SHORT COMMUNICATIONS

POST-FLEDGING DEPENDENCE PERIOD AND ONSET OF NATAL DISPERSAL IN BEARDED VULTURES (*GYPAETUS BARBATUS*): NEW INSIGHTS FROM GPS SATELLITE TELEMETRY

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The time period between the first flight from the nest and the onset of dispersal is one of the most critical stages in the life history of birds (Weathers and Sullivan 1989). This time span, referred to as the post-fledging dependence period, is critical for the development of young birds because during this time juveniles must learn to become self-sufficient, acquire flight skills, find food resources and exploit them efficiently (Bustamante and Hiraldo 1989, Bustamante and Negro 1994, Soutullo et al. 2006a, Delgado et al. 2009). As a consequence, the post-fledging dependence period is of particular importance for the conservation of species with delayed breeding (Ferrer 1993, Soutullo et al. 2006a, Cadahía et al. 2008, López-López et al. 2013). However, despite the high risk of mortality during this stage (Lack 1954), our knowledge about the length of this period and the spatial ecology of birds throughout is still rather limited for most avian species. This is also the case for the Bearded Vulture (*Gypaetus barbatus*), a long-lived, cliff-nesting, obligate scavenger currently listed as a ''priority species'' by the European Union (Annex I of the European Birds Directive), for which very few studies have focused on this critical stage (Ferguson-Lees and Christie 2001). Two previous works on the post-fledging dependence period of this species, one conducted in South Africa (Brown 1990) and the other in the Pyrenees Mountains in Spain (Sunyer 1991), were both based on visual observations and conventional terrestrial radio-tracking of one and seven birds, respectively. Recently, Margalida et al. (2013) reported a description of the

movements of pre-adult Bearded Vultures tracked by satellite telemetry in Europe (including data of individuals from the wild Pyrenean population and the reintroduced populations in the Alps and southern Spain), although no specific analysis of the movement patterns during the post-fledging dependence period was conducted. Our objective in this study was to examine the spatial ecology of Bearded Vultures during the post-fledging dependence period using modern GPS satellite telemetry.

METHODS

Study Area and Bird Tagging. Our study took place in the Pyrenees Mountains (42°37′N, 0°39′E) and in the Cantabrian Mountain range (43°11′N, 4°51′W), northern Spain. Both regions are mountainous, rugged areas, one within the Eurosiberian biogeographic region (Pyrenees) and the other encompassed within the Atlantic biogeographic region (Cantabrian Mountains). The climate is characterized by severe winters with abundant snow cover and by temperate and dry summers (AEMET and IPMA 2011). The population of Bearded Vultures within the Pyrenees is the only remaining natural population in Spain; the population in the Cantabrian Mountains was extirpated in the 1950s (Hiraldo et al. 1979). Our study was conducted as a part of a long-term conservation and research program conducted by the Foundation for the Conservation of the Bearded Vulture (FCQ).

We captured nine Bearded Vultures as nestlings and equipped them with GPS satellite transmitters (PTTs) between 2009 and 2012. We captured three birds in their nests when they were between 85 and 105 d old; the remaining six nestlings were raised in captivity, from eggs obtained from wild pairs with repeated reproductive failure, and released into the wild by means of the hacking technique (Newton 1979). Hereafter, the birds tagged in

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Table 1. Bearded Vultures monitored with GPS satellite telemetry during the post-fledging dependence period in Spain.

INDIVIDUAL	SEX	TRANSMITTER	GEOGRAPHIC AREA	HATCH DATE	FLEDGING DATE	REARING METHOD	CURRENT STATUS†	NUMBER OF LOCATIONS
BV#1	♂	ARGOS/GPS	Pyrenees	16 February 2009	26 June 2009	hacking	alive	592
BV#2	♂	ARGOS/GPS	Pyrenees	5 March 2009	24 June 2009	wild	alive	853
BV#3	♀	GPS/GSM	Cantabrians	1 March 2010	9 July 2010	hacking	alive	388
BV#4	♀	GPS/GSM	Cantabrians	25 February 2010	9 July 2010	hacking	dead	434
BV#5	♀	ARGOS/GPS	Pyrenees	17 March 2011	20 July 2011	hacking	alive	463
BV#6	♀	GPS/GSM	Pyrenees	30 March 2011	3 August 2011	hacking	alive	514
BV#7	♂	ARGOS/GPS	Pyrenees	28 February 2011	7 July 2011	wild	alive	709
BV#8	♂	GPS/GSM	Cantabrians	25 March 2012	2 August 2012	hacking	alive	432
BV#9	♀	GPS/GSM	Pyrenees	15 March 2012	15 July 2012	wild	alive	1218

† January 2014.

the nests will be designated the ''wild'' birds and the young released via hacking will be referred to as ''captive'' in origin. The wild birds were all captured in the Pyrenees, and, of the six captive birds, three were released in Ordesa and Monte Perdido National Park (Pyrenees) and three in Picos de Europa National Park (Cantabrian Mountain range; Table 1). The hacking tower consisted of a battery of cages placed 5 m aboveground, in which nestlings were independently housed. Birds were initially provisioned with food using a puppet resembling an adult bird to avoid imprinting on humans. Following previous studies (Brown 1990, Sunyer 1991) and before the expected fledging age was reached (around 110 d old), we opened the cages. We recorded the date of the nestlings' first flight; after the first flight occurred, the hacked young were supplied with food at a rate simulating natural conditions.

Four birds were equipped with 70-g PTT-100 ARGOS/GPS transmitters manufactured by Microwave Telemetry (Columbia, Maryland, U.S.A.) and five birds with 100-g CTT-1100 GPS/GSM transmitters supplied by Cellular Tracking Technologies (Somerset, Pennsylvania, U.S.A.; Table 1). ARGOS/GPS transmitters were programmed to obtain GPS fixes every 2 hr on a 12 hr on/12 hr off duty cycle (07:00 H to 19:00 H, Greenwich Mean Time). GPS/GSM transmitters were programmed to record a location every 15 min when the animal was within a 10-km radius of the natal area (or release point) and one location/min when the bird was beyond this threshold. All individuals were also equipped with conventional 20-g TW51 VHF radio-tracking transmitters, manufactured by Biotrack (Wareham, Dorset, United Kingdom; 4-yr battery life expectancy), to allow us to locate the birds in case of injury or technical failure of the satellite transmitter. VHF transmitters were glued to the PTTs. The PTTs were attached using a backpack-style harness as described in Bögel (1994). In all cases the total weight of the package, includ-

ing the transmitters, the harness and the patagial/humeral tags or metal leg rings was <3% of the bird's body mass (Kenward 2001, Urios et al. 2010). We collected blood samples for sex determination by genetic analysis (López-López et al. 2011).

Data Analysis. In order to investigate the post-fledging dependence period, locations were grouped into 15-d periods after fledging (hereafter called ''period'' in the analyses). This allowed comparison with previous studies (Brown 1990, Sunyer 1991). Thereby, the post-fledging dependence period was analyzed with respect to the fledging date (i.e., the day when the first flight took place), given that there was individual variation in that date (from 24 June to 3 August; Table 1). We did not use the birds' age as the reference for calculations in order to avoid possible bias due to differences in the age at fledging. The fledging date was assessed by the combination of systematic field visits to the birthplaces/release points and visual inspection of the GPS locations. The onset of natal dispersal, and hence the end of the post-fledging dependence period, was assessed by means of the ''observed location pattern'' method as described in Cadahía et al. (2008). This method is based on the visual observation of the pattern of locations and assumes that the onset of natal dispersal happened the first day after the abrupt departure from the natal area and subsequent settlement in a different range, without return (Walls and Kenward 1998). Field observations at ossuaries and vulture restaurants located in the study area were also conducted as a part of the long-term monitoring program of the species in the Pyrenees in order to record the presence of marked individuals at these places.

Spatial Parameters. The following spatial parameters were calculated: (1) average distance of all locations to natal nest or release point, recorded for each 15-d period; (2) size of the area explored, calculated using 100%

Minimum Convex Polygon (MCP), 95% fixed kernel and 50% fixed kernel home ranges; (3) cumulative size of the explored area; (4) distance between the centroids of consecutive MCPs; (5) increase in size of the explored area (i.e., difference in the size of areas used consecutively); (6) overlap between consecutive MCPs; (7) distance between two consecutive roosting places (i.e., places where birds stay overnight, obtained from the first and last locations of each day); and (8) distance covered in 2 hr (only for birds equipped with ARGOS/GPS PTTs). Different levels of space use were assessed by means of the MCP, 95% kernel and 50% kernel, which represent a common standard approach in spatial ecology studies (Worton 1989, García-Ripollés et al. 2011, Cumming and Cornélis 2012, Campioni et al. 2013, López-López et al. in press). The Least Squares Cross Validation method was used to calculate the smoothing parameter (Silverman 1986). Computations were performed using Geospatial Modelling Environment software (Beyer 2012) and represented in Esri® ArcMap 10.0 (http://www.esri.com/). Importantly, a preliminary analysis showed that there was no significant correlation between the number of locations used for the analyses and home-range size, using either the MCP ($r = 0.41$, $r^2 = 0.17$, $t = 1.19$, $P = 0.27$), the 95% kernel ($r = 0.42$, $r^2 = 0.18$, $t = 1.22$, $P = 0.26$) or the 50% kernel ($r = 0.55$, $r^2 = 0.31$, $t = 1.76$, $P = 0.12$; $n = 9$ in all cases). This preliminary test of the effect of sample size on the home-range size is critical because it allows the elimination of possible bias in the estimation of space use due to individual variability (Kernohan et al. 2001).

Statistical Analysis. We used Linear Mixed Models (LMMs) to investigate the effect of "period," "sex," and "origin" on ranging behavior. Hence, these three variables were included as fixed effects in the analyses. LMMs are particularly useful for analyzing longitudinal data when individuals are measured repeatedly over time (i.e., there is temporal pseudo-replication due to repeated measurement of the same individuals; Zuur et al. 2009). Therefore, "individual" was incorporated as a random effect. When necessary, dependent variables were normalized using log-transformations allowing the specification of a normal error distribution with an identity link function in the LMMs.

Spatial parameters were included as dependent variables in LMMs; each parameter was tested separately. The geographic region (Pyrenees and Cantabrian mountains) was not included in the analyses because of limited sample size and because we lacked some of the possible combinations of origin and geographic area (i.e., there were no "wild" birds in the Cantabrian Mountains).

To find the best model structure using LMMs, we followed the top-down strategy suggested by Zuur et al. (2009). Initially, we fitted a full factorial model ("beyond optimal model" *sensu* Zuur et al. 2009), and we then tried different models, varying the structure of fixed effects. These models were compared using the maximum likelihood estimation for fitting. Finally, having selected the best structure of fixed effects, we determined the best model using the restricted maximum likelihood estimation (Zuur et al. 2009). Models were validated by checking for homoscedasticity and normality of the residuals. To that end, relevant model diagnostic graphs were computed (residuals against fitted values, residuals against each explanatory variable, histogram of residuals and normality Q-Q plots; Zuur et al. 2009). In all cases, diagnostic graphs showed that models assumptions of normality and homogeneity of variance were met (results not shown). For random effects we reported the intraclass correlation coefficient and a generalized R^2, calculated as the squared correlation between the fitted values of the model and the observed values of the data (Zheng and Agresti 2000). The former measures the correlation between observations from the same individual and can be interpreted as a measure of consistency of the results, and the latter provides information about the amount of variation in the data explained by the random effect (i.e., between-individual variation; Campioni et al. 2013, López-López et al. in press). Computations were run with the "nlme" extension for R (Pinheiro et al. 2013).

Differences in fledging date and onset of dispersal due to the sex and origin of the birds were evaluated by means of nonparametric Mann-Whitney tests using Statistica version 10.0 (www.statsoft.com). Tests were two-tailed and the significance level was set at $\alpha = 0.05$. Descriptive values are presented as mean ± standard deviation.

RESULTS AND DISCUSSION

A total of 5603 GPS fixes were used for the analyses, with an average of $623 ± 269$ fixes/individual (range = 388–1218, $n = 9$; Table 1). No differences were found in the number of GPS fixes obtained in relation to the type of transmitter (ARGOS/GPS vs. GPS/GSM; Mann-Whitney, $U_{4,5} = 5.00$, $Z = 1.22$, $P = 0.22$). Notwithstanding, the performance of the two types of transmitters was different. Whereas ARGOS/GPS transmitters sent signals uninterruptedly throughout the post-fledging dependence period, GPS/GSM transmitters operated irregularly, sending high number of locations during most of the time, but with some periods with no transmission. This happened because of the ruggedness of the terrain, putting the transmitters out of range in some remote areas.

Age at First Flight. First flight occurred when birds were $126 ± 7$ d old (range = 111–134 d, $n = 9$). No differences were observed in the age at first flight, either between sexes (Mann-Whitney, $U_{4,5} = 10.00$, $Z = 0.00$, $P = 0.99$) or between wild and released birds (Mann-Whitney, $U_{6,3} = 2.00$, $Z = 1.84$, $P = 0.07$). Our results were similar to those reported in South Africa ($126 ± 2$ d, $n = 3$, Brown 1990) and slightly higher than those reported in the Spanish Pyrenees ($119 ± 7.4$ d, $n = 7$, Sunyer 1991; $123 ± 6$ d, $n = 20$, Margalida et al. 2003). Fledging took place between late June and early August. The earliest flight ever recorded of a young Bearded Vulture in the Pyrenees was 17 May 2010 (Ascaso and Gil 2010).

Post-fledging Behavior. Birds remained in their natal or release areas for the first 2 mo after fledging. They then started to progressively increase the distance from their natal area (Fig. 1a), with the maximum size of the explored area between 61 and 90 d after fledging (Fig. 1b). After this, birds returned to their natal or release areas and remained nearby, making occasional medium- to long-distance exploratory flights up to 55–60 km (maximum recorded distance = 60.6 km, 89 d after fledging). These pre-dispersive exploratory flights or ''excursions'' (Walls and Kenward 1998, Cadahía et al. 2008) have also been reported in other raptors such as the Common Buzzard (*Buteo buteo*) and the Bonelli's Eagle (*Aquila fasciata*) and are particularly important because they allow birds to develop a cognitive map of the area that they will use later, during the post-fledging dependence period (O'Keefe and Nadel 1978). During this early stage of the post-fledging dependence period, young Bearded Vultures started to break bones at ossuaries, initially with the parent birds (the first observation of a juvenile in this study was on 13 August 2010) and after some time (ca. 50–70 d after fledging), independently (P. López-López unpubl. data). Moreover, from the third–fourth weeks after fledging, juveniles started to use some vulture restaurants located close to the nesting/release areas. The earliest record of a juvenile Bearded Vulture (not tracked in this study) recorded at a vulture restaurant occurred on 6 July (J. Sesé pers. comm.), but typically juvenile Bearded Vultures start visiting vulture restaurants regularly from mid-August to early September (P. López-López unpubl. data).

The cumulative size of the explored area varied notably among individuals, increasing remarkably after 61 d after fledging (Fig. 1c, d). Birds tended to progressively drift away from the natal or release areas. The distance between the centroids of the areas used consecutively ranged from 4 to 9 km (Fig. 1e), and the overlap of consecutive MCPs decreased after the first 2 mo after fledging, ranging from 20 to 60% (Fig. 1f). A similar progressive distancing from the natal area was reported by Margalida et al. (2013), who found a quadratic relationship between daily distance covered by Bearded Vultures and total dispersal distance with age.

The home-range area recorded in our study (maximum cumulated MCP = 2852 km^2; maximum cumulated 95% kernel = 358 km^2; Fig. 1c) was notably higher than has previously been reported. Brown (1990) reported ranges using MCP in South Africa of 42 km^2, 78 km^2, and 168 km^2 during the third, fourth, and fifth month after fledging, respectively. In Spain, Sunyer (1991) estimated a maximum cumulative area of 65 km^2 in the fourth month after fledging using the MCP. Because a similar analytical method was used in all studies (MCP), the differences between our results and those previously reported may be explained by the difference in tracking methods. The use of GPS satellite telemetry, which is much more accurate than ground radio-tracking, allowed the detection of long-distance movements beyond the range of observation and/or coverage of radio signal. It also allowed discrimination between the pre-dispersive exploratory flights and the true dispersal (Cadahía et al. 2008).

The results of the LMMs showed significant differences in the size of the explored areas, either according to MCP, 95% kernel, or 50% kernel, in relation to the time after the first flight (i.e., ''period'') of the post-fledging dependence period. The variables ''sex'' and ''origin'' were not included in the best models (Table 2), thus suggesting that no differences in spatial parameters were found between sexes and between captive and wild birds. Nevertheless, these results should be interpreted cautiously due to the limited sample size. LMMs for the degree of overlap between the centroids of consecutive MCPs, distance between the centroids of areas used consecutively, and distance between consecutive roosting places, showed no effects of ''period'' or ''sex.'' The variable ''origin'' was included in the best models but its effect was not significant ($P = 0.167$, $P = 0.103$, $P = 0.256$, respectively; detailed table of results not shown). LMMs for the distance to natal/release point and distance covered within 2 hr showed a significant effect of ''period'' but not ''sex'' or ''origin'' in these spatial parameters (Table 3). Again, this suggests that no differences in the pattern of spatial parameters were found between sexes and between captive and wild birds during the post-breeding dependence period.

Bearded Vultures used many different nocturnal roosting places during the post-fledging dependence period. Fifty-five percent of consecutive roosting places were located <1 km from each other and only 5% were located >10 km away (Fig. 2). The length of movements recorded at 2-hr intervals increased with the time elapsed since the first flight (Fig. 3a). In the first 4 wk after fledging, most (84–94%) movements within 2-hr intervals were <3 km, with the distance increasing progressively as time went on (Fig. 3a). Long-distance movements (>15 km in 2 hr) represented 20% of the frequency of movements in the last weeks of the post-fledging dependence period (Fig. 3a). In relation to the time of day, the great majority of long-distance movements took place from early morning until noon (Fig. 3b). Bearded Vultures, like other soaring raptors, make use of thermal and deflected updrafts that favor long-distance movements with minimal energetic cost (Soutullo et al. 2006b, García-Ripollés et al. 2011, Ainslie 2014). Short-distance movements became more frequent later in the day, making up 86–96% of the time in the evening (Fig. 3b).

Onset of Natal Dispersal. Birds departed from natal areas at 193 ± 40 d after the first flight (range = 143–231 d, $n = 5$), which corresponded to an average age of juveniles of 317 ± 38 d (range = 272–361, $n = 5$). No differences were observed in the onset of dispersal either between sexes (Mann-Whitney, $U_{3,2} = 2.00$, $Z = 0.58$, $P = 0.56$) or between wild and captive birds (Mann-Whitney, $U_{3,2} = 2.00$, $Z = 0.58$, $P = 0.56$), although our tests were limited by small sample size (detailed data were only available for five out of the nine birds).
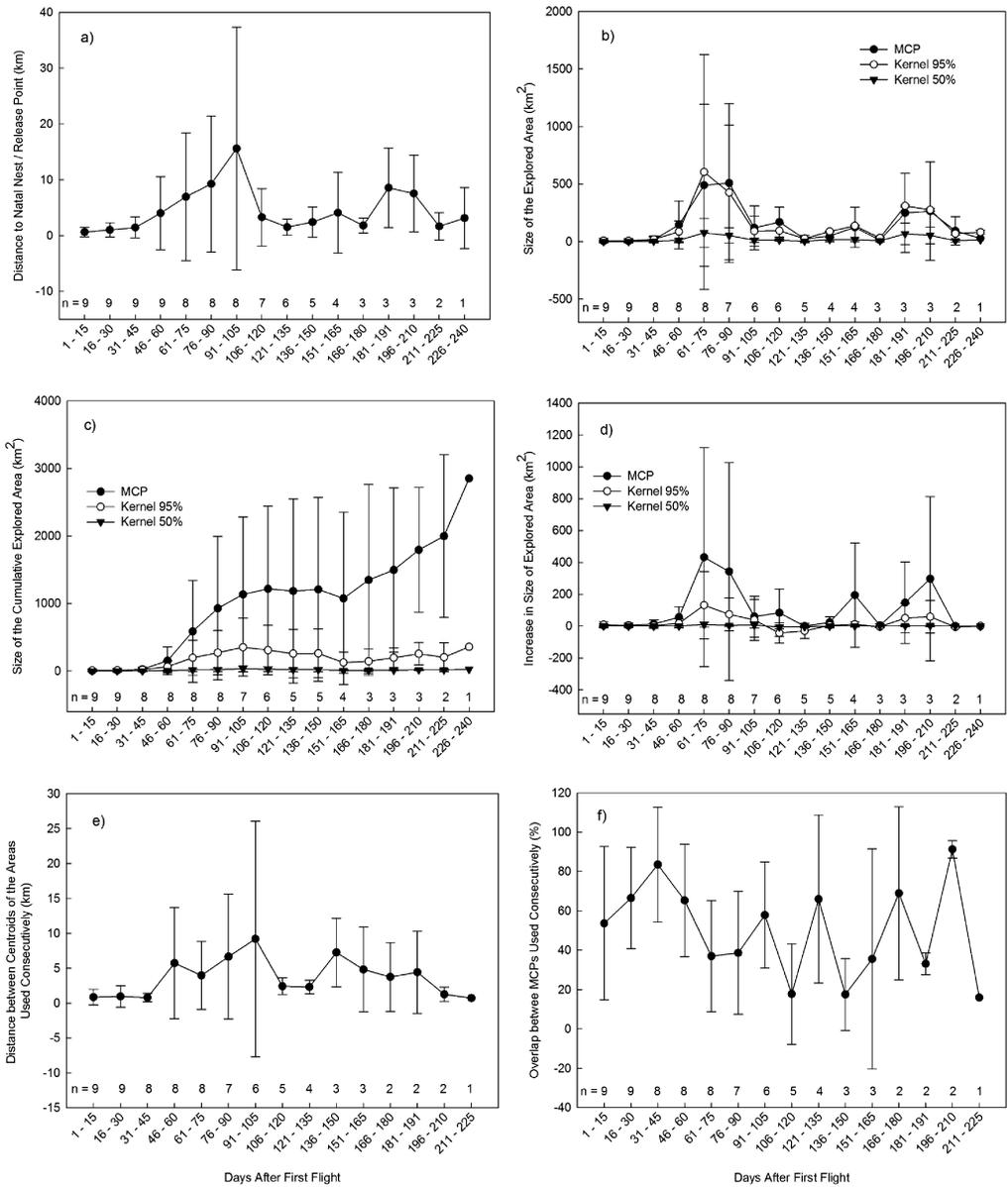
Figure 1. Post-fledging dependence period of nine Bearded Vultures tracked by GPS satellite telemetry in Spain. Data were grouped at intervals of 15 d from the fledging date. Panels indicate: (a) Average distance of all locations recorded for each period to natal nest or release point; (b) size of the area explored calculated using MCP, 95% kernel, and 50% kernel; (c) size of the cumulative explored area (i.e., the area corresponding to the period 16–30 d also includes locations recorded from 1 to 15 d after the first flight, and so on); (d) distance between centroids of consecutive MCPs; (e) increase in size of the explored area; (f) overlap between consecutive MCPs. Values are expressed as average value ± standard deviation (vertical bars). n indicates the sample size (number of individuals) for which each average was calculated. The sample size was different in each period because of the different length of the post-fledging dependence period between individuals.

Table 2. Linear mixed models of home range size according to Minimum Convex Polygon (MCP), kernel 95% and kernel 50% as response variables. The variables "period," "sex," and "origin" were included as fixed effects and "individual" was incorporated as a random effect (see details in Methods). Abbreviations: SD = standard deviation; LCI = lower confidence interval; UCI = upper confidence interval; ICC = intraclass correlation coefficient.

Model Type		MCP						KERNEL 95%						KERNEL 50%				
	SD	LCI 95%	UCI 95%	DF	F	P	SD	LCI 95%	UCI 95%	DF	F	P	SD	LCI 95%	UCI 95%	DF	F	P
Random effects Individual	0.425	0.189	0.959				0.488	0.245	0.972				0.513	0.263	1.001			
Residual	0.888	0.737	1.069				0.714	0.592	0.861				0.691	0.573	0.834			
R^2	0.551						0.670						0.671					
ICC	0.187						0.318						0.355					
Fixed effects Intercept				1,55	37.031	<0.001				1,55	35.482	<0.001				1,55	2.497	0.120
period				15,55	2.905	0.002				15,55	4.172	<0.001				15,55	4.420	<0.001

Table 3. Linear mixed models of spatial parameters as response variables. The variables "period," "sex," and "origin" were included as fixed effects and "individual" was incorporated as a random effect. Abbreviations: SD = standard deviation; LCI = lower confidence interval; UCI = upper confidence interval; ICC = intraclass correlation coefficient.

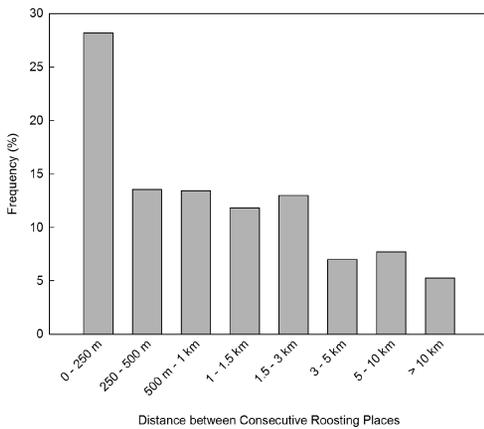| Model Type		DISTANCE NATAL/RELEASE POINT						DISTANCE TWO-HOURS				
	SD	LCI 95%	UCI 95%	DF	F	P	SD	LCI 95%	UCI 95%	DF	F	P
Random effects Individual	0.395	0.241	0.646				0.185	0.080	0.427			
Residual	0.526	0.516	0.536				0.779	0.753	0.806			
R^2	0.441						0.125					
ICC	0.360						0.053					
Fixed effects Intercept				1,5579	514.818	<0.001				1,1692	7.934	0.005
period				15,5579	44.745	<0.001				15,1692	11.283	<0.001

Figure 2. Distance between consecutive roosting places (i.e., places where birds stay overnight as obtained from the first and last locations of each day).

Previous studies estimated the onset of dispersal as between 95 and 247 d after the first flight, which corresponded to an age of between 206 and 364 d (Sunyer 1991). Although our results fell within these ranges, according to our data the onset of dispersal was later than that previously reported (i.e., the lower limit of the range was higher, 143 vs. 95 d in the case of the time since the first flight, and 272 vs. 206 d of age). This is probably due to the different methods used for tracking the birds (terrestrial radio-tracking vs. GPS satellite telemetry), which allowed us to discriminate clearly between pre-dispersive exploratory flights and the exact onset of dispersal (Cadahía et al. 2008). The individual variation observed in the time of the onset of dispersal was in agreement with the results observed in other raptors such as eagles, kestrels, kites, and buzzards (Bustamante and Hiraldo 1989, Ferrer 1992a, 1992b, Bustamante and Negro 1994, Walls and Kenward 1998) and New World vultures (Wallace and Temple 1987) and Old World vultures (Robertson 1985, Donázar and Ceballos 1990, Yamaç and Bilgin 2012). Finally, the onset of dispersal overlapped with the adults' next breeding season. In most cases juveniles became independent once their parents were incubating, which is in agreement with previous studies (Brown 1990, Sunyer 1991). The high parental investment during the breeding period (Margalida and Bertran 2000, Margalida et al. 2003) and the long length of the post-fledging dependence period in the Bearded Vulture, one of the longest documented for birds, may help ensure the survival of the young.

PERÍODO DE DEPENDENCIA POST EMPLUMAMIENTO DE *GYPAETUS BARBATUS*: NUEVAS EVIDENCIAS A PARTIR DE TELEMETRÍA SATELITAL

RESUMEN.—Utilizamos telemetría satelital para estudiar el periodo de dependencia post emplumamiento de tres
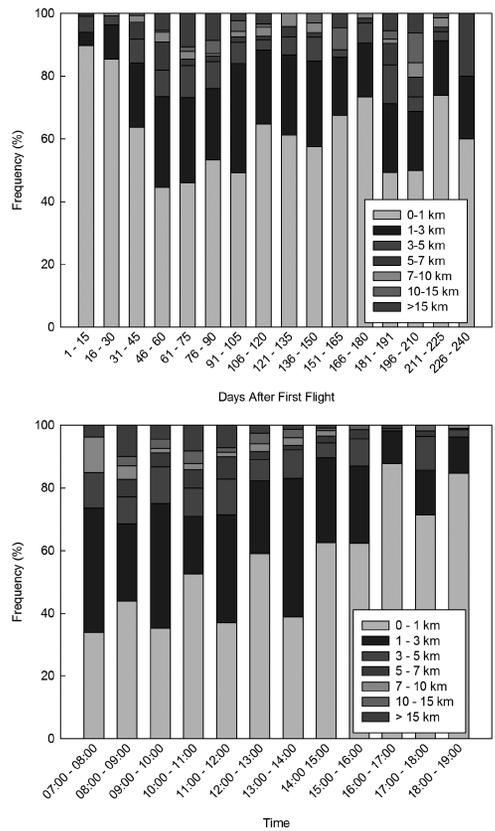

Figure 3. Frequency of movements recorded at 2-hr intervals categorized by distance ranks during the entire post-fledging dependence period (upper panel), and time budget showing the frequency of movements throughout the day (lower panel).

individuos silvestres y seis individuos cautivos de *Gypaetus barbatus*. El primer vuelo tuvo lugar cuando los pollos tenían 126 ± 7 días de edad (rango = 111–134 días) y el inicio de la dispersión ocurrió a los 193 ± 40 días desde el primer vuelo (rango = 143–231 días). Los jóvenes permanecieron en sus áreas natales (o de liberación, en el caso de aves criadas en cautiverio) durante los primeros dos meses desde la fecha de emplumamiento. Luego, comenzaron a incrementar progresivamente la distancia a sus áreas natales; durante este tiempo, la mayoría de los desplazamientos de larga distancia (>15 km) tuvieron lugar antes del mediodía. Los tamaños de las áreas de acción registrados en este estudio fueron superiores a los descritos con anterioridad para la especie, principalmente debido a la diferencia en los métodos de rastreo empleados: la telemetría satelital permitió la detección de movimientos de larga distancia más allá del rango de medición del rastreo por radio convencional. Finalmente, la adquisición de la independencia

(i.e., emancipación) se solapó con la siguiente temporada de cría de los adultos.

[Traducción de los autores editada]

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