

Nocturnal flights by Bearded Vultures *Gypaetus barbatus* detected for the firsttime using GPS and accelerometer data

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ABSTRACT

Capsule: We document previously undescribed nocturnal flight behaviour by Bearded Vultures *Gypaetus barbatus* using a combination of accelerometer and global positioning system (GPS) information.

Aims: To study the nocturnal flight activity of the Bearded Vulture and determine whether nocturnal flights could be linked to foraging behaviour.

Methods: We used both accelerometer and GPS location data of 11 Bearded Vultures in the Spanish Pyrenees along with 88 carcasses monitored with camera traps.

Results: Over half (55%, n = 11) of the individuals tracked were recorded flying between 0.7 and 6.1 km on at least 19 different nights, including 37% that occurred when less than 20% of the moon was illuminated. Bearded Vultures displayed feeding activity in only 8.2% of the 146 feeding events existing during the hour after dawn and the hour before dusk.

Conclusions: Our findings suggest that foraging benefits do not explain the nocturnal flights. Disturbances or adverse weather conditions may result in the abandonment of an overnight roosting site. This could also explain why individuals recovered in the field showed impact injuries.

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The nocturnal activity of diurnal raptors is a topic that has attracted increasing attention of ornithologists over the last century (Kendeigh 1934, Moore 1945). A recent comparative evolutionary analysis of 120 vision genes based on retina transcriptome sequencing suggested that a substantial visual modification was found in owls compared with diurnal raptors. The strong selection for nocturnal vision in owls may compensate for their loss of the genes involved in daylight or colour vision, suggesting a sensory trade-off (Wu *et al.* 2016).

With respect to diurnal raptors, nocturnal behaviour has recently been documented: during migration in the Osprey *Pandion haliaetus* (DeCandido *et al.* 2006); in Swainson's Hawks *Buteo swainsoni* and Turkey Vultures *Cathartes aura* (Riba-Hernández *et al.* 2012); during arrival at roosting sites in migrant Levant Sparrowhawks *Accipiter brevipes* (Yosef 2003); in Peregrine Falcons *Falco peregrinus* while hunting and feeding (Wendt *et al.* 1991, Rejt 2004a, 2004b); and in Lesser Kestrels *Falco naumanni* in both natural (Gustin *et al.* 2017) and artificial light conditions (Negro *et al.* 2000). However, most of these observations only provide anecdotal evidence of this unusual behaviour of a diurnal raptor, describing a particular event observed at night. Until recent years, technical limitations on monitoring diurnal avian species at night were probably the main factor preventing more extensive and regular tracking of nocturnal activity. Nevertheless, with the abundance of modern transmitters currently deployed on different species, we can easily determine the frequency of nocturnal activity displayed by diurnal species.

Vultures are diurnal scavengers which feed mainly on the carcasses of wild and domestic ungulates and forage over large areas (Houston 2001). The temporal and spatial unpredictability of carcass availability requires scavengers to forage over extensive areas during daylight (Ruxton & Houston 2004). However, observations of nocturnal activity suggest that vultures could occasionally visit carcasses at night. Several researchers have documented both New and Old-World vultures which have developed nocturnal scavenging behaviour (Naoroji 2006, Charette *et al.*

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2011, Mateo-Tomás & Olea 2018). Nocturnal feeding may benefit individuals by reducing interspecific and intraspecific competition and providing them with advantages over other diurnal competitors (Charette et al. 2011), but this behaviour also has potential costs. For example, the risk of being predated or injured at night could overtake the benefits of competition avoidance since avian scavengers appear to be less efficient at night than nocturnal mammalian scavengers whose nocturnal rate of net energy intake is normally higher (Ruxton & Houston 2004, Spiegel et al. 2013). In some species (including mammals), nocturnal activity appears to be strongly influenced by the amount of available moonlight (Russell 1991, Fernández-Duque 2003). In the case of diurnal raptors, occasional nocturnal flights by migrating raptors may represent an adaptive behavioural response to varied or changing weather or feeding conditions encountered en route (Russell 1991).

In general, large raptors use the energy of the landscape's updrafts to minimize travelling energy costs (Ruxton & Houston 2004). They exploit rising thermal uplifts, convection cells caused by the day-time heating of the land surface by solar radiation, and orographic uplifts, caused by deflection of air masses resulting from their collision against steep terrain (Bohrer *et al.* 2012). However, there are no thermal uplifts at night due to the absence of sun, so nocturnal flights will be more prevalent in lighter-weight raptors species (i.e. presenting a low mass to wing surface area ratio) whose flight strategies are not based on soaring but which profit mainly from orographic uplifts for flying.

Here we document the previously undescribed nocturnal flight behaviour by Bearded Vultures *Gypaetus barbatus*, using a combination of accelerometer and global positioning system (GPS) tracking data. In addition, we analysed diurnal and nocturnal feeding events on experimental carcasses with the help of camera traps, to establish whether nocturnal flights could be linked to the foraging behaviour of this species.

Methods

We marked 11 Bearded Vultures in the Spanish Pyrenees with GPS-GSM 50 g Ornitela and E-obs Bird Solar 57 g transmitters, between 2018 and 2019 (Table 1). The transmitters on each bird were programmed differently, but all recorded accelerometery and positional data 24 h a day from 1st October 2018 to 15th April 2019. We considered nocturnal flight activity as any spatial displacement during the night initially detected through GPS location data which were then confirmed, when possible, by acceleration data, to avoid the transmitters' horizontal inaccuracy. Based on our stationary tests the transmitters were accurate to within 4.5-25 m, as they were influenced by a rough orography and device orientation due to animal movement. Accelerometery can only provide information on a bird's behaviour during the precise seconds registered, while the GPS data can describe the general movement and spatial position of the animal through time. Distances travelled by vultures were calculated using basic trigonometry and flight speed was consequently the distance covered during the time between consecutive locations. We recorded a total of 38,601 nocturnal locations and 81,490 twilight locations, defining the beginning and end of the nocturnal period (also called 'night') based on the timing of astronomical twilight (data in www. timeanddate.com). We also monitored 88 carcasses of wild and domestic ungulates (Sheep Ovis aries, Goat Capra hircus, Wild Boar Sus scrofa and Roe Deer Capreolus capreolus) using camera traps in the same study area during December 2017 to January 2019, to determine whether nocturnal behaviour could be related to foraging movements.

The carcasses were monitored with Moultrie camera traps (M-990i GEN2 10MP and M-999i 20MP) programmed to take a set of three photographs when movement was detected and wait 15 s before taking the next series of photographs.

Results

Nocturnal flights

The nocturnal activity data recorded 55% (n = 6) of the tracked individuals flying between 0.7 and 6.1 km on at least 19 different nights (Table 1). We summarize the most striking cases below.

First, on 24th November 2018, a non-territorial adult (Coto) had been perched at a roosting site since 15:00 (Coordinated Universal Time – UTC). The night of 24th–25th November was defined from 18:04 to 5:18. From GPS and accelerometer records, it abandoned this roost between 03:00 and 3:30 on 25th November 2018 and flew over a small town before perching again at a new nocturnal roosting site between 3:30 and 4:01, where it remained until 10:00 (Figure 1(a, b)). It flew 4.9 km between the two roost sites, while 97% of the moon was illuminated.

Second, on 3rd March 2019 (when the night of 3rd-4th March was defined as 19:19-4:51), Coto travelled

Table 1. Detailed characteristics of the 11 Bearded Vultures *Gypaetus barbatus* tracked for nocturnal activity between 1st October 2018 and 16th April 2019 in the Pyrenees. The *periods* described are always delimited by the time of the two GPS locations covering the nocturnal flight, but do not necessarily strictly define the time during which the bird is actually flying (the bird's flight normally takes only a few minutes within these *periods of nocturnal activity*). For this parameter, italic letters correspond to strictly nocturnal times (defined through the end and onset of astronomical twilight), bold letters denote twilight times, and normal font letters correspond to periods including times of several of the aforementioned phases of the day. Universal Time Coordinated (UTC) time was used in all cases.

Name	Age class (years)	Transmitter type	Days tracked	Night Flight Activity	Night data provision (%)	Twilight (Dusk)	Night	Twilight (Dawn)	Periods of nocturnal activity
Bolisna	Ad (>7)	E-obs	197	Yes (2 nights)	0.29	17:26–19:01 17:51–19:25	19:01–5:14 19:25–4:43	5:14–6:48 4:43–6:16	18:00–18:30 & 18:30–6:50 23:22–00:02 & 00:30–2:11 & 3:10–3:51
Cano	Juv (0–1)	E-obs	197	No	2.03	-	-	-	-
Coto	Ad (8)	E-obs	187	Yes (8 nights)	11.76	16:48-18:23	18:23-4:51	4:51-6:27	20:31-5:00
						16:25-18:04	18:04–5:16	5:16-6:55	19:30–20:30 & 2:30–4:00
						16:25-18:04	18:04–5:18	5:18-6:56	3:00-4:00
						16:22-18:04	18:04–5:37	5:37-7:19	17:00–21:31
						16:34–18:16	18:16-5:42	5:42-7:23	18:00-23:01
						16:56-18:34	18:34–5:36	5:36-7:14	19:00–20:00
						17:31–19:05	19:05-5:08	5:08-6:42	18:01-23:00 & 23:31-00:30 & 3:00-4:00
						17:45–19:19	19:19–4:51	4:51-6:25	19:25–19:40
Espluga	Juv (0–1)	Ornitela	197	No	11.90	-	-	-	-
Galbana	Ad (>7)	E-obs	69	Yes (3 nights)	4.52	16:20-18:02	18:02–5:32	5:32-7:14	17:30-19:00 & 19:00-20:00 & 1:00-3:00
						16:20-18:02	18:02–5:33	5:33-7:14	17:00-19:00 & 19:00-20:31 & 23:31-1:31 & 2:30-3:30
						16:21-18:02	18:02–5:33	5:33–7:15	18:00–19:30
Genova	Ad (>7)	E-obs	131	Yes (2 nights)	18.68	16:21-18:02	18:02–5:25	5:25-7:04	19:00–19:30 & 23:30–00:00
						16:34–18:16	18:16–5:42	5:42-7:23	18:30–21:00
Lluna	Juv (0–1)	Ornitela	197	No	10.37	-	-	-	-
Lluvia	Ad (>7)	E-obs	188	Yes (1 night)	18.72	17:47–19:21	19:21–4:48	4:48-6:21	1:15–1:40
Moleta	Ad (>7)	E-obs	155	Yes (3 nights)	9.75	16:59–18:37	18:37–5:35	5:35–7:13	2:00–2:30
						17:13–18:49	18:49–5:25	5:25-7:01	2:30–3:30
						17:11–19:46	19:46-3:12	3:12-4:47	2:20–4:21
Segarra	Juv (0–1)	Ornitela	197	No	1.87	-	-	-	-
Viu	Juv (0–1)	Ornitela	197	No	10.11	-	-	-	-

25th November 2018



Figure 1. (a) Route of a nocturnal movement by a non-territorial adult Bearded Vulture *Gypaetus barbatus* derived from three GPS locations recorded in the Pyrenees (Spain) from 3:00 to 4:01 during the night of 24th–25th November 2018, when 97% of the moon was illuminated. Notice that at 3:30 the bird is clearly flying over a small town. It flew 4.9 km considering a straight-line distance. (b) Accelerometery data from an E-obs transmitter on 25th November 2018 between 00:00 and 5:00 visualized using the Acceleration Viewer program. At the top, the yellow marks show the GPS locations registered in parallel to the accelerometery activity. Red, green and blue lines correspond to the acceleration in the *X*, *Y* and *Z* axes respectively, reflecting a flapping flight moment at 3:30, while the GPS locations registered at the same time indicated a 'ground-speed' of 10.66 m/s.

6.1 km between 19:25 and 19:40 between two nocturnal roosting sites, again flying close to a small town and over farmland, while only 8% of the moon was illuminated. Coto achieved a minimum flight speed of 24.4 km/h, the highest minimum speed registered for all the nocturnal displacements analysed (Table 1, online supplementary Figure S9).

Third, a non-territorial adult (Galbana) occupied the same nocturnal roosting site located close to a village over three consecutive days from 15:30 on 11th December 2018 to 10:00 on 14th December 2018 (night defined from 18:02 to 5:33), despite the accelerometery and nocturnal GPS data indicating that it suffered unsettled nights, and made multiple short



Figure 2. Feeding activity around nocturnal hours by avian scavengers of the study area. We detected 64 feeding events in 28 carrions at night and twilight periods, having place only 2 feeding events at night, both carried out by Griffon Vultures. Bearded Vultures presented feeding activity at the two periods of one hour after dawn (4 feeding events) and one hour before dusk (8 feeding events), considering a total of 146 feeding events recorded in 46 carrions for these two 1 h periods.

nocturnal flights over a maximum distance of 0.5 km. During those three nights Galbana travelled frequently between two slopes of the same valley, each time flying over both a road and a river, while the fraction of the moon illuminated was between 18% and 38% (Table 1, online Figures S10-S12).

In a fourth case, a territorial adult (Moleta) flew 3.9 km between 2:30 and 3:30 on the morning of 7th February 2019 (when the night of 6th–7th February was defined from 18:49 to 5:25), with only 3% of the moon illuminated, changing its night roosting site and coming to rest on a hill next to a small city inside its own territory (Table 1, online Figure S17).

Feeding behaviour

We recorded 847 feeding events at the 88 monitored carcasses. We detected feeding activity during the night and at dawn and dusk (both defined by the civil twilight) at 32% of the carcasses (n = 28), recording a total of 64 (7.6%) feeding events. Of these 64, only 3.12% (*n* = 2) occurred during the night at two different carcasses visited by Griffon Vultures Gyps fulvus, which were recorded feeding until 18:54 and 22:15 on 1st November 2018 and 15th December 2018, respectively. Analysing the two periods of one hour after the end of the dawn civil twilight and one hour before the beginning of the dusk civil twilight, we observed feeding activity at 52.3% (n = 46) of the carcasses monitored, documenting 146 feeding events; with only 8.2% (n = 12) carried out by Bearded Vultures. Consequently, we only detected Bearded Vulture feeding activity during the two periods of one hour after dawn and one hour before dusk (Figure 2).

Discussion

The cases of nocturnal flights by Bearded Vultures suggest that nocturnal flight could be more common than previously realized. In fact, Turkey Vultures have been documented flying at night when the moon was full and other environmental factors were favourable (Tabor & McAllister 1988). Our findings show that most of the tracked flights were in the area surrounding the nocturnal roosting site. However, in Pyrenean Bearded Vultures, during the non-breeding period maximum distance reached from the initial point per day ranged between 0.14 ± 0.21 km and 16.83 ± 21.01 km in the case of non-territorial adults, 3.72 ± 8.4 km for territorial adults, and 5.7 km in the case of juveniles (Margalida et al. 2016, García-Jiménez et al. 2018). Interestingly, all six adults equipped with transmitters in this study showed nocturnal flight activity, but this pattern was not observed among juveniles. Older birds could possibly have better knowledge of their territory and be more confident in flying at night. On the other hand, this age stratified behaviour may also be associated with differences in the transmitters' programming, since adult data records represented 64% of all the night fixes recorded, therefore it is possible that a more intensive nocturnal accelerometery and GPS tracking on juveniles would also detect some nocturnal activity within this age class.

Bearded Vultures probably benefit from their lighter wing loading $(0.56 \text{ g/cm}^2 \text{ for the Bearded Vulture,})$ 0.60 g/cm^2 for the Egyptian vulture Neophron percnopterus and 0.77 g/cm² for the Griffon Vulture, Donázar 1993) which allows them to utilize weaker orographic uplifts than many other vulture species. Although the reasons behind nocturnal flights are still unknown, it seems that foraging benefits could be excluded as a general explanation. Our results suggest that Bearded Vultures almost exclusively fed by day, and that there was no link between their nocturnal flights and foraging behaviour. In addition, the specialized osteophagous diet of the Bearded Vulture seems to have certain advantages because bones remain edible for much longer periods than the soft tissues required by meat-eating vultures (Houston & Copsey 1994, Margalida & Villalba 2017). In fact, dry bones retain 90% of the protein found in fresh bones (Margalida & Villalba 2017) enabling Bearded Vultures to effectively store bones to be consumed at a later stage (Margalida & Bertran 2001, Margalida 2008).

Based on our results, it seems that although nocturnal feeding activity could be more common than expected in this diurnal species, the nocturnal flights of Bearded Vultures are not related to foraging behaviour. This contrasts with nocturnal feeding activities we observed on Griffon Vultures (3% of both nocturnal and twilight feeding events, n = 2, Figure 2), as it has been previously documented in this and other Gyps vulture species (Naoroji 2006, Mateo-Tomás & Olea 2018). It may be that some individuals are able to benefit from artificial light and are not concerned about flying close to villages or paved roads, even at night (on 58% of nights on which nocturnal flights were made by four adults, flights were close to, or over man-made structures). Presumably, disturbances (e.g. provoked by the presence of wild and domestic ungulates) or adverse weather conditions may result in the sudden abandonment of an overnight roosting site even when the moon is not at its brightest. In this sense, predatory animals (e.g. Red Fox Vulpes vulpes, Stone Marten Martes foina), might visit regularly nesting or roosting sites of Bearded Vulture because of the food they store (Margalida & Bertran 2003, authors pers. obs.) and cause disturbance at night. Indeed, 37% of the nocturnal flights analysed occurred when less than 20% of the moon was illuminated (online Table S1). This behaviour could explain the cases of individuals recovered in the field showing impact injuries (authors unpubl. data). Even though interspecific and intraspecific interactions frequently produce serious injuries (Blanco et al. 1997), nocturnal flights must carry an increased risk of collision accidents, especially

at low moonlight intensities. Since we currently only have a small number of nocturnal flight records, we cannot yet distinguish between the different hypotheses discussed here, or be sure how common nocturnal flight behaviour is either in Bearded Vultures or other diurnal raptor species. Future research on diurnal raptors should take nocturnal movements and foraging ecology into account, in order to improve our knowledge regarding the ecological and conservation consequences of such behaviour.

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References

- Blanco, G., Traverso, J.M., Marchamalo, J. & Martínez, F. 1997. Interspecific and intraspecific aggression among griffon and cinereous vultures at nesting and foraging sites. *J. Raptor Res.* **31:** 77–79.
- Bohrer, G., Brandes, D., Mandel, J.T., Bildstein, K.L., Miller, T.A., Lanzone, M., Katzner, T., Maisonneuve, C. & Tremblay, J.A. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and Turkey vultures. *Ecol. Lett.* 15: 96–103.
- Charette, M., Pelletier, F. & Calme, S. 2011. Observation of nocturnal feeding in black vultures (*Coragyps atratus*). *J. Raptor Res.* 45: 279–280.

- DeCandido, R., Bierregaard, R.O.J., Martell, M.S. & Bildstein, K.L. 2006. Evidence of nocturnal migration by Osprey (*Pandion haliaetus*) in North America and Western Europe. J. Raptor Res. 40: 156–158.
- **Donázar, J.A.** 1993. Los Buitres Ibéricos: biología y conservación. J.M. Reyero Editor., Madrid.
- Fernández-Duque, E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behav. Ecol. Sociobiol.* 54: 431–440.
- García-Jiménez, R., Pérez-García, J.M. & Margalida, A. 2018. Drivers of daily movement patterns affecting an endangered vulture flight activity. *BMC Ecol.* 18: 39.
- Gustin, M., Giglio, G., Pellegrino, S.C., Frassanito, A. & Ferrarini, A. 2017. New evidences confirm that during the breeding season Lesser Kestrel is not a strictly diurnal raptor. *Ornis Fenn.* **94**: 194–199.
- Houston, D.C. 2001. Vultures and Condors. Colin Baxter, Granton- on-Spey.
- Houston, D.C. & Copsey, J.A. 1994. Bone digestion and intestinal morphology of the Bearded Vulture. *J. Raptor. Res.* 28: 73–78.
- Kendeigh, S.C. 1934. The role of environment in the life of birds. *Ecol. Monogr.* 4: 299–417.
- Margalida, A. 2008. Presence of bone remains in the ossuaries of Bearded Vultures (*Gypaetus barbatus*): storage or nutritive rejection? *Auk.* **125:** 560–564.
- Margalida, A. & Bertran, J. 2001. Function and temporal variation in the use of ossuaries by Bearded Vultures (*Gypaetus barbatus*) during the nestling period. *Auk* 118: 785–789.
- Margalida, A. & Bertran, J. 2003. Interspecific and intraspecific kleptoparasitic interactions of the Bearded Vultures (*Gypaetus basrbatus*) at nesting areas. *J. Raptor Res.* 37: 157–160.
- Margalida, A. & Villalba, D. 2017. The importance of the nutritive value of old bones in the diet of Bearded vultures *Gypaetus barbatus. Sci. Rep.* 7: 1–5.
- 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: 35746.

- Mateo-Tomás, P. & Olea, P.P. 2018. Griffon Vultures scavenging at night: trophic niche expansion to reduce intraspecific competition? *Ecology* 99: 1897–1898.
- Moore, A.D. 1945. Winter night habits of birds. *Wilson Bull.* 57: 253–260.
- Naoroji, R. 2006. Birds of Prey of the Indian Subcontinent. Christopher Helm, London.
- Negro, J.J., Bustamante, J., Melguizo, C., Ruiz, J.L. & Grande, J.M. 2000. Nocturnal activity of Lesser Kestrels under artificial lighting conditions in Seville, Spain. *J. Raptor Res.* **34**: 327–329.
- Rejt, L. 2004a. Nocturnal behaviour of adult peregrines at the nest during nestling period. *Vestn. Zool.* 38: 87–90.
- Rejt, L. 2004b. Nocturnal feeding of young by urban Peregrine Falcons (*Falco peregrinus*) in Warsaw (Poland). *Pol. J. Ecol.* 52: 63–68.
- Riba-Hernández, L., Akresh, M., Martínez, D.A. & Hernández, W. 2012. A nocturnal flight record of Swainson's hawks (*Buteo swainsoni*) and Turkey vultures (*Cathartes aura*) during fall migration in Costa Rica. *J. Raptor Res.* **46:** 234–235.
- Russell, R.W. 1991. Nocturnal flight by migrant "diurnal" raptors. J. Field Ornithol. 62: 505–508.
- Ruxton, G.D. & Houston, D.C. 2004. Obligate vertebrate scavengers must be large soaring fliers. *J. Theor. Biol.* 228: 431–436.
- Spiegel, O., Harel, R., Getz, W.M. & Nathan, R. 2013. Mixed strategies of griffon vultures' (*Gyps fulvus*) response to food deprivation lead to a hump-shaped movement pattern. *Move. Ecol.* 1: 5.
- Tabor, S.P. & McAllister, C.T. 1988. Nocturnal flight by Turkey Vultures (*Cathartes aura*) in southcentral Texas. *J. Raptor Res.* 22: 91.
- Wendt, A., Septon, G. & Moline, J. 1991. Juvenile urbanhacked Peregrine Falcons (*Falco peregrinus*) hunt at night. *J. Raptor Res.* 25: 94–95.
- Wu, Y., Hadly, E.A., Teng, W., Hao, Y., Liang, W. & Liu, Y. 2016. Retinal transcriptome sequencing sheds light on the adaptation to nocturnal and diurnal lifestyles in raptors. *Sci. Rep.* 6: 33578.
- Yosef, R. 2003. Nocturnal arrival at a roost by migrating Levant Sparrowhawks. J. Raptor Res. 37: 64–67.