Breeding behaviour and time-activity budgets of Bonelli's Eagles *Aquila fasciata*: marked sexual differences in parental activities

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ABSTRACT

Capsule: Differences in parental investment between sexes and stage of the breeding period were found in Bonelli's Eagles *Aquila fasciata*.

Aims: To describe the sexual differences in parental behaviour of Bonelli's Eagles and to assess the sex-specific pattern of variation in parental investment in relation to the breeding period.

Methods: Between 2006 and 2016, we monitored the parental behaviour of 11 pairs of Bonelli's Eagles during the incubation and chick-rearing periods in southeastern Spain. Observations were made using 20–60× telescopes from points overlooking the territory at a distance of about 500–800 m from the nest.

Results: Our results reveal a marked division in parental duties in Bonelli's Eagles. Females invested more effort in incubation, nest attendance, chick feeding and nest-building, while males contributed more to food provisioning. Nest attendance and feeding by females decreased with time, and both parents adjusted their provisioning effort in relation to nestling age. Most changeovers took place during the middle of the day, when male provisioning rates and temperatures reach their maximum.

Conclusion: Intersexual differences are discussed in the context of the prey capture difficulty hypothesis, which proposes that intra-pair prey differences, due to large sexual size dimorphism, should be particularly advantageous among raptors that pursue agile prey.

Parental care in a wide range of animals is defined as the set of activities that progenitors develop to ensure offspring viability, often at a cost to their own survival and reproduction (Royle *et al.* 2012). Previous studies have documented the prevalence of different modes of parental care in birds: the use of geothermal heat to incubate eggs, brood parasitism, male-only care, female-only care, biparental care and cooperative breeding (Cockburn 2006). Biparental care is very common in birds, where it occurs in over 90% of species (van Rooij & Griffith 2013) although the type of care provided by each sex may differ substantially (Webb *et al.* 2010).

In monogamous bird species, the parental roles of sexes are divided to cover specific activities. For instance, females contribute more to offspring care and males contribute more in territory defense (Clutton-Brock 1991). In altricial species, such as raptors, where the offspring are entirely dependent on the parents for food, care and defense at the nest, reproductive success is often limited by parental provisioning rates (Royle

et al. 2006), nest attendance (Evans & Stutchbury 2012) and different territory-defense behaviours (Kontiainen *et al.* 2009, Cain *et al.* 2015). However, parental investment involves energy expenditure by the breeders, which may have a negative effect on their fitness and future reproduction through trade-offs with survival (Nur 1988). Given that the future potential of each parent could be improved if the other partner contributed more to the total investment in the progeny, there is an interesting conflict between the sexes (Trivers 1972, Westneat *et al.* 1990, McNamara *et al.* 2003, Houston *et al.* 2005, Sonerud *et al.* 2014).

Raptors and owls are known for their asymmetric parental roles; females perform most or all of the incubation, brooding and feeding of the offspring, while males hunt and provide most of the prey (Byholm *et al.* 2011, Eldegard & Sonerud 2012). However, the evolution of these asymmetric parental sex roles is still poorly understood (Sonerud *et al.* 2014). Role differentiation during the breeding period has been related to the reversed sexual size

dimorphism (RSD) hypothesis (i.e. females have become larger to form a larger egg or to increase incubation efficiency, or males have become smaller for more efficient hunting or territory defense: Amadon (1975), Massemin *et al.* (2000)), although recent reviews on RSD do not favour this hypothesis as the likely cause of RSD in birds of prey (Krüger 2005). An alternative, the 'prey capture difficulty' hypothesis (Andersson & Norberg 1981, Margalida *et al.* 2007), suggests that predators of agile prey using structurally complex hunting habitats should face selection for small males to increase efficiency in catching such prey.

Bonelli's Eagle *Aquila fasciata*, a socially monogamous species, exhibits moderate reversed sexual dimorphism in comparison with other bird-eating raptors (Byholm *et al.* 2011, Zuberogoitia *et al.* 2013), as females are about 29.5% larger than males (García *et al.* 2013). Thus, we would expect a degree of asymmetric parental roles greater than that found in raptors with no or little reversed sexual dimorphism (e. g. vultures; see Margalida & Bertran 2000a), but not as marked as in species with stronger reversed sexual dimorphism such as species in the genus *Accipiter* (Byholm *et al.* 2011).

Little is known about parental care in Bonelli's Eagle. Previous studies have compiled some descriptive data, not quantitatively assessed, on parental activities (Blondel *et al.* 1969, Glutz *et al.* 1971, Arroyo *et al.* 1976, Pérez-Mellado *et al.* 1977, Real 1983). It has been suggested that parental care in this species exhibits a dichotomy in sex roles: female play the larger role during the incubation and chick-rearing periods, whereas the male is the main food provisioner during incubation and at least part of nesting period, but invests little effort in incubation, brooding and feeding (Cramp & Simmons 1980). Thus, this paper presents the first quantitative assessment of parental investment in Bonelli's Eagle. An understanding of parental behaviour in this species and other raptors is crucial for effective monitoring and, ultimately, for their conservation (Fernández-Bellón *et al.* 2017).

Our study focused on the parental investment and time budgets of a small population of Bonelli's Eagles (11 pairs) breeding in a semi-arid Mediterranean area of southeastern Spain. The aims of this paper are (1) to describe the sexual differences in parental behaviour of Bonelli's Eagles during the incubation and chick-rearing period; (2) to assess the sex-specific pattern of variation in parental investment in relation to the breeding period. We discuss our results in the context of the few studies carried out on this species, and other Mediterranean eagles (Margalida *et al.* 2007, Bassi *et al.* 2017), the RSD hypothesis and the prey capture difficulty hypothesis.

Methods

Study area

The study was conducted in the south and centre of the Murcia Region, southeastern Spain (37°48′N 1°22′W), a mountainous region with alternating dry riverbeds, wastelands, irrigated cultivated areas and urbanized areas in the foothills. The area has a semi-arid Mediterranean climate, with mean annual precipitation of less than 250 mm. Natural vegetation is concentrated on abrupt slopes and the bottom of the ravines, and is dominated by perennial grasses and xerophytic shrub communities, alternating with small patches of Aleppo pine forest.

Study species

The Bonelli's Eagle is a long-lived and territorial species that builds its nests on cliffs or, exceptionally, in trees (Cramp & Simmons 1980). It is characterized by an egg-laying date in mid-January, a modal clutch size of two eggs and a mature reproduction age of 3.5 years (Cramp & Simmons 1980). In Western Europe, the Bonelli's Eagle diet is based principally on the European Rabbit *Oryctolagus cuniculus* complemented by pigeons (*Columba* spp.), Red-legged Partridges *Alectoris rufa* and other birds (Moleón *et al.* 2009).

Nowadays, Bonelli's Eagle is considered to be 'endangered' in Spain according to International Union for the Conservation of Nature (IUCN) categories (Real 2004) and as 'least concern' worldwide (BirdLife International 2016). The estimated population in Europe ranges from 1100 to 1200 breeding pairs (BirdLife International 2015) but the stronghold of the Bonelli's Eagle European population is the Iberian Peninsula, with 733–768 breeding pairs (Del Moral 2006). The European population has experienced a decline in the past few decades, mainly due to (1) negative demographic balance caused by an increase in non-natural mortality (casualties from power lines and direct persecution) and a decrease in productivity due to the decline in the European Rabbit (Real *et al.* 2001, Moleón *et al.* 2012) and (2) habitat loss in the breeding and foraging areas caused by human disturbance and, conversely, land abandonment affecting prey availability (Ontiveros *et al.* 2004, 2005).

Field methods

Intensive monitoring of 11 breeding pairs was carried out during the period 2006–16. Each pair was monitored only during one reproductive event. In

total, 1726 hours of monitoring was spread over 160 days. The observations were performed weekly from sunrise to sunset. The monitoring of pairs began between January and February of each year, coinciding with egg-laying and incubation, and ended when the eaglets fledged (May–June). During the incubation period, we performed 624 hours of observation spread over 64 days (mean ± sd = 9.75 ± 1.19 hours of observation per pair, range: 6.5–13.0 hours), whereas for the chick-rearing period 1102 hours was spread over 96 days (mean ± sd = 11.48 ± 2.08 hours of observation per pair, range: 5.5–14.5 hours). The mean (±sd) altitude of Bonelli's Eagle nests monitored in this study was 384.5 ± 133.8 m above sea level ($n = 11$; range 150–550 m).

Given that the Bonelli's Eagle has undergone a dramatic decline in recent decades and is now listed as endangered in Europe (BirdLife International 2015), carrying out behavioural studies on the species necessarily implies the adoption of precautions to avoid disturbing the breeding birds. Therefore, observations were made using 20–60× telescopes from vantage points which allowed for a good view of the nest (500–800 m). These distances did not appear to alarm the birds or alter their behaviour (González et al. 2006, Martínez et al. 2019).

Sex was determined by direct observation based on the sexual dimorphism exhibited by the species – males have smaller wingspan and paler plumage than females, which tended to be larger, darker and with a greater contrast between ventral and dorsal feathers (García et al. 2013, Forsman 2016). The age of the birds was determined according to the characteristics of their plumage (immature, subadult and adult; Vincent-Martin & Ponchon 2013, Forsman 2016). The pairs in our study displayed adult plumage, except in two territories where the females exhibited a subadult plumage classed as 'young adult', indicating they were four years old (Forsman 2016).

To analyse the contribution of the two sexes to parental tasks during the breeding season, we examined the following activities: (1) incubation and changeovers; (2) nest attendance, (3) nestling feeding duration; (4) provision of material to the nest during the incubation and chick-rearing periods and (5) provision of food during the incubation and chick-rearing periods. Incubation was defined as the period between laying and hatching of the first egg (incubation lasts from 39 to 41 days; Arroyo et al. 1995) and was subdivided into 6 week-long periods. In this context, we first estimated the incubation effort (in minutes) as a percentage of the time each sex spent incubating at the nest with respect to the total hours of

observation per day. The chick-rearing period was defined as the period between hatching of the first egg and fledging of the last eaglet (fledging period 60–65 days; Cramp & Simmons 1980) and was subdivided into 9 week-long periods. Thus, secondly we recorded: (1) nest attendance (in minutes) as a percentage of the time each sex invested in nestling brooding with respect to the total hours of observation per day; (2) the duration of feeding events (in minutes) as a percentage of the time each sex spent feeding the nestlings with respect to the total hours of observation per day and (3) frequencies of visits by each sex per day to the nest and their purpose, including changeovers and the provision of nest material and food.

Data analysis

To analyse the contribution of each sex to parental investment and to quantify the sex-specific involvement in parental care and nesting activities during incubation and chick-rearing periods, we ran generalized linear mixed models (GLMM) fitted with the Laplace approximation (Bolker et al. 2009). Six behavioural parameters were considered as response variables: incubation, nest attendance and nestling feeding duration under Gaussian distribution, and provision of food, provision of nest material and changeovers under Poisson distribution (log-link function). Sex (male and female) and week (number of weeks from the incubation onset to the hatching date and to the first fly of the nestlings) and their interaction were considered as predictive variables. To account for possible effects of correlation factors in the data, territory identity was included as a random factor in all cases. All analyses were performed using the software R 3.6.0 (R Development Core Team 2019) and the packages piecewiseSEM (Lefcheck et al. 2018), lme4 (Bates et al. 2019), car (Fox et al. 2019) and nlme (Pinheiro et al. 2019).

Results

Females invested significantly more effort than males in incubation, the provision of nest material during incubation and chick-rearing, and nestling attendance and feeding, whereas males invested most of their parental effort in provisioning the females and nestlings (Tables 1 and 2).

Incubation, nest attendance and feeding

The contribution of females to incubation did not decline as the incubation phase progressed (Figure 1,

Table 1. Percentage of time spent (in hours) by Bonelli's Eagles in incubation, nest attendance, feeding, provisions of nest material and food per day at their nests in the incubation and chick-rearing periods.

Period	Activity	Sex	% Time (mean)	Items delivered per day (mean)	sd	Min	Max
Incubation	Egg incubation	Males	7.45		7.31	0.00	29.44
		Females	82.42		12.49	46.08	100.0
Incubation	Provision of nest material	Males		0.29	1.04	0	7
		Females		0.92	1.19	0	5
Incubation	Prey deliveries at nest	Males		0.45	0.66	0	2
		Females		0.00	0.00	0	0
Chick-rearing	Nest attendance	Males	1.29		3.38	0.00	21.26
		Females	33.48		28.54	0.00	98.97
Chick-rearing	Feeding	Males	0.21		0.88	0.00	5.55
		Females	6.09		4.33	0.00	21.30
Chick-rearing	Provision of nest material	Males		0.44	1.21	0	9
		Females		2.59	3.44	0	15
Chick-rearing	Prey deliveries at nest	Males		1.53	1.06	0	5
		Females		0.61	0.77	0	4

Table 2. Results of GLMM for incubation, nest attendance and feeding (in hours). Significant values are highlighted in bold type. Reference value for sex is male (1) and female (2).

	Values	Estimate	se	t-value	P
Incubation	Intercept	7.555	2.930	2.578	
	Factor (Sex)2	76.105	4.144	18.362	**<0.001**
	Week	−0.029	0.769	−0.038	0.719
	Factor (Sex)2: Week	−0.332	1.087	−0.306	0.759
Nest attendance	Intercept	6.928	5.995	1.156	
	Factor (Sex)2	119.179	8.175	14.577	**<0.001**
	Week	−0.522	0.514	−1.014	**<0.001**
	Factor(Sex)2: Week	−7.930	0.726	−10.921	**<0.001**
Feeding	Intercept	0.058	1.322	0.044	
	Factor (Sex)2	12.305	1.834	6.707	**<0.001**
	Week	0.013	0.115	0.120	**<0.001**
	Factor (Sex)2: Week	−0.586	0.162	−3.597	**<0.001**
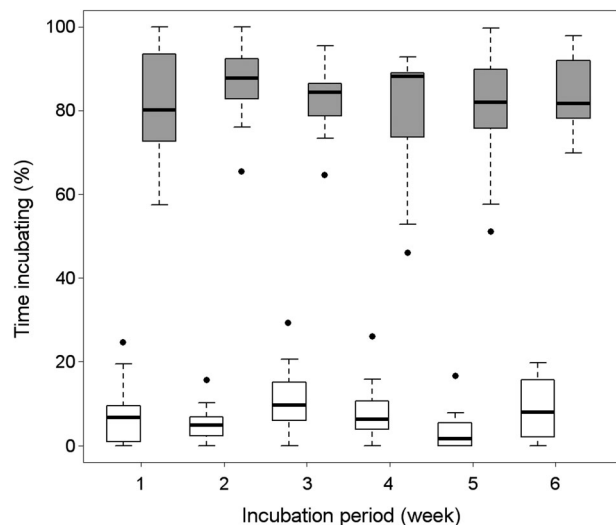
Figure 1. Tukey box plot for incubation contribution by male (white) and female (grey) Bonelli's Eagles. The line within the box represents the median, the horizontal lines are the first and third quartiles (50% of observations fall between the two, i.e. in the box). Vertical lines depict intervals including other data up to 1.5 times the interquartile distance.

Table 2) and males contributed with short periods (mean ± sd = 43.78 ± 43.54 min, range = 0–165) while females fed or rested. Time spent in nest attendance was also higher for females than males and declined as the chick-rearing period progressed, falling during the last period, i.e. pre-fledging (Figure 2(a)), when parents did not attend the eaglets in the nest.

Overall, we observed 87 changeovers during incubation (1.34 changeovers/day of observation, range: 0–4). The changeover rate was constant throughout the incubation period (Table 3). Most changeovers took place during the middle of the day (Figure 3).

During the chick-rearing period, the time invested in nestling feeding differed between the sexes, as females spent much more time than their partners in feeding eaglets. The time that females devoted to feeding decreased significantly after the fourteenth week (Table 2, Figure 2(b)).

Food provisioning

During incubation, we observed 29 provisions of food. All cases were prey items provided by males to females. Males invested significantly more effort in delivering prey items to the nest (71.36% of the 206 food deliveries observed in the chick-rearing period). This effort did not significantly vary with time (Table 3) and both sexes provided more food between the eleventh and thirteenth week (Figure 2(c)).

Bringing of nest material

Females contributed most of the nest material delivery activity during incubation (78 events; Table 1) and, although males also contributed to this task during the chick-rearing period, their investment was significantly lower than that of females (292 events; Table 3, Figure 4).
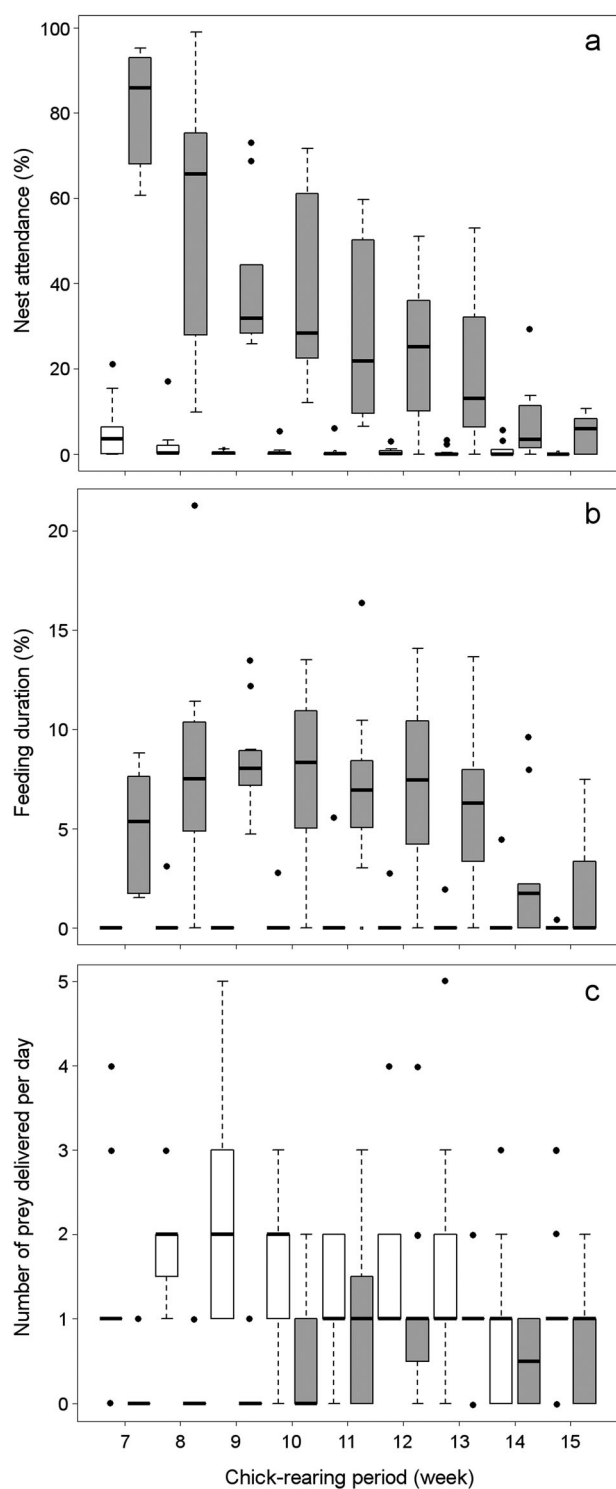
Figure 2. Tukey box plot for (a) nest attendance, (b) feeding and (c) provision of food at the nest throughout the chick-rearing period after the first egg has hatched by male (white) and female (grey) Bonelli's Eagles. The line within the box represents the median, the horizontal lines are the first and third quartiles (50% of observations fall between the two, i.e. in the box). Vertical lines depict intervals including other data up to 1.5 times the interquartile distance.

Table 3. Results of GLMM for provision of food and nest material, and changeovers (items per day). Significant values are highlighted in bold. Reference value for sex is male (1) and female (2).

|	Values	Estimate	se	z-value	P
Food provisioning	Intercept	0.942	0.361	2.611	**<0.01**
	Factor (Sex)	−3.561	0.760	−4.684	**<0.001**
	Week	−0.049	0.032	−1.498	0.134
	Factor (Sex)2: Week	0.232	0.063	3.665	**<0.001**
Provision of nest material	Intercept	−1.400	0.768	−1.822	0.068
	Factor (Sex)2	2.196	0.724	3.032	**<0.01**
	Week	0.005	0.059	0.094	0.924
	Factor (Sex)2: Week	−0.040	0.064	−0.630	0.528
Changeovers	Intercept	0.097	0.274	0.354	0.723
	Week	0.040	0.064	0.636	0.525
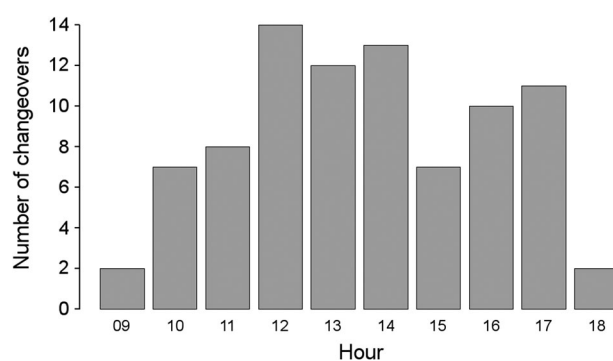
Figure 3. Pattern of changeovers by Bonelli's Eagle in relation to the time of the day.

Discussion

Avian incubation is energetically demanding and, within species with biparental incubation, the contribution of each sex can vary widely (Klimczuk et al. 2015, Zuberogoitia et al. 2018). Indeed, our findings pointed to intersexual differences in parental behaviour during incubation, a task primarily carried out by females with males temporarily relieving them (Newton 1978, Deeming 2002), and their effort did not change as the incubation period progressed. In Bonelli's Eagles, the regular presence of at least one of the parents at the nest is necessary to protect the clutch from extremes of temperature (AlRashidi et al. 2010, Deeming & Reynolds 2015) and potential predators (Ontiveros 2016). Although the contribution of males was modest, as mentioned above, it was greater than that documented by other authors for the same species (Arroyo et al. 1976, Pérez-Mellado et al. 1977, Real 1983). A possible explanation could be the limited number of hours dedicated to observing one pair in
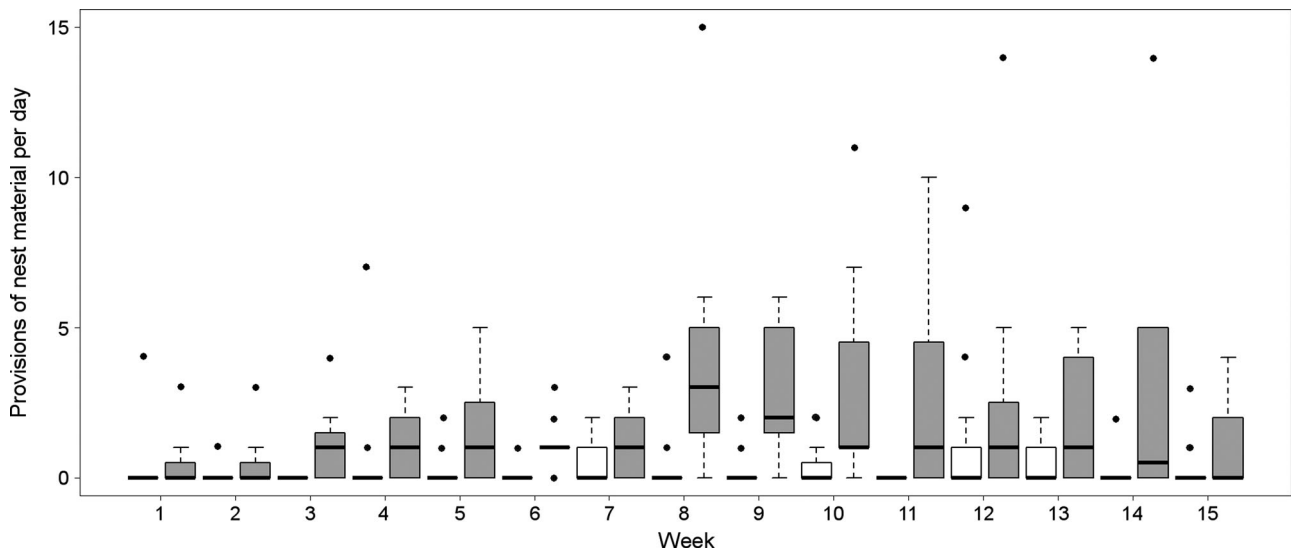
Figure 4. Tukey box plot for provision of nest material throughout incubation and chick-rearing by male (white) and female (grey) Bonelli's Eagles. The line within the box represents the median, the horizontal lines are the first and third quartiles (50% of observations fall between the two, i.e. in the box). Vertical lines depict intervals including other data up to 1.5 times the interquartile distance.

previous studies. On the other hand, the contribution of Bonelli's Eagle males to the incubation task was similar and lower than that recorded for other eagles, such as the Spanish Imperial Eagle *Aquila adalberti* (Margalida *et al.* 2007) and the Golden Eagle *Aquila chrysaetos* (Collopy 1984, Bassi *et al.* 2017), respectively. In contrast, our findings show that female Bonelli's Eagles accounted for most of the incubation time, a similar pattern to that reported in this species and other eagles in the Mediterranean region (Cramp & Simmons 1980, Margalida *et al.* 2007, Bassi *et al.* 2017).

Incubation behaviour precludes foraging, so energy constraints may be significant (Drent *et al.* 1985, Reid *et al.* 2002, Margalida *et al.* 2006). In birds, females must compensate their energy needs required for incubation with the thermal needs for embryo development (Bulla *et al.* 2015a), and these opposing demands limit both the proportion of time the female incubates and the time spent searching for food (Bambini *et al.* 2019). According to Matysioková & Remeš (2014), males can contribute directly and indirectly to the resolution of this conflict of females in two ways: (1) sharing incubation with the females and (2) feeding the incubating females. During incubation, changeovers are necessary to share breeding costs (Marasco & Spencer 2015) and, as a common trait of biparental incubation, could allow females to have enough time to recover their energy reserves, which have been consumed in their previous incubation session (Bulla *et al.* 2015b). The pattern of changeovers was similar to those observed in other cliff-nesting

raptors (Margalida & Bertran 2000a, Bassi *et al.* 2017), where changeovers mostly took place in the central hours of the day (Figure 3). Thus, Bonelli's Eagle females were more often off-nest during the warmer period of the day (Bulla *et al.* 2014), when foraging conditions were presumably better for mostly food transfers carried out by males during incubation (51.72%, *n* = 29). The contribution of prey to the nest fell exclusively to males during incubation. In all prey transfers, the females relieved from 'nest duty' moved to nearby perches, where they consumed the prey while the males incubated. Male provisioning of incubating females can have important consequences for the pair bond maintenance, mate-guarding and greater incubation efficiency (Stein *et al.* 2010, Zuberogoitia *et al.* 2018). In addition, incubation feeding can increase nest attentiveness by reducing the amount of time the female spends foraging off the nest (Jawor & Breitwisch 2006, Evans & Stutchbury 2012, Matysioková & Remeš 2014), reducing the risk for developing embryos (Olson *et al.* 2006) and as a result, favouring greater hatching success (Stein *et al.* 2010). Therefore, male help is indispensable for increasing nest attentiveness in incubating females, either in the form of incubation feeding or the direct incubation of eggs (Matysioková & Remeš 2014, Zuberogoitia *et al.* 2018).

Both sexes participated in the task of repairing and rebuilding the nest with fresh and dry plant material during the incubation and chick-rearing periods, although the contribution of the females to this task

was significantly greater than that of the males. The structure of the nest in Bonelli's Eagles is damaged by the regular activity of adults and chicks in the nest, and the intake of prey and the progressive accumulation of remains promote parasite activity in the nests (Margalida & Bertran 2000b, Ontiveros et al. 2008). Our model showed that the contribution of the female in providing nest material (dry and fresh branches) was significantly greater as the reproductive period progressed, reaching its maximum during the first part of the growth period of the chicks. This pattern would respond to the need to increase the stability of the structure and the amount of green plant material (*Retama sphaerocarpa*, *Ephedra fragilis*, *Olea europaea*, *Stipa tenacissima* and principally *Pinus halepensis*) in the nests to reduce a load of ectoparasites (Protocalliphora fly larvae) during chick growth. Previous studies have documented that the supply of fresh plant material to the nest fulfils these functions, as well as that of regulating the temperature of the nest (Wimberger 1984, Margalida et al. 2007, Gwinner et al. 2018); all factors which could determine greater reproductive success in the Bonelli's Eagle (Ontiveros et al. 2008).

During the period of chick growth, nest attention tasks, feeding and the contribution of prey to the nest, were not shared equally among the parents, similar to observations made in other raptor species (Margalida et al. 2007, Keeley & Bechard 2017). Females contributed significantly more than males to nest attention, while males participated sparingly in the care of the chicks, leaving their contribution to brief stays in the nest to cover and protect young chicks with their body (<10–12 days) and the regular contribution of prey to females and chicks. For many raptor species, the males provide little help with brooding but deliver most of the food for the young (Newton 1978, Collopy 1984, Holthuijzen 1990, Good et al. 2001, Meyer et al. 2004, Margalida et al. 2007, Bassi et al. 2017). In contrast, the females remained for long periods in the nest for the first two weeks after hatching (with chicks 1–2 weeks of age), but nest maintenance decreased significantly as the growth period of chicks progressed (Katzenberger et al. 2015, Keeley & Bechard 2017, Bassi et al. 2017). During the first days of the breeding period, when chicks become more vulnerable to weather conditions and predators (Margalida et al. 2007, Katzenberger et al. 2015, Keeley & Bechard 2017), females are completely dependent on males, who hunt and provide food for females and chicks (Katzenberger et al. 2015). The progressive decrease in nest maintenance by females from week 8 on (Figure 2 (a)) could be a response to the need to devote more

effort in the search for prey to meet the increase in energy requirements of the chicks as the breeding period progresses (Margalida et al. 2007, Bader & Bednarz 2011). From 50 to 56 days (weeks 14–15) onwards the parents' investment in nest maintenance was minimal, which is probably related to the proximity of the start date of the first flights of the chicks out of the nest between 60 and 65 days (Cramp & Simmons 1980). On the other hand, unlike other Mediterranean eagles, in which both parents feed their chicks (Margalida et al. 2007), the contribution of the male Bonelli's Eagles to this task was anecdotal, with this parental activity falling almost exclusively on females. In this context, our model showed that the time spent on feeding decreased as the growth period of chicks progressed, with a further decline in this task after the tenth week (chicks of 22–28 days) and minimal investment in the two weeks prior to the first flights of the chicks out of the nest (Figure 2(b)). These findings are similar to those available for Spanish Imperial Eagles and Golden Eagles (Margalida et al. 2007, Bassi et al. 2017).

The task of providing prey to the nest fell mostly on males. Their contribution was significantly higher as the breeding period progressed, peaking when the chicks were between 8 and 21 days old (weeks 8–9; Figure 2(c)). The contribution of females to this task was sporadic during the first three weeks after hatching, but increased significantly after the fourth week of the chick growth period (chicks more than 22 days old; Figure 2(c)). With this strategy both parents adjusted the effort to provide food according to the age of the chicks: their contribution was maximum during the mid-part of the chick-rearing period (chicks between 36 and 49 days) and decreased significantly in the two weeks before fledging (Figure 2(c)). This pattern may be due to two factors: (1) the eaglets' greater energetic requirements (Margalida et al. 2007) and (2) the peak in prey demand, which is likely to occur in the middle stages of brood development when growth rates are highest, decreasing slightly when broods are close to fledging (Newton 1979, Steen et al. 2012).

In the context of the RSD hypothesis, the fact that Bonelli's Eagle exhibits a moderate degree of RSD (García et al. 2013) means that a less marked division of parental role than that found in our study might be expected. Therefore, our results do not support the RSD hypothesis and are more similar to those found in raptors species with a higher degree of RSD whose diet is based on birds (Simmons 2000, Byholm et al. 2011). Since pigeons, Red-legged Partridges, corvids and other medium-sized birds are agile prey and difficult to

catch, but constitute the bulk of the diet of Bonelli's Eagle (Moleón *et al.* 2009), we suggest that the RSD of the species could be better explained by the prey capture difficulty hypothesis (Andersson & Norberg 1981, Margalida *et al.* 2007) than by the division of parental roles during the breeding period (Miranda *et al.* 2018). This hypothesis postulates that if predators pursue types of prey that move rapidly in hunting habitats with structural complexity, the selection of small males could be favoured (Krüger 2005, Sonerud *et al.* 2014, Pérez-Camacho *et al.* 2018), so they would be more efficient in catching such prey (Penteriani *et al.* 2013, Pérez-Camacho *et al.* 2015).

Our research represents an important contribution to the knowledge of parental investment in Bonelli's Eagle. Nevertheless, these results should be considered as preliminary since future studies with larger sample sizes and carried out in different landscapes and climatic conditions could, potentially, provide different results. In conclusion, this study shows marked intersexual differences in parental activities: females contributed significantly more than males in all parental activities except for the provision of prey. Consequently, sex and phase of the reproductive period are profiled as two reliable predictors of parental investment in Bonelli's Eagle. In the context of the RSD, our results could be better explained by the prey capture difficulty hypothesis than by the division of parental roles during reproduction. Future studies will evaluate the relevance of spatial facets of the niche (hunting habitat and territoriality) and diet (size and agility of prey) in the evolution of the RSD of this and other raptors showing moderate RSD.

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