of the birds' body weight and all individuals were released unharmed. Only high-quality Argos Location classes (i.e. LCs 3, 2 and 1) were used in this study. We also included some LC 0 locations when they were consistent with the birds' movements in terms of distance covered and time elapsed between locations (for a similar approach see e.g. Cadahía *et al*., 2010; Mellone *et al*., 2012a,b). Data recorded for this study are publicly available upon request in Movebank (https://www.movebank.org/).

The size of the home range was computed using fixed-kernel density methods. To allow comparison with similar studies, we computed the 100% Minimum Convex Polygon (MCP), the 95% kernel (K_{95}) and the 50% kernel (K_{50}). The 100% MCP represents the maximum area of activity, the K_{95} the home range, and the K_{50} the core area of activity (Worton, 1989; Seaman and Powell, 1996; e.g. Urios *et al*., 2010; Mellone *et al*., 2012b).

TABLE 1

Histories of nine non-breeding bearded vultures tracked by ARGOS satellite telemetry in the Pyrenees between 1999 and 2006. Abbreviations: SFS = Supplementary Feeding Station; NP = Natural Park.
[Datos básicos de nueve quebrantahuesos no reproductores seguidos mediante telemetría satelital ARGOS en los Pirineos entre 1999 y 2006. Abreviaturas: SFS = punto de alimentación suplementaria; NP = parque natural.]

Bird	Age at capture	Sex	Type of PTT	Date of capture	Place of capture	First and last location dates	Tracking period (days)
BV1[a]	Subadult	Female	Battery	13 Jan 1999	Guara NP (SFS)	13 Jan 1999-04 Sep 1999	234
BV2[b]	Adult	Male	Battery	13 Apr 2000	Garcipollera (SFS)	24 Jun 2000-18 Jul 2002	754
BV3[b]	Subadult	Male	Battery	09 Apr 2002	Garcipollera (SFS)	22 Apr 2002-10 Jun 2002	49
BV4[†]	Subadult	Male	Solar	09 Nov 2004	Guara NP (SFS)	13 Nov 2004-13 Jul 2005	242
BV5[b]	Juvenile	Female	Solar	09 Nov 2004	Guara NP (SFS)	26 Nov 2004-29 Nov 2005	368
BV6[†]	Subadult	Female	Solar	15 Nov 2004	Guara NP (SFS)	22 Nov 2004-15 Jul 2005	235
BV7[a]	Subadult	Female	Solar	22 Nov 2004	Guara NP (SFS)	24 Nov 2004-02 Sep 2006	647
BV8[b]	Juvenile	Female	Solar	18 May 2005	Benasque (nest)	02 Oct 2005-26 Jul 2006	297
BV9[a]	Juvenile	Female	Solar	01 Jun 2005	Guara NP (nest)	14 Jun 2005-28 Jan 2006	228

Current status (September 2014): [a] alive, [b] missing, [†] dead.

The smoothing parameter was determined by least square cross validation (Silverman, 1986). Only locations recorded from individuals with at least 30 locations were included in home range analyses, the minimum number recommended for unbiased estimates of HR size (Kenward, 2001; Seaman *et al.*, 1999). In addition, two spatial parameters were calculated: the average (SD_{mean}) and maximum (SD_{max}) spider distance, which represent a measure of spread, calculated as the distances from each location to the arithmetic centre of the home range (Hooge and Eichenlaub, 2000). Home ranges and spatial parameters were computed using the Animal Movement Analyst and Home Range extensions for ArcView 3.2 (Rodgers and Carr, 1998; Hooge and Eichenlaub, 2000). Statistical analyses were computed in STATISTICA version 10.0 (StatSoft Inc., www.statsoft.com). Statistical significance was set at $p < 0.05$. Descriptive values are presented as mean ± standard deviation. We did not perform comparisons between sexes, ages or different periods of the year due to limited sample size.

On average the nine bearded vultures were tracked for 339 ± 223 days (range = 49-754 days), sending a total of 427 high-quality locations. No differences in the number of locations received were detected between PTT types (Mann-Whitney test, $Z = -0.516$; $p = 0.606$). The satellite transmitters did not work as expected; three of them stopped working prematurely for unknown reasons and very few locations were obtained (table 2). Therefore, only six individuals of the nine captured for this study provided enough data and were used in the analyses (table 2).

Individual and average values of home range and core area size are reported in table 2. Home range size was not correlated with the number of locations (MCP_{100}: $r = 0.589$, $p = 0.219$; K_{95}: $r = 0.109$, $p = 0.836$; K_{50}: $r = -0.072$, $p = 0.892$, $n = 6$ in all cases). Bearded vultures ranged extensively across the whole Pyrenean mountain range during the tracking period and none of the birds left this area, remaining on both the southern and northern slopes of the Pyrenees (fig. 1). There was partial overlap among all individuals' home ranges (MCP_{100}), encompassing an area of 831 km^2. This area was located between the southern sector of Ordesa and Monte Perdido National Park and the northern end of Sierra and Cañones de Guara Natural Park (Huesca, Spain).

Overall, home range sizes, calculated as MCPs or according to fixed kernel density estimates, were larger than those reported in previous studies, in which visual observations or conventional radio-tracking were used (table 3). Thus, as might be expected, the use of satellite tracking technology as opposed to other methods allows broader foraging areas to be obtained because of its lack of spatial bias (Sokolov, 2011; Cadahía *et al.*, 2010). The home range sizes reported in the present study were smaller than those reported in South Africa and slightly larger than those reported in the Pyrenees or in the Alps. Unfortunately, the recent work of Margalida *et al.* (2013) did not include a quantitative assessment of home range size to compare with our study. Previous studies have reported that juvenile birds are highly mobile during their long juvenile dispersal period (Heredia, 1991; Gil *et al.*, 2010; Urios *et al.*, 2010; Margalida *et al.,* 2013). A combination of factors, which would include searching for food, territory exploration, looking for a partner or interactions with conspecifics, may explain the vast distances recorded. Bearded vultures increase their home range progressively, starting with short movements close to their natal territories (López-López *et al.*, 2014a), before finally settling in a breeding territory, irrespective of the acquisition of full adult plumage (Antor *et al.*, 2007; López-López *et al.*, 2013a). Once birds become adults and settle in a territory, home range seems to decrease abruptly (Gavashelishvili and McGrady, 2007).

TABLE 2

Home range size and spatial parameters of non-breeding bearded vultures tracked by ARGOS satellite telemetry in the Pyrenees between 1999 and 2006. In some cases, the insufficient number of locations did not allow calculations. Abbreviations: MCP = Minimum Convex Polygon; K = Kernel; SD = spider distance.
[Área de campeo y parámetros espaciales de quebrantahuesos no reproductores monitorizados mediante telemetría satelital ARGOS en los Pirineos entre 1999 y 2006. En algunos casos el número insuficiente de localizaciones no permitió los cálculos. Abreviaturas: MCP = Mínimo Polígono Convexo; K = kernel de probabilidad; SD = distancia "spider"]

ID	Number of locations	Home range (km^2)			Spatial parameters	
		$MCP_{100\%}$	$K_{95\%}$	$K_{50\%}$	SD_{mean} (km)	SD_{max} (km)
BV1*	43	4929	6209	558	32	56
BV2*	58	19691	22916	4470	69	132
BV3	10	945	1796	194	14	34
BV4*	41	7178	5603	680	39	136
BV5	18	978	1973	265	24	45
BV6*	69	19008	21019	3423	56	153
BV7*	129	16993	8717	513	36	137
BV8	14	1155	3665	640	35	60
BV9*	45	4544	6128	825	46	99
mean ± sd*	64 ± 34	12057 ± 7239	11765 ± 7999	1745 ± 1741	46 ± 14	119 ± 36

* Only individuals with at least 30 locations were used for calculations

There were 26 SFS located across the area encompassed within the bearded vultures' home ranges. Taking into account satellite telemetry records, 104 of 427 total locations were recorded less than five km from SFS (24.36% of the total records); 44 locations were less than three km from SFS (10.30%); and three locations were inside SFS (0.70%). All individuals were seen feeding inside SFS during the tracking period. The mean number of observations of birds feeding inside SFS (on different days and excluding locations received in the first few days after trapping) was 5.67 ± 1.94 (range = 3-8; n = 51 observations). The average distance from locations to SFS was 25.41 ± 25.23 km (range = 0.12-133.25, n = 427) and the average distance from the median centres of the core areas (K_{50}) to the closest SFS was 7.35 ± 9.53 km (range = 1.48-26.58, n = 6). All individuals included SFS within their home ranges and core areas of activity. The average number of SFS within home ranges was 15 ± 6 (range = 10-22) according to MCP_{100}, and 6 ± 2 (range = 3-8) according to K_{50}, without significant differences among individuals (Chi-square test, MCP_{100}: χ^2 =

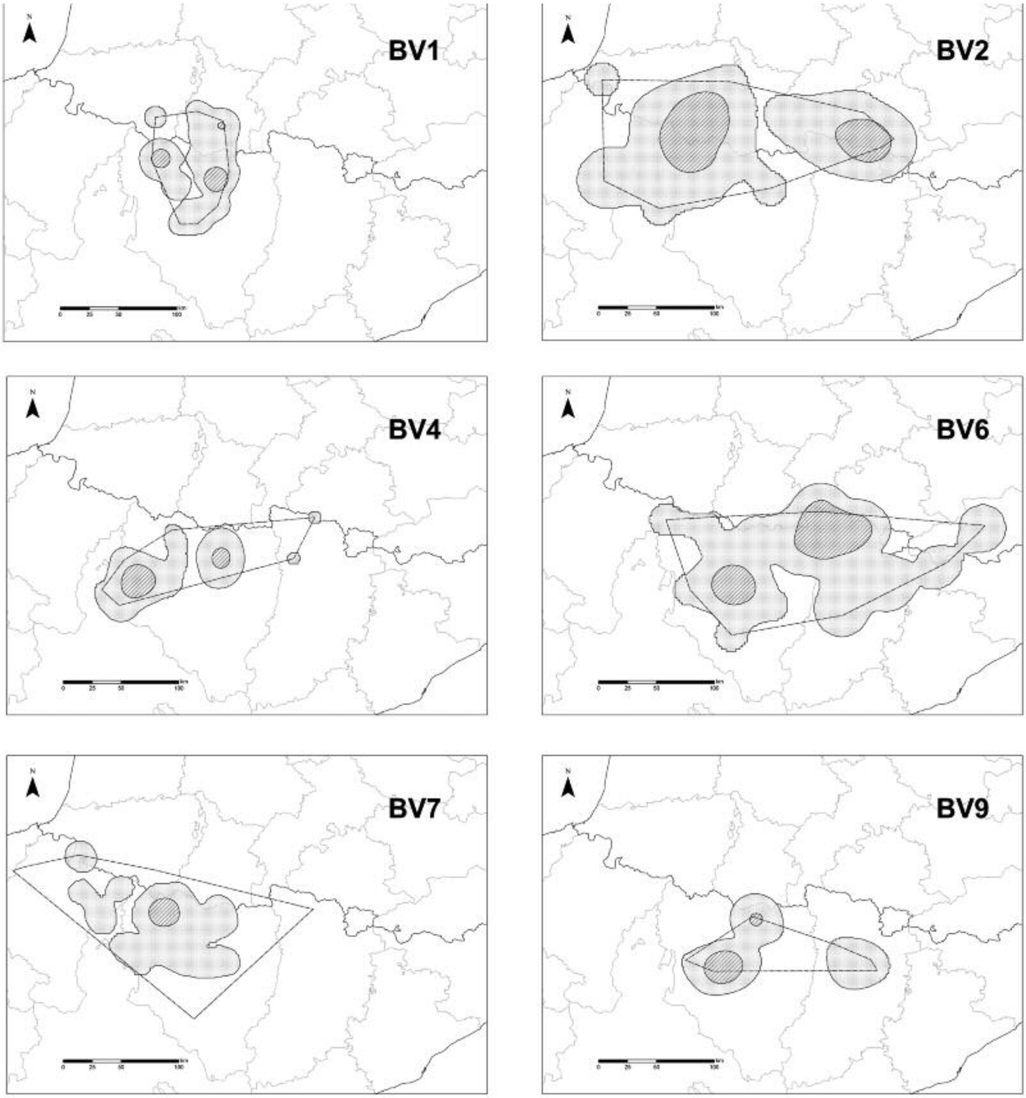

FIG. 1.—Ranging behaviour of six bearded vultures in the Pyrenees. The 100% MCP (dashed line), K_{95} (dotted area) and K_{50} (hatched area) are shown. Spanish and French Administrative units (pale grey) are shown. Note the scale invariance to allow comparison of range size among individuals.
[Área de campeo de seis quebrantahuesos en los Pirineos. Se muestran el MCP100% (línea discontinua), el K_{95} (área de puntos) y el K_{50} (área rayada). Las regiones españolas y francesas se muestran en gris claro. Nótese la invariancia de escala para permitir la comparación entre individuos.]

10.53, d.f. = 5, p = 0.061, K_{50}: χ^2 = 6.21, d.f. = 5, p = 0.286, with Yate's correction for continuity). It is notworthy that one of the most important Pyrenean SFS (Escuaín, Huesca, Spain), which has provided continuous supplementation of food since the 1980s, was within all the bearded vultures' ranging areas. The most used SFS were those at Garcipollera

TABLE 3

Summary of home range sizes recorded for bearded vultures around the world. Abbreviations: MCP = Minimum Convex Polygon; K = Kernel; Min = minimum; Max = maximum.
[Resumen del área de campeo del quebrantahuesos a nivel mundial. Abreviaturas: MCP = Mínimo Polígono Convexo; K = Kernel; Min = mínimo; Max = máximo.]

Region	Age	Method used and home range area (km^2)	Tracking method	Number of individuals	Source
South Africa	Juvenile	MCP100 = 38500; K95 = 16719; K50 = 3196	satellite telemetry	1	Urios *et al.,* (2010)
Alps	Juvenile	MCP: min = = 384 – max = 6362	satellite telemetry	7	Zink and Izquierdo (2011)
Pyrenees	Juvenile	MCP: min = = 4800 – max = 10450	radio-tracking	3	Gil and Díez (1993)
Pyrenees	Juvenile	max. cumulative MCP100 = 2852; K95 = 358	satellite telemetry	9	López-López *et al*., (2014a)
Pyrenees	Juvenile Immature	cumulative MCP: min = 950 – max = = 10294	radio-tracking	7	Heredia (1991)
Caucasus	Adult	K95 = 206	satellite telemetry	1	Gavashelishvili and McGrady (2007)

(57.14% of cases), Escuaín (28.57%) and Yaso-Loporzano (29.57%), all in Huesca province (Spain).

All bearded vultures include predictable sources of food into their home range. This is particularly important in the case of inexperienced birds (< 3 years old), which often remain near SFS for long periods (Sesé *et al*., 2005). This behaviour seems to be usual in other scavengers (e.g. griffon vultures and Egyptian vultures) for which satellite-tracking data has also shown how vultures were temporarily linked to particular SFS and that predictable sources of food are major determinants of their ranging behavior, even in the case of adults (García-Ripollés *et al*., 2011; López-López *et al*., 2013b, 2014a, 2014b; Monsarrat, *et al*., 2013; Zuberogoitia *et al*., 2013). Given that some of the Pyrenean SFS have been operative since the 1980s (e.g. Garcipollera, Escuaín) it is not surprising that bearded vultures of all age classes have taken advantage of these predictable sources of food. This has facilitated a population increase and the avoidance of potential sources of mortality resulting from vagrancy (Sesé *et al*., 2005; Oro *et al*., 2008). Notwithstanding, the relationship between ranging behaviour, food predictability and landscape features still requires further research. The research programs underway, which include accurate GPS satellite tracking, will definitely improve our understanding of the spatial ecology and behaviour of this endangered species.

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