Nest-Building Effort is Not An Indicator of Male Quality In Bonelli's Eagles, *Aquila fasciata*

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Abstract

Raptors often use a variety of materials to build their nests (natural, such as branches, but also non-natural objects), presumably due to their insulating properties, their suitability to advertise occupancy of the nest, and to decrease pathogen and parasite loads. The amount of branches used in a nest is an indicator of parental quality and is often associated with increased breeding success. However, in raptors where both sexes collaborate in nest construction, it is unclear whether the effort expended by males (taking the amount of material carried to the nest as the potential predictor) could constitute an honest signal of parental quality to female conspecifics. We examined data on sex, type of material brought to the nest, breeding experience, timing, and nest-building investment prior to egg-laying from 32 identifiable Bonelli's Eagles (*Aquila fasciata*) during the pre-laying period to investigate the relative contribution of the sexes to the amount of nest material gathered. We asked: (1) whether the nest-building investment of males could provide information to the females about their quality; and (2) whether the amount of material delivered to the nest by the male was related to breeding success. Despite the considerable investment of males in nest-building during the pre-laying period, our results indicate that this effort is not a consistent indicator of male quality to the female.

Therefore, male nest-building behaviour and investment by Bonelli's Eagles cannot be considered as an extended expression of their phenotype (an extended phenotypic signal). Nest-building behaviour by males in the early and late stages of nest-building, and the fact that males were not significantly more active builders, are discussed in the contexts of signaling nest occupancy to conspecifics and competitors, the decrease of parasite loads, and the strengthening of the pair-bond during the pre-laying period.

Introduction

Many animals use a wide variety of materials, designs, nest-site, and building techniques to build nests for shelter and reproduction[1,2,3]. Nests are essential structures for reproduction in some mammals and the majority of birds, and provide shelter and protection from inclement weather and predators for the eggs and nestlings[4,5]. Unlike animals that do not build their own nests, instead using the abandoned nests of heterospecifics to lay eggs and rear their young[6,7], many species expend considerable time and energy in the construction of one or multiple elaborate nests for breeding[8,9], with varying degrees of differential parental investment (i.e., exclusively maternal, paternal, or biparental; see[10]. Although there is currently no consensus on the adaptive significance of building multiple nests and its effects on breeding success[11], one of the hypotheses that has attracted more interest among researchers has been that they act to attract mates[12,13,14,15,16]. This hypothesis postulates that individuals could signal their current status, or the quality of their territory, through the construction of multiple nests [17,18,19]. In addition, in those species where the elaboration of the nest falls to both sexes, it could be a sexually selective behaviour that allows each sex to collect reliable information on the quality of its mate[20].

Avian nests are often concealed and camouflaged[2], but many species build prominent nests or use conspicuous materials for nest ornamentation[21]. Previous studies have suggested that birds and mammals select materials for nest-building based on their thermal or structural properties[22], which provide important benefits for the eggs and young[23,24]. For example, the use of feathers, fresh fragments of aromatic plants, or even cigarette butts as nest materials can play a key role reducing the adverse effects of pathogenic bacteria and parasites on eggshells[25] and nestlings[26,27], so improving the growth and condition of chicks at fledging[28] to increase parental breeding success[29,30]. These direct benefits alone often make it beneficial to choose mates most able to build well-constructed nests[31,32,4].

At the same time, the type of nest material can provide indirect benefits for builder birds. For example, during bird courtship displays, the degree of nest decoration and the speed and/or efficiency of gathering and transporting nest material may have additional or complementary functions, such as signaling: the extended phenotype of mate quality [33,34,35]; genetic quality[14]; nest-site occupancy; social status to potential intruders[21]; breeding experience[36,37] and the willingness to attract partners and to invest in reproduction[20,38]. The nest-building experience of a mate may be an important factor influencing how and where nests are built in order to improve breeding success, because their previous experience enables them to optimize the nest characteristics to their particular requirements, or possibly because experience is a surrogate of quality[39]. Previous experience can influence decisions relating to the choice of nest-material[36,40]. In addition, experience in nest-building plays an important role in decision making in future building endeavors, because a bird will have had practice in how to use different materials from its environment to build a nest or to increase the speed of construction[41]. Therefore, if we assume that nest-building ability is not wholly genetically determined [42,37], older and more experienced males could gather more nest-building material than younger, less experienced males which would construct simpler nests than older birds. This behaviour could encourage females mated to more active males to make greater parental investments compared to females mated to less active males.

Previous research has shown that male displays of nest-building ability act as inter-sexual signals to attract females, mainly by the addition of green materials, flowers, feathers, and even stones to the nest[17,43,30]. Males contribute to nest-building in many different avian species. Because nest-building is a costly activity in terms of both time and energy, and has fitness consequences, it would pay females to encourage male nest-building behaviour[5]. In this way, the number and size of items gathered for a nest could provide females with information on male condition or willingness to invest in reproduction[20]. To date, two hypotheses have been postulated to explain why females increase their parental effort when caring for the offspring of attractive males: (1) the partner-compensation hypothesis (PCH) postulates that females mated to attractive males elevate their own level of care to achieve increased reproductive success[44,45] and (2) the differential allocation hypothesis (DAH) postulates that females mated to more attractive males are willing to contribute greater levels of parental investment compared with females mated to less attractive males[46,33].

While investigations into extended phenotypic signals have been principally carried out on a variety of passerine species[47], this topic has not yet been explored in other avian groups, such as raptors. Previous studies documenting the supply of nest-material to cliff nests by several raptor species have focused on: the functional aspects of decreasing ectoparasite loads in nests[29,48]; indicators of nest-site selection criteria[49] social dominance; territory quality; means of signaling nest occupancy[21]; and indicators of the evolutionary load of past tree-nesting behaviour[50]. Although the parental behaviour of both sexes of Bonelli's Eagle (*Aquila fasciata*) during breeding has been recently studied[51], the role of nest-building behaviour has been generally poorly explored in raptors. Bonelli's Eagles build multiple large nests which they use alternately between years[29]. Bonelli's Eagle nests consist of a large basal structure of hard materials (sticks) and a nest cup lined with the green branches of aromatic trees and shrubs, and other materials such as fresh and dead grasses[52]. Both sexes build the nests throughout the 3–4 month period before egg-laying, although females may build while males gather nest-material[52]. This raises the possibility that nest-building *per se* can be used as a signal of male quality by females, if male nest-building behaviour and stick supply are consistent traits of a given male. An experimental approach is essential to disentangle whether stick supply to the nest serves as a signal or is an inherent indicator of mate quality. Our research is also of wider interest, because studies on the functionality of nest-building behaviour in biparental species are relatively uncommon compared to those on species where nest-building falls exclusively on either males or females[47].

The objectives of our study were: (1) to describe the nest-building behaviour of Bonelli's Eagles during the pre-laying period; (2) to assess a possible relationship between a male's nest-building effort and his experience (quality); and (3) to investigate a possible relationship between male traits and reproductive success in this species. We hypothesized that male investment in nest-building (taken as the number of branches carried to the nest) could act as an honest signal informing female conspecifics of the parental quality of their mates. If this were the case, females would benefit from choosing mates with good nest-building abilities. We therefore predicted correlations between males which made a high contribution to nest-building and their experience and increased fecundity.

Material And Methods

The species

Our model species, the Bonelli's Eagle, is a large-sized eagle which inhabits mountainous areas across the Palearctic, Indo-Malayan and, marginally, the Afro-tropical regions[53]. It is a long-lived, sexually dimorphic species, and is monogamous and territorial. It builds its own nests using materials gathered by both sexes before egg-laying[54]. Bonelli's Eagles build large, open, perennial nests mainly on cliffs and sometimes in trees[55], with platforms composed of tree and shrub sticks and branches that can be reused for several years, or even decades, as new materials are added every breeding season[29,54]. The existence of alternative nests is often associated with competitive exclusion and ectoparasite deterrence[56].

Their clutch size ranges from one to three (less than 1% of clutches having three eggs[57]). Their diet is generalist, based principally on the European Wild Rabbit (*Oryctolagus cuniculus*) complemented with medium-sized birds such as pigeons (*Columba* spp., Red-legged Partridges (*Alectoris rufa*) and corvids, as well as Ocellated Lizards (*Timon lepidus*)[54]. Regarding its reproductive biology, there is detailed information on the copulatory behaviour of territorial pairs at nest-sites prior to egg-laying[58], and the parental investment of both sexes during breeding[51]. This last study revealed 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 the provision of food.

Bonelli's Eagle is considered to be a flagship conservation species[59,60]. It typically inhabits semiarid and arid landscapes with sparse woodland, and is declining in numbers and range throughout the Mediterranean region. In Spain, which holds about 80% of the European breeding population, its numbers have been in decline since the early 1980s[61] and it is nowadays classified there as Endangered according to the IUCN Red List[62] and as of Least Concern worldwide[63]. The estimated European population ranges from 1,100–1,200 breeding pairs[64], with strongholds in the Iberian Peninsula of 711–745 breeding pairs[65].

The Study Area

Our study was carried out in a large area in the Murcia and Almería provinces, southeastern Spain (37º 59 ´ N, 1º 29´ W). The climate is typically Mediterranean, with mean annual rainfall ranging from 200–400 mm. The vegetation consists of scrubland with small patches of Aleppo Pine (*Pinus halepensis*), interspersed with non-irrigated and irrigated crops in the foothills, plains, and valleys (for more details see[58]).

Field Work

Our study population consisted of 16 Bonelli's Eagle pairs, nesting on cliffs at altitudes of up to 900 m. During 2010–2016, pairs were monitored from October to one week after egg-laying (between January–February). Pairs were observed once a week. On each observation day, we recorded the nest construction activity during the daylight hours from 06:00–18:00, the shortest observation period being 4 hours (interrupted due to adverse weather) and the longest being 12 hours. In total, 4,131 hours of nest monitoring were carried out using 20–60× telescopes, from points overlooking the territories at a distance of about 600–800 m from the nest. This distance did not appear to alarm the birds or affect their behaviour[58].

Following[66], nest visits were recorded during each observation period, regardless of whether males or females arrived with or without nest-material. At each nest visit, we recorded for each sex: (1) the type of material brought to the nest, whether fresh material (mainly green branches used for building the nest

structure and decoration, and lining the interior of the nest) or hard material (mainly withered branches and sticks used for building the nest structure); (2) the date and time of material supply to the nest; (3) the number of branches or sticks supplied/individual/day (nest-building effort); (4) the return of a previously identified individual to a specific nest; and (5) the sex of an individual.

Individual Identification

Capture-recapture methods involving identification based on photographs is recognized as a reliable method to monitor wildlife populations and assess ecological aspects such as population size and structure, survival, site-fidelity, occupancy, lifetime reproductive success and other variables[67,68,69,70,71]. Following previous studies on vultures[72] and raptors, including Bonelli´s Eagle[67,73,74], we took photographs of individual Bonelli's Eagles using camera traps placed on rock perches[74] and a digital camera mounted on a digiscoping adaptor attached to a spotting scope in a hide[72]. Territorial Bonelli's Eagles could be recognized from these photographs of perched individuals (Fig. 1) using variations in plumage colour (cheek, general colour of the breast and neck), and especially in the pattern of pigmentation (throat, and particularly the leg-feathers; see[75]. The ability to recognize individuals on this basis persisted from year to year[74]. Using these photographs, we could use individual identifications to assess male behavior as a possible surrogate for the degree of their investment in nest-building. We identified all of the individuals from 16 breeding attempts by 16 pairs (one breeding attempt per pair). In total, 32 individuals (16 females and 16 males) were identified with certainty during the study period.

For analytical purposes, the monitoring season was divided into 16 weeks during the pre-laying period (weeks 1–16, counting backwards from the moment of egg-laying). Results were then aggregated into four, month-long time-periods (a discrete quantitative variable, range: 1–4; October–January) to assess the monthly distribution of the types of material gathered for nest-building (hard or fresh) by males and females. The pre-laying period spanned the time between the last pre-dispersal flights of the young Bonelli's Eagles of the previous clutch[76,77], the beginning of courtship and nest-building in mid-October, up to the moment of egg-laying[58]. We determined the onset of laying by direct observation (i.e., onset of incubation and changeovers). Laying dates were recorded with a maximum error of ± 1 day.

Using our individual identifications, the experience of each known individual in a territory was determined by the number of consecutive years spent in the same territory, provided that the individual concerned was seen to be installed in the territory when first observed[69]. In addition, the monitored territories were visited at least four times post-laying to record the number of fledglings and to gather data on productivity. Nestlings observed at ≥ 50 days old were assumed to have fledged successfully[78,79].

Data analysis

All statistical analyses were performed with R 4.0.4[80]. We tested six hypotheses in total. For hypotheses 1–5, we first applied a generalized linear mixed model (GLMM) to assess the factors determining the

amount of material (number of branches) carried to the nest by parents and to explore whether the investment of males in nest-building could act as an honest signal informing female conspecifics on their parental quality, fighting ability and social dominance. To test these hypotheses, we quantified the daily rates of nest-material supply as the response variable under a negative binomial distribution. We included a bird's sex and experience and the week as possible predictors of nest-building investment. Hypothesis 1 postulated that males invested more effort than females in nest-building. We then explored the possible differences between the sexes in relation to the type of material delivered to the nest (hard or fresh). Hypotheses 2 and 3 postulated that males gather higher proportions of either hard or fresh materials, respectively, than females. Hypothesis 4 postulated that male nest-building investment depends on male experience, expressed as the number of years that a male has bred in the same territory (as the predictive variable). Hypothesis 5 postulated that the addition of material by males increased throughout the pre-laying period. To account for possible correlation effects between the factors in the data, male/female identity was included as a random factor.

Hypothesis 6

explored whether male nest-building investment affected breeding productivity, because females may increase their parental effort by preferentially investing in the offspring of attractive males. We performed a second GLMM using the breeding quality index (hereafter, BQI) as a response factor under a normal distribution. BQI was defined as an individual's ability to produce offspring compared with the average success of others in the same year. BQI was calculated as the difference between the number of eaglets fledged for a particular individual/territory and the average number of eaglets in the monitored territories in the same year[81]. In this analysis, male nest-building investment was considered as a predictive factor determining productivity. Male identity was again considered as a random factor. Mean values are reported with their confidence intervals. Statistical significance was set at $P < 0.05$.

Results

The materials used for nest construction comprised principally hard and fresh branches, principally of Aleppo Pine, with a small number of shrub species (Table 1). During the pre-laying period, males (mean: 2.00; 95% CI: 1.42–2.82) were more active than females (mean: 1.64; 95% CI: 1.17–2.30) in construction activity, although the difference was not significant (Table 2). The supply of material to the nest began 16 weeks prior to egg-laying. In both sexes, there were two peaks in construction activity: the first, between 112–78 days prior to egg-laying (October and early November); and the second, between 35 days prior to egg-laying and clutch completion (end December and January). In contrast, the supply of nest-material was very low between 77–36 days prior to egg-laying (Fig. 2).

Table 1
The nest-building investment by Bonelli's Eagles in 16 territories in southeastern Spain in terms of the type of material supplied to the nest per day. Mean, 95% CI, number, and percentages (in brackets) of sticks and branches of the different plant species (N = 778) of green (fresh) and non-green (hard) material, supplied by both sexes.

Plant species	Fresh material (%)	Hard material (%)
Pinus halepensis	303 (63.65)	3 (0.99)
Stipa tenacissima	9 (1.90)	6 (2.00)
Olea europaea	5 (1.05)	0
Anthyllis cytisoides	1 (0.21)	0
Ephedra fragilis	2 (0.42)	0
Pistacia lentiscus	32 (6.72)	0
Chamaerops humilis	1 (0.21)	10 (3.31)
Retama sphaerocarpa	29 (6.10)	1 (0.33)
Rosmarinus officinalis	1 (0.21)	0
Unidentified	93 (19.53)	282 (93.37)
Total items	476 (61.18)	302 (38.82)
Males investment (mean, 95% CI)	1.30 (0.96–1.65)	0.89 (0.65–1.13)
Females investment (mean, 95% CI)	1.13 (0.78–1.47)	0.65 (0.41–0.89)

Table 2
Results of generalized linear mixed models for testing the six hypotheses examined. The values of the z and t statistics are also shown. Mean values are shown with their 95% confidence intervals. SE (Standard Error), *P < 0.005

	Estimate	**SE**	***z* value**	***P***
Hypothesis 1				
Intercept	0.896	0.353	2.533	0.011
Sex	-0.200	0.216	-0.925	0.355
Hypothesis 2				
Intercept	-0.172	0.502	-0.344	0.731
Hard material	-0.193	0.300	-0.645	0.519
Hypothesis 3				
Intercept	0.314	0.416	0.756	0.450
Fresh material	-0.191	0.262	-0.729	0.466
Hypothesis 4				
Intercept	0.477	0.302	1.575	0.115
Male experience	0.035	0.031	1.121	0.262
Hypothesis 5				
Intercept	0.812	0.269	3.01	0.002
Week	0.010	0.030	0.33	0.741
	Estimate	**SE**	t-**value**	P
Hypothesis 6				
Intercept	1.500	0.323	4.642	0.000
Male nest-building investment	0.001	0.009	0.198	0.846

During the pre-laying period, the amount of hard and fresh material gathered showed a temporal variation in both males and females (Fig. 3a and b; Tables 2 and 3). The peak of supply of hard material took place between weeks 16–12 prior to egg-laying, while a greater amount of fresh material (green plants) was brought during the last five weeks prior to egg-laying. There were no inter-sexual differences concerning the amount of either type of material gathered: hard (males, mean: 0.69; 95% CI: 0.42–1.12 *vs* females, mean: 0.57; 95% CI: 0.37–0.88) and fresh (males, mean: 1.13; 95% CI: 0.77–1.65 *vs* females, mean: 0.93; 95% CI: 0.63–1.38).

Table 3
Mean and SD (in brackets) for the observed materials supplied to the nest by male and female Bonelli's Eagles, per month, throughout the pre-laying period (divided into 4-month intervals).

Material	Sex	October	November	December	January
Hard	Male	1.96 (3.22)	0.91 (2.13)	0.71 (1.56)	0.45 (0.87)
	Female	1.34 (1.84)	0.66 (1.44)	0.58 (1.24)	0.33 (0.75)
Fresh	Male	1.03 (1.95)	0.60 (1.81)	1.28 (2.91)	2.05 (2.60)
	Female	1.15 (3.34)	0.60 (1.46)	1.26 (2.77)	1.42 (2.00)

During the day, Bonelli's Eagles showed two peaks of material gathering: between 09:00–12:00 h; and later in the day (16:00 h). In addition, both sexes showed similar nest-building activity (Fig. 4).

The nest-building effort of males during pre-laying was not significantly related either to their level of breeding experience at the territory, or to the week (Table 2). In addition, there were no significant relationships between the amount of material carried to the nest by males and their reproductive performance (Table 2).

Discussion

Our observations showed that Bonelli's Eagles selected their nest-site and began bringing hard and fresh material up to four months prior to egg-laying[52]. The onset of eagle visits to the nest, in October, and the start of nest-building using larger quantities of fine and coarse dry branches, might be related to the need to create a larger nest structure, including size, thickness, mass, and cup volume, which can influence the nest's thermal properties[23,22]. This buffers the impact of adverse environmental conditions on the development of embryos and nestlings[82] and signals nest occupancy by increasing the visibility of the nest-site to conspecifics and competitors (e.g., Golden Eagles, *Aquila chrysaetos*), even at large distances[83,21].

Our results showed temporal changes in the types of material supplied to the nest: the supply of hard material occurred in the early visits to the nest and during the start of nest-building, whereas the supply of green material tended to increase as the laying date approached (Fig. 3a and b). Previous studies have shown that green material brought to the nest can regulate the nest temperature and may help to decrease ectoparasite and pathogen loads[84,85,50] and improve breeding success[29]. Although fresh nest-material was gathered from vegetation rich in resins, including nine plant species, the most abundant plant delivered to the nests was greenery from pines (Table 1). Pines are characterized by a high level of aromatic compounds, highly repellent to insects[29,28].

Previous studies have highlighted the important pair-bond existing between territorial Bonelli's Eagles throughout the year[86,87,88]. During the pre-laying period, while copulation activity occurred principally in

the evening, with a progressive increase from the afternoon onwards[58], both sexes showed the strongest nest-building activity during the morning, with a strong peak between 09:00–11:00 h, showing that birds worked together on nest construction activities (Fig. 4).

Behavioural studies exploring the function of nest-building behaviour in biparental species are scarce[47]. In raptors, both partners invest in nest construction[89,66,90]. Thus, if male investment in nest construction is a consistent trait of any particular male, it is likely that females will use male nest-building effort to assess male parental quality and that the amount of branches and sticks that males deliver to the nest would become a sexually selected trait[20,33]. Previous studies describing biparental care in Bonelli's Eagles have shown a sex-biased specialization in parental duties[51,91]. Females invested significantly more effort than males in gathering nest-material during the breeding season[51]. In contrast, our findings show that during the pre-laying period, the construction activities of males were important, and although the males provided slightly more material they were not more active builders than the females. In fact, our model does not demonstrate that sex is important in explaining the amount of material supplied to nests. Therefore, neither sex appears to use the nest-building process as a signal of their mate's quality. Our results, therefore, do not lend weight to Hypothesis 1. Neither were any inter-sexual differences observed with regard to the type of nest-material gathered (hard and fresh). This finding is consistent with the results of[66], who found that in Pyrenean Bearded Vultures (*Gypaetus barbatus*), there were no observed inter-sexual differences concerning the amount supplied of either of the two common nest-materials used (branches and wool). Therefore, our results do not support Hypotheses 2 or 3.

However, breeding experience could be a decisive factor determining the investment effort of males[83,92]. If the nest-building abilities of males are not wholly genetically determined, breeding experience could influence decisions relating to nest material choice[36,40] and the amount of material gathered for nest construction[37]. In this way, younger eagles, with less experience of nest construction, should supply lower amounts of sticks and branches than older, more experienced eagles[37]. However, our model did not demonstrate any importance of this factor in explaining the effort of nest-building by males, thus rejecting Hypothesis 4.

In some bird species where both partners put similar effort into nest construction, the pair may reduce their effort as the laying date approaches[93,94]. In other taxa, the parents carry material to the nest throughout the entire breeding season (until after the chicks fledge[9]). In Bearded Vultures, for example, males invest more effort in nest-building than females, showing a peak of construction activity between 4–2 weeks prior to egg-laying[66]. These studies showed a progressive increase in material delivered to the nest throughout the pre-laying period. However, our results indicated a bimodal response of males to nest-building (Figure 3a), rejecting Hypothesis 4. This pattern could be explained by the fulfilment of two adaptive functions: (1) signaling occupancy of the nest against conspecifics and competitors (e.g., Golden Eagles) at the beginning of courtship; and (2) accumulation of the maximum amount of green material as the laying date approaches, with the aim of reducing the parasite and pathogen loads in order to maximize the viability of the eggs and the chicks.

Previous researches have shown that males may signal their condition, health, or parental quality to mates by building large or elaborate nests or by intense nest-building activity[20,33,47]. At first glance, one might expect that male investment in nest-building could act as an honest signal informing females about their parental quality. Male nest-building behaviour could therefore be considered as a sexually selected trait: females might pair with males which are active builders, regardless of their construction ability (good or bad), and females would adjust their reproductive investment based on the nest-building investment exhibited by their mates. Nevertheless, our analysis did not find a relationship between male nest-building investment and consequent reproductive performance. In this respect, our results are not consistent with the DAH[33], thus rejecting our sixth hypothesis.

Conclusions

Our results indicate that male investment in nest-building does not appear to serve as a signal of male quality and, therefore, does not act as an honest signal to indicate their parental quality to their mates. Male nest-material provisioning rates therefore do not have a positive impact on reproductive success. However, given that nest-building imposes high costs in both time and energy[1], high levels of male nest-building could help females reduce their energy expenditure and help them to maintain optimal physical condition for reproduction[95]. This, in turn, supports the idea that a balanced distribution of nest-building activity, and of parental care in general, is beneficial to the breeding effort of a pair[93].

Declarations

Ethic statements

Bird-photographing procedures, camara trapping and monitoring of Bonelli´s Eagles were conducted under permits and following the protocols approved by the competent Regional Government of Region of Murcia (Resolución AUF/2020/0107). All the work was conducted in accordance with relevant national and international guidelines, and conforms to all legal requirements in compliance with the Ethical Principles in Animal Research.

Data availability

All data generated or analysed during this study are included in this published article (and its Supplementary Information files).

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Author contributions

J.E.M. conceived the idea of the research, conducted fieldwork, created the databases and performed the statistical analysis, edited tables and wrote the manuscript with significant contributions from I.Z. and A.M. J.F.C. performed the statistical analysis and edited figures and photos. All authors (I.Z., J.F.C., M.A. y A.M.) contributed to the literature review and strategic planning, reviewed manuscript drafts and gave final approval for publication.

Competing interests

The authors declare that no competing interests.

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Figures

Figure 1

An adult male photographed during the 2008 breeding season (a) and a different male at the same nest during the 2012 breeding season (b). In both cases, the nest was occupied by the same female. Note the differences in the pigmentation of the cheek, throat and leg-feathers (see coloration patterns in García et al., 2013).

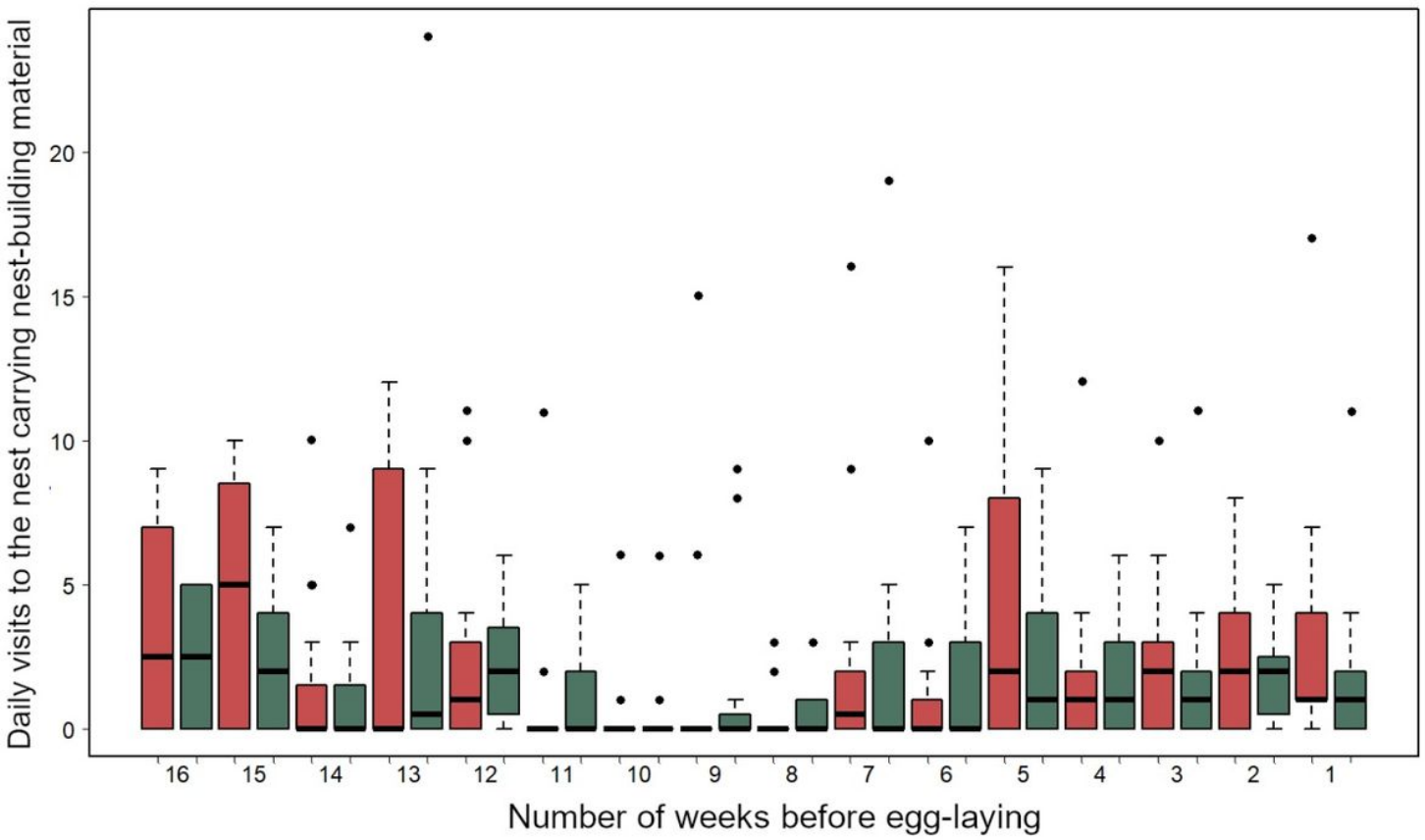

Figure 2

Tukey box plot for the provisioning of nest-building material during the pre-laying period by male (red) 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 the observations fall between the two, i.e., are in the box). Vertical lines depict intervals including other data up to 1.5 times the interquartile distance, and points represent outlying data.

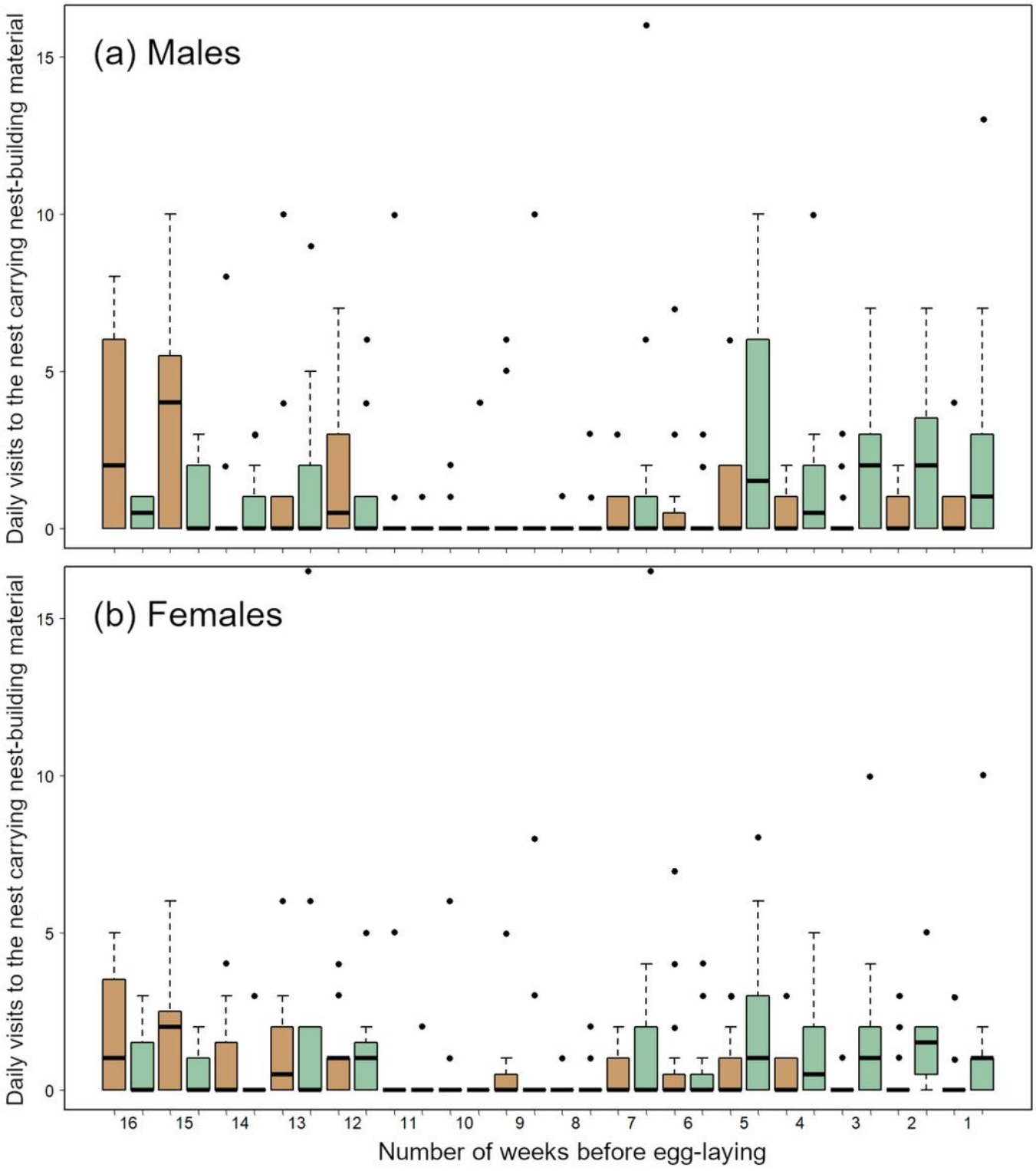

Figure 3

a, b. Tukey box plot for the provisioning by male Bonelli's Eagles of hard (brown) and fresh (green) nest-building material during the pre-laying period. The line within the box represents the median, the horizontal lines are the first and third quartiles (50% of the observations fall between the two, i.e., are in the box). Vertical lines depict intervals including other data up to 1.5 times the interquartile distance, and points represent outlying data.

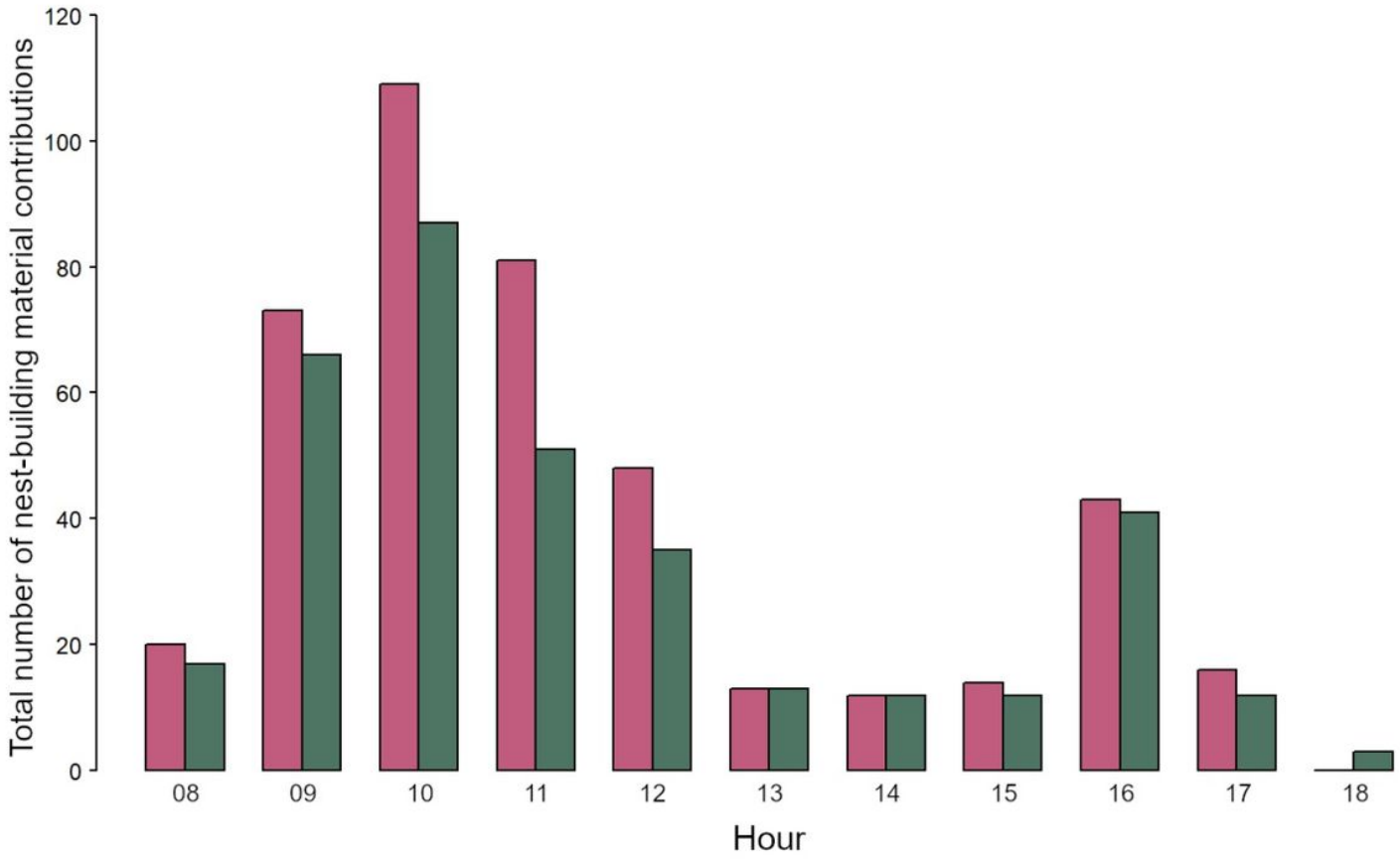

Figure 4

Hourly pattern of nest-building material supply to the nest by Bonelli's Eagles during the pre-laying period: males (violet) and females (grey).

Supplementary Files

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- DataMartinezetalSciRep.xlsx