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Tri-axial accelerometry shows differences in energy expenditure and parental effort throughout the breeding season in long-lived raptors

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Abstract

Cutting-edge technologies are extremely useful to develop new workflows in studying ecological data, particularly to understand animal behavior and movement trajectories at the individual level. Although parental care is a well-studied phenomenon, most studies have been focused on direct observational or video recording data, as well as experimental manipulation. Therefore, what happens out of our sight still remains unknown. Using high-frequency GPS/GSM dataloggers and tri-axial accelerometers we monitored 25 Bonelli's eagles *Aquila fasciata* during the breeding season to understand parental activities from a broader perspective. We used recursive data, measured as number of visits and residence time, to reveal nest attendance patterns of biparental care with role specialization between sexes. Accelerometry data interpreted as the overall dynamic body acceleration, a proxy of energy expenditure, showed strong differences in parental effort throughout the breeding season and between sexes. Thereby, males increased substantially their energetic requirements, due to the increased workload, while females spent most of the time on the nest. Furthermore, during critical phases of the breeding season, a low percentage of suitable hunting spots in eagles' territories led them to increase their ranging behavior in order to find food, with important consequences in energy consumption and mortality risk. Our results highlight the crucial role of males in raptor species exhibiting biparental care. Finally, we exemplify how biologging technologies are an adequate and objective method to study parental care in raptors as well as to get deeper insight into breeding ecology of birds in general.

Key words: biologging, GPS, movement ecology, ODBA, space use, telemetry

Cutting-edge tracking technologies have facilitated progress in studies about animal movements and behavior (e.g., Kays et al. 2015; López-López 2016; Tucker et al. 2018; Wang 2019), physiology and energetic requirements (e.g., Laich et al. 2011; O'Mara et al. 2019), and conservation (e.g., Berger-Tal and Lahoz-Monfort 2018; Katzner and Arlettaz 2020). However, key aspects of the life history

of organisms such as parental care remain poorly investigated by means of tracking technologies (but see Kavelaars et al. 2018). In this regard, biologging technologies provide an exceptional set of tools to gain deeper insight into the complex behavioral responses of animals that are eventually expressed as parental care.

Parental care can be considered any activity carried out by progenitors to increase the survival and biological fitness of their offspring, regardless of any cost to the parents (Clutton-Brock 1991; Royle et al. 2012). In the case of birds, the majority of the species exhibit biparental care (Lack 1968), with both sexes contributing to chick rearing (Cockburn 2006). Nonetheless, the sort and amount of care effort could differ between sexes (Webb et al. 2010; Goymann et al. 2016), some of them as a consequence of size dimorphism (Schoenjahn et al. 2020), age (Møller and Nielsen 2014), and phylogenetic affiliation (Cockburn 2006). This cooperation has a synergistic effect on the offspring's biological fitness, particularly when there is sex-biased task specialization, leading the progeny to a better chance of survival (Pilakouta et al. 2018). However, parental care implies high individual cost for the parents, shrinking their fitness with an evolutionary trade-off between current breeding success and parents' future condition (Trivers 1972; Nur 1988; Clutton-Brock 1991; but see Williams 2018). In consequence, the more parental investment the more energy parents are expected to spend, because feeding the offspring is a demanding task due to an increase in ranging effort and traveling costs (Royle et al. 2012), which ultimately results in a conflict between offspring and parents and between both parents (Clutton-Brock 1991). Therefore, linking energy expenditure on a fine spatial and temporal scale to parental activities is vital to understand how parents take behavioral decisions during the breeding season.

Nowadays, the development of tri-axial accelerometers combined with high-frequency GPS dataloggers provides information on 3 spatial axes (i.e., heave, sway, and surge) for each input of movement that can be used to compute the amount of energy required for movement (Stothart et al. 2016; Lear et al. 2017). Although parental care is a phenomenon well documented in the literature (e.g., Royle et al. 2012; Kokko 2018), parental care studies have been traditionally done using focal sampling methods (i.e., direct observations) (e.g., Arroyo et al. 1976; Pérez-Mellado et al. 1977; Martínez et al. 2020), video recording (Sonerud et al. 2014; Keeley and Bechard 2017), and radio-tracking methods (Muriel et al. 2015; Maury et al. 2020). In the case of birds, field observations provide important information such as prey items delivered to the offspring, nest, and chick attendance, and incubation time-budgets (van Rooij and Griffith 2013; Wagner et al. 2019). However, visual observations are limited by the amount of people recording behavior and usually result in imperfect monitoring effort during short time periods and/or limited sample size. The same happens with video recordings, which do not take into account the surroundings of the focal area, typically the nest. In contrast, GPS dataloggers allow monitoring of several individuals in an unbiased and continuous way, compensating thus for the fact that an observer only can track a few individuals for a bounded period of time in a restricted space. Notwithstanding, very few studies have used GPS telemetry to study parental care on birds so far (Brown et al. 2013; Kavelaars et al. 2018; Austin et al. 2019; Sotillo et al. 2019) and only one study used this technology with raptors to study foraging strategies during the breeding season (Hernández-Pliego et al. 2017). Hence, to the best of our knowledge, despite the advent of GPS/ACC telemetry, tri-axial accelerometry has been ignored to further investigate parental care in

raptors. In addition, new tools to analyze recursive movement patterns allow assessing the repetitive use of specific locations like nesting sites or other places of ecological relevance (Berger-Tal and Bar-David 2015; Bracis et al. 2018). Recursive analysis of movement trajectories allows gauging the amount of parental investment by each individual throughout the entire breeding season by analyzing the temporal and spatial patterns of revisitation. Thereby, revisitation analyses provide new insights into the life history of individuals and, ultimately, useful information for management and conservation (Bracis et al. 2018).

Here, we studied ranging behavior, energy expenditure, and nest attendance, considered as the recursive movement pattern, of a long-lived endangered raptor, the Bonelli's eagle *Aquila fasciata*, during the breeding season by means of high-frequency GPS/GSM telemetry. Our main goal was to describe and quantify sex-biased task specialization and energy expenditure patterns in parental care investment between sexes and across different periods of the breeding season. In particular, we aim to respond 2 questions: (i) how does the daily time at nest (i.e., residence time), daily travel distance, and overall energy expenditure differ between males and females during the different stages of the breeding season?; and (ii) are there differences between sexes in the relative energy expenditure per breeding stage? As other raptors of similar size, the Bonelli's eagle is a slightly reversed size dimorphic bird of prey that shows biparental care. Thereupon, we hypothesize that a role diversification between both sexes should be expected (Newton 1979; Cramp and Simmons 1980), with females spending more time in the nest while males act as providers, hunters, and deliver prey to the nest. Under this scenario, we would expect a compensation of efforts, with different time and resource allocation as a result of sex differences in role behavior. Males should spend most of the time away from the nest and thus would need larger energy requirements related to the movements if compared with females. On the other hand, as eagles need high prey detectability areas in order to find food, we hypothesize that male individuals living in less suitable territories must expend extra energy during the most demanding periods of breeding season (i.e., incubation and chick-rearing).

Material and Methods

Study area

The study area was located in eastern Spain, including northern Valencia and southern Castellón provinces. Eagles' breeding territories were located inside the Natura 2000 protected areas and their surroundings, comprising Sierra Calderona and Sierra de Espadán Natural Parks (from 40°09′N to 39°36′N and from 0°44′W to 0°05′E), the more coastal parts of the Iberian System. The area covers approximately 1,600 km², from sea level to 1,106 m above sea level. The climate is Mediterranean, with mean temperatures during the breeding season varying from 17°C (coastal areas) to 8°C in the inner highlands. Geologically, the study area stands out for its red sandstones and limestones, which includes an abrupt landscape with a considerable number of hills, which are suitable for nesting eagles. Furthermore, the study area, and particularly the surroundings, is a highly human populated area that results on periodic patterns of disturbance of wildlife due to recreational activities (Perona et al. 2019). Moreover, there is an extensive network of power lines, roads, and other artificial infrastructures that represent a potential source of mortality. Further details on description of the study area are available in López-López et al. (2007).

Study species

The Bonelli's eagle is a long-lived resident raptor distributed across the Palearctic, Indo-Malayan, and, to a lesser extent, across the Afrotropical regions (Ferguson-Lees and Christie 2001). It inhabits coastal regions and mid-altitude mountain areas throughout the Iberian Peninsula, which holds 60% of the European population (Del Moral and Molina 2018). Unlike other large eagles such as the Golden eagle *Aquila chrysaetos* or the Spanish Imperial eagle *Aquila adalberti*, its range overlaps many urban areas across the Mediterranean region (Muñoz et al. 2005; Carrascal and Seoane 2009). Consequently, the species has experienced an important population decline due to human pressure including habitat degradation, direct persecution by shooting and poisoning, and presence of artificial infrastructures, such as power lines, which comprise one of the main mortality risks for this species (Chevallier et al. 2015). The species is legally listed as Vulnerable in Spain (Royal Decree 139/2011) and as Endangered according to IUCN National Red List due to rapid reduction in important areas of its breeding range (Real 2004).

The Bonelli's eagle is a dimorphic bird of prey with females being slightly larger than males. Previous studies have described biparental care for this species with a sex-biased specialization in parental tasks, with females taking more care of the nest and males focusing on providing prey (Pérez-Mellado et al. 1977; Martínez et al. 2020), similar to other large raptors (Margalida et al. 2007; Bassi et al. 2017). Although this species shows strong annual fidelity to its territory (Martínez-Miranzo et al. 2016), it is vulnerable to changes in prey availability (Martínez-Miranzo et al. 2019). Therefore, it is of vital importance to enhance our understanding of the behavioral patterns during the breeding season to improve its delicate conservation status.

Monitoring

Overall, 25 territorial Bonelli's eagles, 12 females and 13 males, from 12 different territories were trapped by means of a folding net remotely triggered at distance between 2015 and 2018 (Table 1). Both individuals of each territory were captured at the same time (except for territory #5 where only the male was captured). In case of death of one of the members of the pair, we captured the replacing individual as well. All individuals were tagged with 48 g solar-powered GPS/GSM dataloggers (e-obs GmbH, Munich, Germany) using a tubular Teflon wing-harness in a backpack configuration. Transmitters did not represent more than 3% of individuals' weight (average = 2.25%, sd = 0.38%) to avoid negative effects on behavior (Kenward 2001). Age was estimated based on plumage characteristics during individual manipulation (Forsman 2016). Transmitter's duty cycle was programmed to record locations and tri-axial accelerometry (33.3 Hz) at 5 min interval from 1 h before sunrise to 1 h after sunset throughout the breeding season. Only individuals who carried out breeding (including success and failure until the day of failure) were considered in this study. Data were stored in the online data repository Movebank and filtered and managed using R version 3.6.1 (R Core Team 2019).

In order to account for temporal variations in space use over the entire breeding period, we divided the data into 4 different periods: (i) courtship, (ii) incubation, (iii) chick-rearing, and (iv) post-fledging. Courtship was considered from 1 January to the actual egg laying day (obtained by means of the combination of fieldwork observations and tracking information including accelerometry). Then, we considered an average span of incubation of 39 days from egg laying to hatching date (Gil-Sánchez 2000). We considered an average of 63 days after hatching as the "chick-rearing period" (Cadahía et al. 2008). Finally, the "post-fledging period" was

Table 1. Summary information of 25 territorial Bonelli's eagles tracked by GPS/GSM telemetry in Eastern Spain from 2015 to 2019

Individual	Territory	Tagging date	Sex	Breeding season	Number of locations
1	A	19 May 2015	M	2016	29,910
2	A	19 May 2015	F	2016—2017—2018–2019	118,415
3	A	31 January 2017	M	2017—2018—2019	81,111
4	B	6 October 2015	M	2016	29,235
5	B	6 November 2015	F	2016	29,621
6	B	11 April 2017	F	2019	30,319
7	C	28 October 2015	M	2016—2017—2018	88,397
8	C	28 October 2015	F	2016—2017—2018	66,532
9	D	29 October 2015	M	2016–2017	46,750
10	D	29 October 2015	F	2016–2017	47,170
11	E	8 June 2016	M	2018–2019	58,222
12	E	18 May 2017	F	2018–2019	59,494
13	F	6 June 2016	M	2018–2019	59,195
14	G	13 September 2017	M	2018	12,107
15	G	6 June 2017	F	2018	12,067
16	H	20 April 2017	M	2018	12,665
17	H	6 October 2016	F	2018	8,636
18	I	7 October 2016	M	2017	27,782
19	I	7 October 2016	F	2017	27,300
20	J	5 June 2017	M	2018–2019	50,830
21	J	14 June 2017	F	2018–2019	58,982
22	K	11 July 2017	M	2019	57,828
23	K	11 July 2017	F	2019	55,426
24	L	17 May 2018	M	2019	29,880
25	L	17 May 2018	F	2019	29,063

Notes: The number of locations correspond to a 5-min tracking span. Breeding years correspond to each one of the breeding seasons computed. M, male; F, female.

considered from fledging until 1 July, as this is the date when all chicks in our dataset had fledged.

Movement data analysis and space use

In order to calculate the amount of parental care, we recorded the daily number of revisits and the time spent at the nest. Revisitation analyses were conducted using the R package "recurse" (Bracis et al. 2018). This package computes revisitation metrics for trajectory data. In particular, we considered a radius of 25 m around nest exact location each year (to account for GPS nominal error) and a threshold of 10 min of time difference to exclude excursions outside this radius (Bracis et al. 2018).

Energy expenditure associated with the movement of individuals was calculated from tri-axial accelerometry data as the overall dynamic body acceleration (ODBA). Accelerometer information was recorded at 5-min intervals every day during the breeding season, registering in the 3 different axes (x, y, and z) the amount of movement which can be interpreted as the amount of effort used in flight and movement activities. Thus, we calculated daily ODBA as the sum of ODBA values of the 3 axes using the "ACCstats" function implemented in the "moveACC" R package (Scharf 2018). Raw acceleration data were transformed into physical unit "g" (Laich et al. 2011). ODBA can be considered a proxy of energy expenditure (Gleiss et al. 2011; Qasem et al. 2012; Spivey and Bishop 2013) since it is positively associated with oxygen consumption and carbon dioxide production (Wilson et al. 2006; Laich et al. 2011) and the mechanical work produced by muscles and internal organs (Gleiss et al. 2011; Bishop et al. 2015).

To estimate space use at the individual level, we computed daily traveled distance as the sum of all step-length segments (i.e., distance between 2 subsequent GPS location fixes) recorded within a day using the "amt" R package (Signer et al. 2019). Then, we obtained home range area from each breeding phase (i.e., courtship, incubation, chick-rearing, and post-fledging). Home range areas and correspondent isopleths were obtained from the 95% kernel density estimation (KDE) by using "rhrKDE" function of the "rhr" R package (Signer and Balkenhol 2015).

Space use and energy expenditure can vary in relation to prey availability within each territory regardless of the stage of the breeding season. Moreover, different habitat features can influence prey detectability by raptors (Ontiveros et al. 2005). Hence, to account for the influence of prey detectability on space use and energy expenditure during the breeding period, we calculated a prey detectability index and prey richness for each land cover class of the CORINE land cover (CORINE 2018) within each territory (estimated as the 95% kernel contour). Prey richness was calculated as the presence of main prey species of Bonelli's eagle for each land-cover type, including rock pigeon *Columba livia*, common wood pigeon *Columba palumbus*, stock dove *Columba oenas*, red-legged partridge *Alectoris rufa*, and European rabbit (*Oryctolagus cuniculus*) following López-López et al. (2011) habitat suitability models. Eagles prefer open habitats for hunting (Ontiveros et al. 2005), including grasslands, cereal crops, and low-height scrublands (Martínez et al. 2014). In contrast, forests, intensive crops, and some artificial areas were considered as closed land. Thus, we assigned a detectability value for each land-cover type of CORINE (2018) according to these habitat characteristics of the study area in QGIS 3.8.2. Unavailable, closed, semi-closed, semi-open, and open Corine Land Cover Classes (CLCs) were assigned a value of 0 (i.e., null detectability), 0.25 (low detectability), 0.50 (medium detectability), 0.75 (high detectability), and 1 (full detectability), respectively.

A detailed table of prey detectability values and habitat suitability for each type of prey in each CLC is available as Supplementary Table S1.

We finally related each home range 95% isopleth (with the correspondent number of fixes) to the layers of prey detectability and prey richness by intersecting them in QGIS 3.8.2. Then, we obtained the proportion of locations on each land-cover pixel with correspondent detectability and richness values per individual/breeding phase, calculating the percentage of those locations that correspond to detectability values ≥0.5, considering them as favorable "hunting spots" in subsequent analyses (Ontiveros et al. 2005).

Statistical analysis

We used generalized linear mixed models (Zuur et al. 2009) to: (i) analyze the variation in the number of "revisits" and "residence time" at nest in relation to "daily ODBA," "daily traveled distance," "sex," "age," and "period"; and (ii) to investigate the effect of prey detectability on space use measured as "hunting spots." In the first case, "daily ODBA," "daily traveled distance," and "hunting-spots" were entered in the models as continuous covariates while "sex," "age," and "period" were coded as factors. In addition, in the prey detectability model, "age" and "period" were entered as fixed factors to account for potential variations on space use due to intrinsic and external factors, respectively. We considered "territory," "individual," and "year" as random factors. "Year" was considered nested inside "individual" and the latter nested into "territory" in order to account for non-independence of data (Harrison et al. 2018). Overall, we built 16 different models for each response variable "revisits," "residence time," and "hunting spots." We built 5 simple models for each fixed factor and the rest as a result of different combination of additive fixed factors. Models were computed by using "glmer" function implemented in the package "lme4" for R (Bates et al. 2014).

We calculated the Akaike's information criterion (AICc) corrected for small sample size (Akaike 1974) to select the most parsimonious model for each scale (Burnham and Anderson 2002; Johnson and Omland 2004). We ranked models using AICc and selected the best one according to the lowest AIC_c value (Sakamoto et al. 1986). Following Symonds and Moussalli (2011), we conducted model averaging among the best models (i.e., models differentiating less than 2 AIC_c units) in order to assess the relative contribution of each independent factor by means of the R package "MuMIn" (Barton 2018). To account for the effect of multiple comparisons, we computed corrected *P*-values using the Benjamini–Hochberg multiple comparisons procedure for controlling the false discovery rate (Benjamini and Hochberg 1995). Statistical significance was set at $\alpha < 0.05$. All computations were done in R version 3.6.1.

Results

Overall, 41 individual-breeding events (accounting for an individual breeding or attempting to breed in 1 year) were used in this study. Eagles were tracked on average 266 ± 180 days for females and 268 ± 151 days for males. The total number of GPS locations at 5-min interval was 1.126.937, accounting for 170.67 ± 44.84 GPS locations per day for females and 171.40 ± 46.56 GPS locations per day for males. Breeding success, computed as the percentage of successful pairs divided by pairs initiating reproduction, was 73% in 2016, 45% in 2017 and 2018, and 90% in 2019, whereas the

productivity was 1.75 fledged chicks per territory in 2016, 1.60 in 2017, 1.00 in 2018, and 1.56 in 2019 for the tracked individuals.

The best model for residence time was the additive model with all fixed factors (ODBA, daily travel distance, period, sex, and age), whereas the best model for revisits did not include age (Table 2). Our results show strong negative significant effects on residence time for ODBA (Table 3), which means that the more energy expended on a day the less time eagles spend in their nest. Besides, similar results were found for daily travel distance as a measure of ranging behavior, which suggest that the more distance ranged the less time eagles spent in the nest, linking ODBA and ranging behavior (Figure 1). Conversely, although ODBA and daily travel distance showed significant relationships with the number of visits to the nest, the effect of daily travel distance was slightly positive, thus greater revisitation rates were associated with longer distances traveled. In contrast, the effect of ODBA on nest revisitation rates was negative (Table 3).

Strong differences in residence time were found between both sexes. Males had a strong negative effect on residence time if compared with females. The same result was found for the revisitation analysis, which means that males spent a lesser amount of time at the nest as well as fewer visits than females (Table 3 and Supplementary Figures S1 and S2). In fact, females spent on average 1.35 ± 3.81 h per day during courtship, 10.57 ± 10.73 h per day during incubation, 5.50 ± 6.80 h per day during chick-rearing, and 1.12 ± 2.88 h per day during post-fledging periods at the nest. In contrast, males spent on average 0.28 ± 1.06 h per day during courtship, 0.44 ± 1.01 h per day during incubation, 0.57 ± 1.56 h per day

during chick-rearing, and 0.52 ± 1.72 h per day during post-fledging periods at the nest. In sum, females spent more time on the nest during the incubation period, whereas males spent more time during the chick-rearing period.

On the other hand, we found important differences between sexes in energy expenditure. Males expended more energy measured as ODBA throughout the breeding season. In fact, females shrink energy expenditure related to movements from the courtship to incubation, reaching minimum values during the latter, whereas males tended to increase ODBA until the post-fledging period (Figure 1). On average, males daily accumulated ODBA values were 13.67 ± 5.42 g during courtship, 15.98 ± 6.72 g during incubation, 17.42 ± 5.79 g during chick-rearing, and 14.90 ± 4.24 g during the post-fledging period. However, females' ODBA values were on average 11.07 ± 4.75 g during courtship, 9.69 ± 5.73 g during incubation, 16.11 ± 6.54 g during chick-rearing, and 16.20 ± 5.29 g during the post-fledging period.

Furthermore, we recorded sex differences in the relationship between residence time and ODBA. Males spent the same time at the nest every day across the breeding season no matter the amount of energy expended, whereas females spent a considerable number of hours at nest on days with less energy expenditure (Figure 2A); this difference between sexes seems to disappear with high energy expenditure. Similar results were observed between time at the nest and daily travel distance (Figure 2B), where males' values were always lower than females.

Regarding the relationship between visits, ODBA, and daily travel distance, males' values were generally smaller than female values. Females and males showed similarly stable numbers of nest visits as a function of distance traveled (Figure 2C, D). However, it is worth noting that with accumulated ODBA per day higher than 30 g, the number of visits shrank for females (Figure 2C).

Eagles showed different behavior throughout the breeding season (Table 3). We found strong positive effects for residence time and revisits for incubation and chick-rearing periods, indicating that eagles spent on average much more time at the nest in those periods (Figure 3A, B). Eagles consumed more energy during the chick-rearing period, with increases in both ODBA values and daily travel distance (Figure 1). Similar results were found for the number of visits to the nest, with a considerable decrease in the number of visits during the post-fledging period (Table 3 and Figure 3C, D).

Models of prey detectability showed that territories with high percentages of good hunting spots were positively correlated to daily traveled distance (Table 3). Energy expenditure was negatively correlated with the proportion of adequate habitat for hunting, meaning that in territories with high percentage of favorable hunting spots eagles had less energy expenditure (Table 3). Besides, the percentage of use of areas within the territory with high prey detectability changed throughout the breeding season. Consequently, the relationship between detectability and energy expenditure was only negative during the incubation and chick-rearing period (Figure 4).

Discussion

Based on a data-driven approach, this study sheds light on parental activities of a long-lived vertebrate from the perspective of energy expenditure by means of a cutting-edge technology. Combined GPS/GSM and accelerometry information enable a continuous 24 h/365 days intensive monitoring that provides daily information about the position, movement trajectories, and behavior of several pairs at the same time including both males and females. To the best of our

Table 2. Model selection of the best GLMMs according to AIC_C

Value	Model	df	AIC	ΔAIC_C	AIC_w
Revisits					
	ODBA + DD + Period + Sex	**10**	**21531.7**	**0.00**	**0.65**
	ODBA + DD + Period + Sex + Age	11	21532.9	1.24	0.35
	ODBA + DD + Period	9	21555.2	23.46	0.00
	ODBA + Period	8	21831.3	299.57	0.00
	Period	7	21850.4	318.74	0.00
Residence time					
	ODBA + DD + Period + Sex + Age	**12**	**93191.0**	**0.00**	**0.98**
	ODBA + DD + Period + Sex	11	93199.5	8.48	0.01
	ODBA + DD + Period	10	93222.4	31.32	0.00
	ODBA + Period	9	93495.1	304.05	0.00
	Period	8	93799.1	608.04	0.00
Hunting spots	**Age + Period + ODBA + DD + ODBA*DD**	**11**	**423.93**	**0.00**	**0.98**
	Period + ODBA + DD + ODBA*DD	10	431.39	7.46	0.02
	ODBA + DD	6	446.98	23.05	0.00
	Age + ODBA + DD + ODBA*DD	8	448.01	24.08	0.00
	Age + Period	8	458.21	34.28	0.00

Notes: Only models with less than 2 units of ΔAIC_C were chosen for further analysis. DD, daily distance; df, degrees of freedom; AIC_w, Akaike weight. Significant values (i.e., $P < 0.05$) are higlighted in bold.

Table 3. Generalized linear mixed model (GLMM) results of variation in residence time at the nest and revisits taking into account the energy expenditure (ODBA), ranging behavior (daily distance), breeding season period (courtship, incubation, chick-rearing, and post-fledging), and age (adult/subadult)

Value	Variable	Estimate	Std. error	Statistic	Conf. Low	Conf. High	*P*-value
Residence time	ODBA	−24.986	6.050	−4.130	−36.843	−13.129	**<0.001**
	Daily distance	−55.950	3.834	−14.595	−63.464	−48.436	**<0.001**
	Sex (male)	−208.415	44.230	−4.712	−295.103	−121.726	**<0.001**
	Period (post-fledging)	66.037	10.900	6.058	44.673	87.401	**<0.001**
	Period (incubation)	263.528	9.204	28.631	245.488	281.568	**<0.001**
	Period (chick-rearing)	173.749	8.542	20.340	157.006	190.491	**<0.001**
	Age (subadult)	−32.621	67.128	−0.486	−164.190	98.948	0.626
Revisits	ODBA	−0.076	0.016	−4.612	−0.098	−0.054	**<0.001**
	Daily distance	0.171	0.011	15.743	0.156	0.186	**<0.001**
	Sex (male)	−0.844	0.120	−7.061	−1.005	−0.683	**<0.001**
	Period (post-fledging)	−0.148	0.041	−3.585	−0.204	−0.093	**<0.001**
	Period (incubation)	0.757	0.028	26.719	0.719	0.795	**<0.001**
	Period (chick-rearing)	0.749	0.027	28.101	0.713	0.785	**<0.001**
	Age (subadult)	0.175	0.202	0.868	−0.097	0.447	0.383
Hunting spots	ODBA	−0.555	0.411	−1.348	−1.108	−0.001	0.063
	Daily distance	0.215	0.131	1.641	0.039	0.392	**0.003**
	Age (subadult)	12.414	5.986	2.074	4.357	20.471	0.063
	Period (incubation)	−3.575	1.280	−2.794	−5.297	−1.853	**<0.001**
	Period (chick-rearing)	−6.745	1.692	−3.987	−9.022	−4.468	**<0.001**
	Period (post-fledging)	−9.925	1.858	−5.343	−12.425	−7.425	**<0.001**
	ODBA*Daily distance	−0.001	0.006	−0.192	−0.010	0.007	0.847

Notes: Significant values after Benjamini and Hochberg (1995) correction are highlighted in bold.
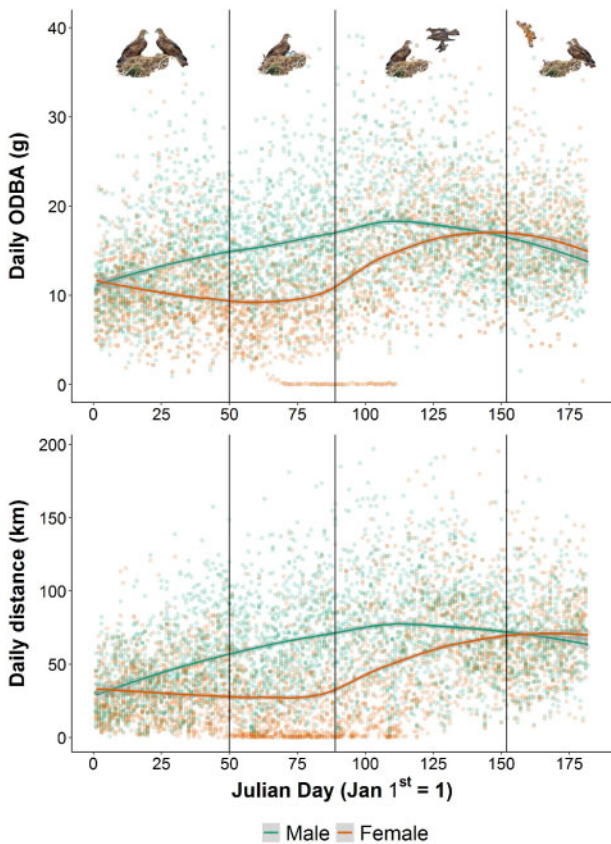

Figure 1. Daily ODBA and daily travel distance throughout the breeding season by sex. 95% confidence intervals around the non-parametric locally weighted scatterplot smoothing are shown in gray. Marked periods are based on average dates, from left to right: courtship, incubation, chick-rearing, and post-fledging.

knowledge, this is the first study using high-frequency data in combination with high-resolution tri-axial accelerometry to study parental care activities in raptors using recursive analysis. In contrast to observational studies, data recorded by GPS/GSM/ACC are not limited to certain periods of time during the day and to single sites (e.g., nests) depending on field effort. In this regard, the increasing availability of high-quality telemetry data opens new avenues of research in the field of behavioral ecology that still remain poorly understood. Interestingly, our results suggest an important role partitioning between both sexes, with the female taking far more care than the male in the nest during incubation and chick-rearing and decreasing effort as the breeding season progresses. Our study also highlights the effort of males far away from the nest, which is usually neglected in parental care studies, providing supporting evidence for a role specialization model.

Residence time can be mainly related to incubation, protection, and nest-attendance. Incubation task implies an energetic trade-off between the energy needs of the incubating adults and the energy requirements for egg development (Bulla et al. 2015). Incubation changeovers and temporary nest desertions are used by females to feed themselves and contribute new material to the nest in order to control temperature and to avoid the proliferation of ectoparasites (Margalida et al. 2007; Ontiveros et al. 2008; Martínez et al. 2020). However, our results reveal that the time spent by the male at the nest is generally scarce throughout the breeding season (Figure 2 and Supplementary Figure S1). This suggests that the female carries out almost all the incubation and egg turning as well as other tasks for chick-rearing. Moreover, in agreement with the reverse size dimorphism theory, the presence of the female in the nest would be favored to provide major protection to the nestlings due to its larger body size (Schoenjahn et al. 2020). Large raptors tend to take large prey, which cannot be swallowed by the nestlings and need to be processed by an adult (Newton 1979; Cramp and Simmons 1980; Sonerud et al. 2013). The larger time spent in the nest by females
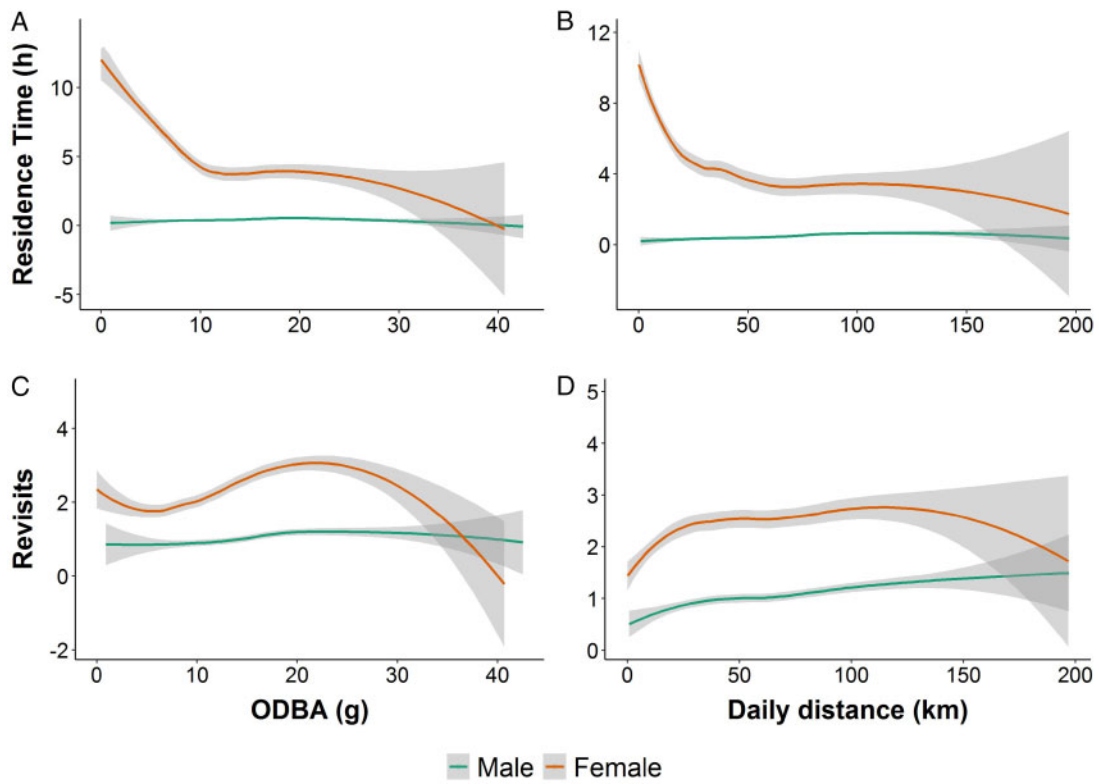
Figure 2. Sex differences in energy expenditure and ranging effort in relation to residence time and number of revisits to the nest. 95% confidence intervals are shown in gray.
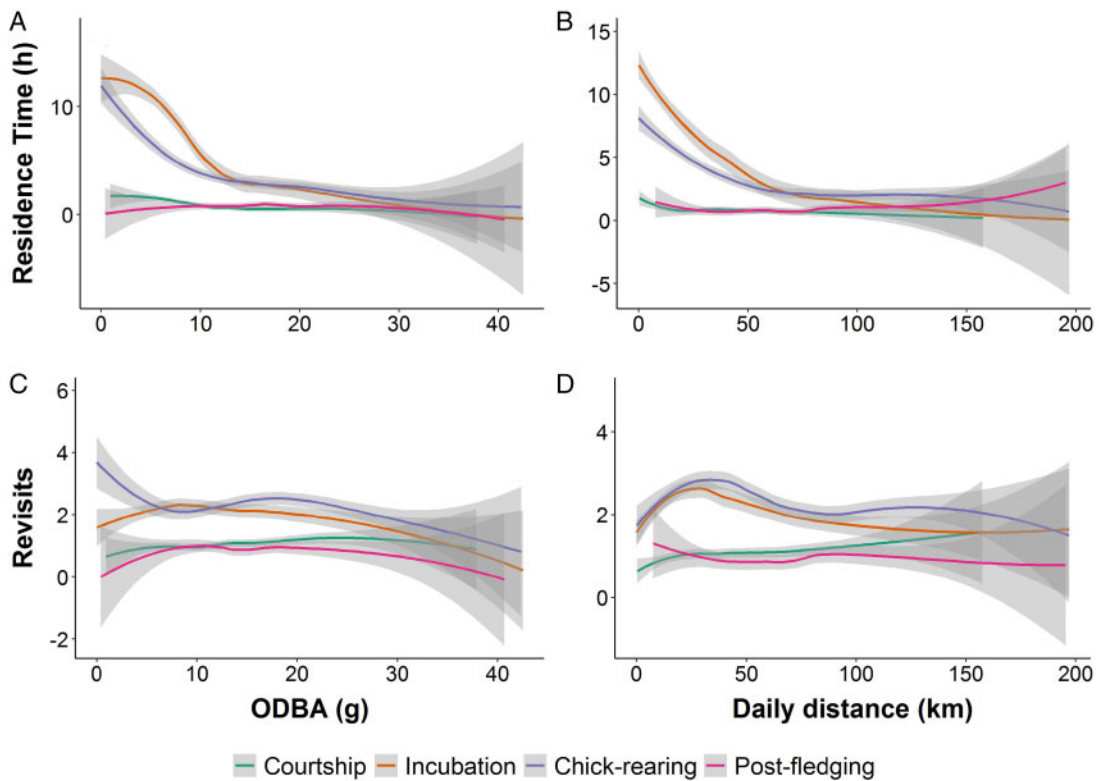

Figure 3. Differences in energy expenditure and ranging effort among different periods of the breeding season in relation to residence time and number of revisits to the nest. 95% confidence intervals are shown in gray.
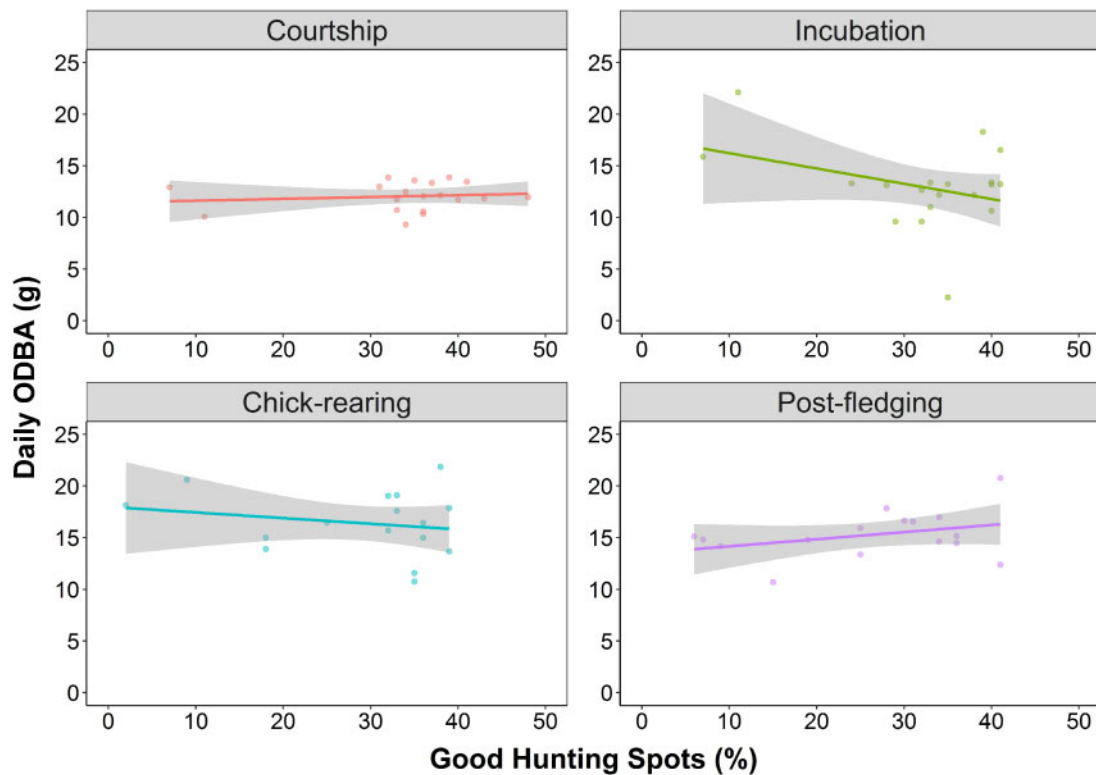
Figure 4. Daily ODBA of males in relation to prey detectability by period of the breeding season. 95% confidence intervals are shown in gray.

implies that this task is executed by them, even if the prey has been captured and delivered by the male (Sonerud et al. 2013, 2014). In the particular case of Bonelli's eagles, similar to other raptors, the male usually delivers the food to the female either in the nest or in its surroundings (Martínez et al. 2020). For example, the probability of prey being directly delivered by a male to 10-day-old nestlings has been reported as lower than 10% in Eurasian Kestrel *Falco tinnunculus* (Sonerud et al. 2013). As most of these events take place away from the nest or take place in very short time intervals (usually less than a minute), recursive analyses would not count them as visits by the male and would partially explain the difference in number of visits recorded in both sexes. If both parents hunt and feed the nestlings, we would expect a spatial–temporal conflict in feeding assistance as well as uncoupled chick-rearing activities (Sonerud et al. 2014). To avoid that, a division of tasks between sexes that prevent disengaged nest attendance and foraging activities would be expected (Sonerud et al. 2013, 2014). This seems to be the case in the Bonelli's eagle. Time spent on the nest decreased as the breeding season progressed (Figure 2). Our results show that the residence time was significantly lower during the later stage of the chick-rearing period as well as once chicks have fledged (Figure 3). During the first steps of the breeding season, the presence of an adult is necessary to protect both the eggs and chicks from low temperatures and potential predation by other birds (Margalida et al. 2007). Once the nestlings can thermoregulate and increase energy requirements, parents need to intensify hunting activity, and thereby females spend more time away from the nest assisting males, increasing their activity consequently (Figure 1). As for the residence time, the number of visits was significantly higher during incubation and chick-rearing periods, decreasing during the post-fledging period (Supplementary Figure S2). Overall, females were more active in visiting the nest than males even if the female remained

much more time on it than males. Visits can be related to food provisioning and maintenance tasks of the nest such as providing new material during the pre-laying period but also during incubation and chick-rearing. Bonelli's eagles build their nest mainly on cliffs and rarely on trees (Cramp and Simmons 1980). Nest structure can be damaged by the activities of chicks and adults and inclement weather conditions (Margalida et al. 2007) and such damage can cause chick mortality due to nest collapse.

As expected, energy expenditure showed strong differences between sexes (Figure 1). Interestingly, males spent much more energy on average than females throughout the breeding season (Figure 2) and this situation was recurrent along our dataset (Supplementary Figure S3). This supports the role specialization in parental tasks provided that ODBA and daily travel distance were negatively related to residence time and number of revisits (Table 3). Many observational studies of parental care focusing only on nest activities tend to underrate the activity of males. This bias increases in studies with limited sample size and where researchers' observations are limited to certain periods of time during the day (see e.g., Martínez et al. 2020). However, our study shows that males compensate for the short time spent in direct nest-attendance and chick-rearing activities by spending more time in hunting and ranging activities. Hence, the distance traveled, computed as daily travel distance, was higher (Figure 1 and Supplementary Figure S4). Moreover, the longer the traveled distance the higher the energy consumption (Figure 1). Increasing energy expenditure implies more area ranged which can be explained because males usually act as providers, hunting most of the time while females remain in the nest. Feeding the nestlings can be considered a demanding task that can result in a conflict between parents and offspring (Royle et al. 2012), due to an increase in the home-range and traveling costs (Sokolov et al. 2014). While some authors disagree with the assumption that parental care

requires a sustained high-intensity activity that could result in strong negative physiological consequences to the parents (Williams 2018), our results of daily ODBA (Figure 1 and Supplementary Figure S3) show a similar outcome to the generally predicted workload for altricial birds as discussed in Williams (2018).

Energy expenditure increased as the breeding season progressed being maximal during the chick-rearing period (Figure 1 and Supplementary Figure S3). During incubation, females decreased substantially their activity to remain in the nest, which was compensated with a stronger effort by males. During the chick-rearing period, females started to increase their activity in order to assist males with foraging activities. Conversely, both parents decreased energy expenditure during the post-fledging period, with female ODBA values higher on average than males. The latter decreased energy expenditure probably to recover from the intense effort spent during previous stages of the breeding cycle. Nevertheless, this outcome was not consistent in all territories (Supplementary Figure S1) suggesting that different individuals choose different strategies, maybe depending on the experience (although we did not find significant differences in age) or territory quality.

The increase of traveled distance was directly linked with an increase in the home range area. Raptors defend a well-established territory throughout the annual cycle, but ranging behavior depends on resource availability and they may need to change home range use in order to find prey (Martínez-Miranzo et al. 2016). This is particularly evident in our study area, densely covered by pine forests, particularly in the inner areas, where eagles have limited access to hunting habitats. Eagles ranged more distant as the breeding season advanced in order to find prey, particularly in low-quality territories where prey availability was low. In fact, our results revealed a correlation between energy expenditure and the percentage of favorable hunting spots in eagles' territories (Figure 4). This means that eagles lengthen their home range in order to find hunting spots where prey availability and prey detectability is easier. This result has a side effect for conservation, since an increase in home range as a consequence of limited prey availability or caused by human disturbance (Perona et al. 2019) could lead eagles to abandon protected areas to forage in areas where the risk of mortality is higher (Pérez-García et al. 2011), eventually increasing their energy expenditure.

In conclusion, this study exemplifies how biologging technologies, and particularly the incorporation of tri-axial accelerometry metrics such as ODBA, are an adequate and objective method to study parental care in raptors as well as to get deeper insight into breeding ecology of birds in general. Further studies incorporating transmitters' calibration measurements in order to correct energy expenditure metrics, as well as those considering species-specific and individual variation in flight types throughout the day, will provide further insight into the trade-offs in energy allocation during key phases of the life-cycle of organisms such as the one here exemplified (i.e., parental care during breeding). Finally, inasmuch as transmitters become miniaturized, future studies will address key questions in behavioral ecology with the full range of bird species, and not only the larger ones that can be currently tracked.

Authors' Contribution

A.M.P., O.E.-C., and P.L.-L. conceived the ideas, designed the methodology, and collected the data. A.M.P., O.E.-C., and J.M.E. analyzed the data. A.M.P. wrote the first draft and P.L.-L. wrote the final version of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

All data used in this study are publicly available upon request to data managers in the online data repository Movebank (www.movebank.org), project 'Bonelli's eagle University of Alicante Spain' (project ID = 58923588), and project 'Bonelli's eagle University of Valencia Spain' (project ID = 193515984).

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest

Authors declare that no conflict of interest exists.

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