Adult coloration of the Bearded Vulture (*Gypaetus barbatus*) in the Pyrenees: relation to sex, mating system and productivity

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Cosmetic coloration is not a common phenomenon among bird species. Adult Bearded Vultures *Gypaetus barbatus* typically show orange coloration in head, chest, belly and tarsus feathers that is the result of mud baths in ferruginous substrates. Several non-mutually exclusive visual signalling hypotheses can be proposed to explain this phenomenon. Coloration could be used to signal: (1) dominance towards conspecifics, with darker birds being dominant (status signalling hypothesis); (2) sex (gender signalling hypothesis) because females are usually more intensely coloured; (3) individual quality for mate choice (quality signalling hypothesis); or (4) different reproductive strategies between individuals (e.g. in polyandrous trios). Here we report results from systematic monitoring of breeding Bearded Vultures in the pre-laying period in the central and western Pyrenees (Spain and France) between 2016 and 2020, including 162 individuals from 70 reproductive units (48 pairs and 22 trios). We classified individuals as being white, pale, medium or dark, and analysed the relationship with sex, mating system (pair or trios) and average productivity across years. Our results showed that the most common form was medium (67%), then pale (22%), dark (9%) and white (2%) morphs. Overall, females were darker than males, but with a large overlap in coloration. In trios, dominant males were darker than subordinate males, although differences were not statistically significant. The mating system (pair or trio) did not influence female coloration. A multimodel comparison showed that the number of years of territory occupation, mating system and their combination (but not coloration) were the best predictors of average productivity. Our results do not support the gender signalling hypothesis. The reproductive strategy signalling hypothesis might be supported because beta males were, on average, paler than males in pairs, but this topic requires further investigations because our results were inconclusive. Finally, that females (thought to be dominant because of their slightly larger size) were on average darker than males agrees with the status signalling hypothesis, although an experimental approach would be needed to formally test this hypothesis.

Keywords: birds, cosmetics, evolutionary ecology, morphs, visual signalling.

Plumage coloration is known to play important roles in the ecology and behaviour of birds, performing functions as varied as feather protection, thermoregulation, concealment from predators and social recognition (Savalli 1995, Bortolotti 2006, Bostwick 2016). At the intraspecific level, individual variation in the degree of coloration is commonly used as a signal to conspecifics, with

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signallers conveying information about themselves – such as presence, individual identity, fighting ability, mating strategy and quality – to receivers (Rohwer 1975, Savalli 1995, Dale 2006).

Coloration is mostly produced through pigments (e.g. melanins and carotenoids) deposited during feather growth or by the structural arrangement of feather tissues (Bostwick 2016). Interestingly, a few species also acquire cosmetic colours by actively applying substances such as uropygial gland secretions, skin secretions, feather powder or soil particles to their plumage (Montgomerie 2006, Delhey et al. 2007). The functions of this behaviour have rarely been investigated and often lack direct supporting evidence. The main hypotheses include sexual signalling, e.g. in the Great White Pelican Pelecanus onocrotalus and the Greater Flamingo Phoenicopterus roseus (Stegmann 1956, Amat et al. 2011), and camouflage, as in the Rock Ptarmigan Lagopus mutus (Montgomerie et al. 2001).

The Bearded Vulture Gypaetus barbatus is an extremely specialized bone-eating raptor distributed throughout mountainous regions of Eurasia and Africa (del Hoyo et al. 1994). In adults, the coloration of the head, chest, belly and tarsus feathers can vary from pure white to deep orange, as a result of mud baths in ferruginous substrates where they acquire chromophoric elements (Berthold 1967, Brown & Bruton 1991, Frey & Roth-Callies 1994, Duchateau & Tellechea 2019). Various hypotheses have been proposed to explain this behaviour in the species, including concealment, feather protection against abrasion or ectoparasites (Brown & Bruton 1991), bacteria control on eggs, nestlings or the bird itself (Arlettaz et al. 2002, Tributsch 2016), and a visual signal towards conspecifics (Negro et al. 1999, 2002, Margalida et al. 2019). This last hypothesis remains promising because experimental studies have found no support for feather protective or antibacterial effects of iron oxides (Frey & Roth-Callies 1994, Margalida et al. 2019, Crespo-Ginés et al. 2021). Moreover, colouring behaviour in the species is mostly performed outside the breeding period (Duchateau & Tellechea 2019), a pattern little in agreement with a health function. It has been proposed that Bearded Vultures exhibiting a higher intensity in their coloration would be dominant individuals (Negro et al. 1999, 2002, Margalida et al. 2019). To support this assumption, females, which are generally slightly bigger than males (López-López et al. 2011), appear more coloured, as is also the case for alpha males in polyandrous trios of these vultures. To express a visual signal toward conspecifics, Bearded Vultures may have to stain their plumage with iron oxides, because carotenoid pigments are rare or absent in their bone-based diet (Negro et al. 1999). Visual status signalling is a widely studied and sometimes debated topic among ornithologists (Senar 1999, 2006, Santos et al. 2011, Sánchez-Tojar et al. 2018a). It allows assessment of a competitor's status (for food, territory or mate) without having to fight – thereby avoiding risky confrontations – even without seeing the individual interact with conspecifics (Rohwer, 1975, Senar, 2006). According to Zahavi and Zahavi (1997), any visual signal, to be honest and thus reliable for receivers, needs to be costly, that is to require a significant investment. Negro et al. (1999) and Margalida et al. (2019) suggest that the cost, in the case of Bearded Vultures, would be the extra time required and/or distance covered to reach adequate colouring places. Therefore, a dark-coloured individual would particularly signal to conspecifics its ability to find restricted resources.

Nevertheless, there are other non-mutually exclusive visual signalling hypotheses for this coloration. First, differences in coloration between Bearded Vultures could be involved in sex recognition, as some studies report that females tend to exhibit more orange coloration than males (Negro et al. 1999, Margalida et al. 2012, Sesé 2019). This could be supported by the fact that such gender signalling is mostly expected in species that are sexually monomorphic in appearance (Margalida & Bertrán, 2000, Dale 2006). Second, coloration intensity may signal individual quality (Wilson & Nussey 2010) in a context of intersexual selection (Andersson 1994, Dale 2006). Thereby, following this assumption, in a given sex more coloured Bearded Vultures would be better mates, preferred by their opposite-sex partners, and consequently their breeding performance would be higher than that of less coloured birds.

Coloration polymorphism within the same sex might also signal different reproductive strategies, where individuals adopt various tactics linked to their own genotype and phenotype to maximize their fitness (Gross 1996, Sternalski 2008). A classic example is found in the coloration patterns of the male Ruff Philomachus pugnax, which reflect three distinct strategies (Lank & Dale 2001,

Jukema & Piersma 2006). Exploring this hypothesis could be of particular interest in the case of the Bearded Vulture given that this species often exhibits cooperative breeding, mostly in the form of polyandrous trios (Heredia & Donázar 1990). In some exceptional cases, polygynous trios (Fasce & Fasce 2011, Gil *et al.* 2017) and even some quartets (Margalida *et al.* 1997, Gil *et al.* 2011) have also been reported. For example, in the southern central Pyrenees (Aragón region, Spain), 35% of the territories were occupied by trios in 2018 (Gil *et al.* 2019). Because these polyandrous trios are usually located in traditional breeding areas with higher food abundance (Heredia & Donázar 1990), it is thought that joining a trio may represent an opportunity for floating males to reach high-quality territories (Bertran *et al.* 2009). Previous observations indicate that in polyandrous trios the dominant males (hereafter alpha males) usually exhibit higher colour intensity than subordinate males (hereafter beta males; Negro *et al.* 1999), which seems consistent with the hypothesis of a discrete polymorphism signalling alternative strategies for the purpose of access to a territory and/or reproduction. Nonetheless, our current knowledge about coloration patterns in the Bearded Vulture and their relationship with sex, mating system and breeding performance remains poorly understood.

The main goals of the present study are: (1) to quantify and report the intensity of coloration of breeding Bearded Vultures in the Pyrenees according to sex and mating system (pairs or trios); (2) to analyse the relationship between mates' coloration and the degree of dominance (i.e. whether females exhibit a higher degree of coloration than males and, additionally, whether alpha males show a higher degree of coloration than beta males in trios); and (3) to analyse the relationship between individual coloration and the quality of their breeding territory, with number of years of occupation and average productivity used as proxies of territory quality. Consequently, if the status signalling hypothesis were true, we would expect that dominant individuals would show a higher degree of coloration than subordinate ones (i.e. females vs. males and alpha males vs. beta males) and that, for a given sex, darker individuals would be able to monopolize the oldest and/or most productive territories which would, as a consequence, increase their fitness. If the gender signalling hypothesis were true, we would expect that

females would be, on average, more coloured than their mates both in pairs and in polyandrous trios, with a clear bimodal pattern of individual's colour morph variability (Dale 2006). Furthermore, if quality signalling were the main function of cosmetic coloration in the species, we would expect coloration differences to occur mainly within, and not between, sexes. Lastly, if the reproductive strategy signalling hypothesis were true, we would expect colour intensity differences between alpha and beta males in trios. These four hypotheses are not mutually exclusive.

METHODS

The study area included the administrative regions of Aragón (Spain), Pyrénées-Atlantiques and Hautes-Pyrénées (France), in the central-western area of the Pyrenean mountain range (Fig. 1). To avoid confusion between pairs and trios, we referred to occupied territories as reproductive units (RUs). RUs were observed with 30–60× field spotting telescopes during the pre-laying period (i.e. November to February, with dates ranging from 21 October to 27 February) from 2016 to 2020. This period coincides with the onset of breeding activities, including nest construction, copulation and egg-laying (Bertran & Margalida 1999, Gil *et al.* 2019) and immediately follows that of the maximum activity of plumage baths (Duchateau & Tellechea 2019). We favoured morning and late afternoon 2- to 4-h observation sessions close to known nest-sites, where the birds usually roost together for the night and frequently copulate (Bertran & Margalida 1999, Margalida *et al.* 2012, S. Duchateau, G. Chéliz, J. A. Gil & P. López-López, pers. obs.).

Individuals' sex was determined by observing the position during copulation, or using the wing marks of some individuals ($n = 12$) that were previously captured and sexed using molecular methods (García *et al.* 2009) as part of the species monitoring programme in the central Pyrenees (Gil *et al.* 2019). Body size was not used for sex differentiation, because although females are on average bigger than males (López-López *et al.* 2011), there is an overlap and in many cases this is not a reliable criterion in the field (S. Duchateau, G. Chéliz, J. A. Gil & P. López-López, pers. obs.). All trios included in the study were assumed to be polyandrous (one female paired with two males) according to observed positions
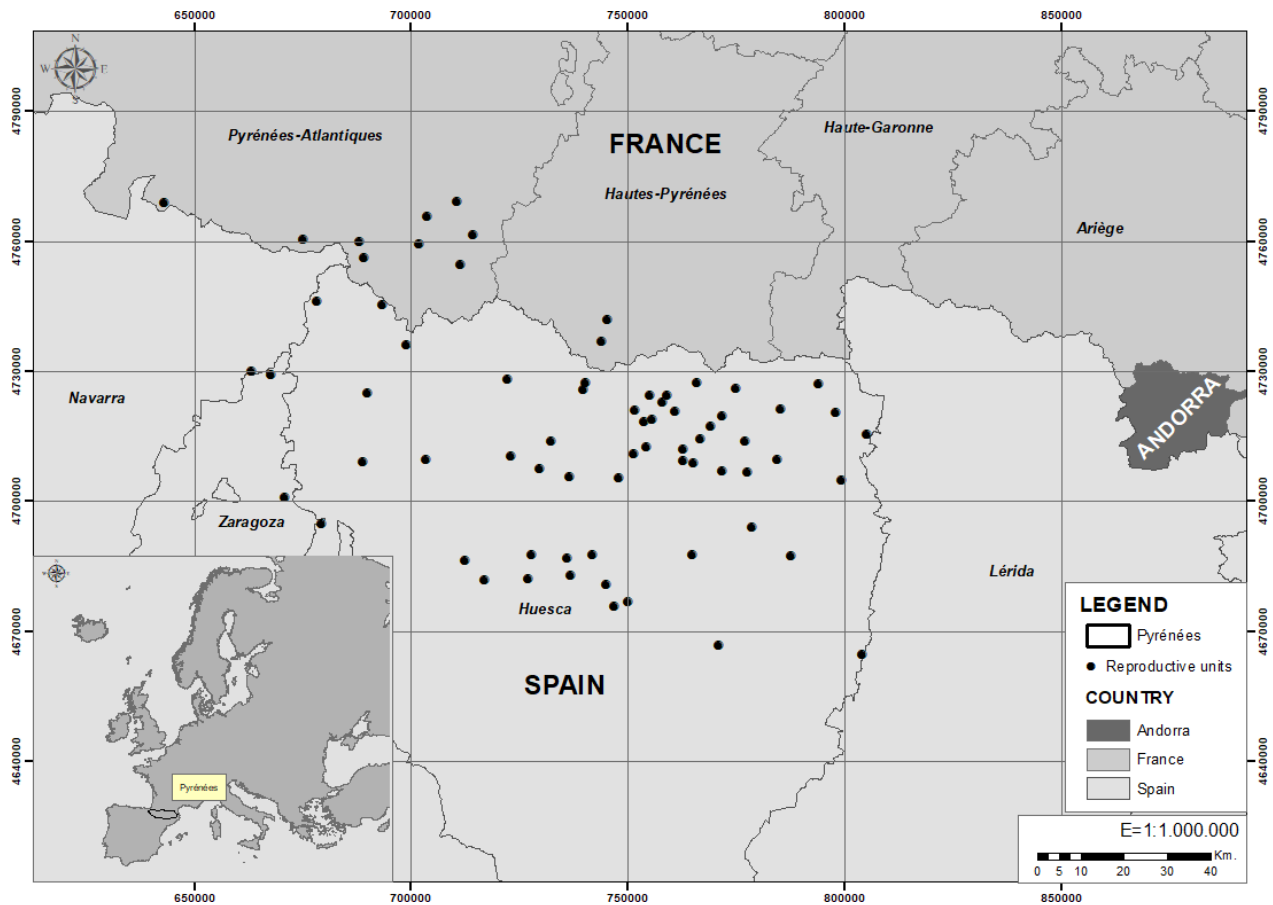
Figure 1. Study area and Bearded Vulture reproductive units included in this study (black circles).

during copulations and to wing marks of some known-sex individuals. Moreover, polygynous trios may present behavioural specificities that were never observed in the RUs taken into account, such as laying in separate nests and lack of aggressive interactions between same-sex individuals (Fasce & Fasce 2011). Because homosexual or even reverse mountings may occur within polyandrous trios (Bertran & Margalida 2003, 2006), we attempted to systematically observe several copulations for each RU in order to reduce this possible bias.

Within trios, the dominant (alpha) males were differentiated from the subordinate (beta) males using behavioural characteristics. Permanent and closer proximity to the female, mate monopolization during copulations, displacement of the other male and threatening postures were attributed to alpha males, whereas attempts to interrupt

copulations were assigned to beta males (Bertran *et al.* 2009). This categorization (alpha vs. beta) was especially carefully done when the two males showed differences in the intensity of body coloration.

Each individual was classified according to the following four types of coloration (or morphs *sensu lato*; Fig. 2): (1) white morph: bird of pure white coloration, even on the front of the neck (e.g. an individual that has never taken ferruginous baths, or that has not taken a bath in many months); (2) pale morph: a whitish bird, but which shows signs of having bathed in ferruginous waters, as it has orange feathers, with the front part of the neck being more orange than the rest of the body; (3) medium morph: a bird that presents no intense orange coloration, with the front part of the neck darker than the back of the head; (4) dark morph: bird of uniformly intense orange colour, even on

the back of the head. Because colour perception differs between birds and humans (Tanaka 2015), numerous studies use spectrophotometers to quantify the colour parameters (i.e. hue, saturation, brightness) and evaluate their variation among individuals. Nevertheless, studies based on human vision usually produce reliable results as well (Andersson & Prager 2006, De Sousa Trigo 2014). In our case, we used coloration scales based on human perception because of the impossibility of capturing and handling birds.

Most of the observation bouts were carried out by the same experienced observer (70.3% of the cases, $n = 159$), complemented by data collected by two other observers. Between-observer variation in morph classification was not calibrated but was subsequently proved to be of no statistical significance ($\chi^2 = 4.290$, df = 4, $P = 0.368$). Likewise, the degree of cloud cover was taken into account during observations in case the luminosity could have any effect on the perception of the degree of coloration of the individuals. There was no statistically significant differences in bird morph classification between sunny ($n = 309$) and cloudy ($n = 28$) conditions ($\chi^2 = 4.718$, df = 2, $P = 0.094$).

To avoid pseudoreplication, a single data point per individual and RU obtained during the first complete and highest quality observation session of each RU was included in the analyses (i.e. observation of the two or three individuals together, with priority given to the observations of copulations and of marked individuals of known sex). Consequently, unless it changed RU during the course of the study, a given individual could not appear more than once in our dataset. We

hypothesized that such changes are infrequent in a long-lived and essentially monogamous species, where pair composition is believed to remain stable across years (Terrasse, 2004, Arroyo *et al.* 2021, S. Duchateau, G. Chéliz, J. A. Gil & P. López-López, pers. obs.). If it exists, this bias might not have involved more than a couple of individuals in our dataset given the relatively short duration of the study. In order to maximize the sample size of trios, only the data of the trio have been kept in the cases of RUs that shifted from a pair to a trio or from a trio to a pair during the study ($n = 9$).

Colour differences were evaluated by comparing the distribution of colour morphs according to sex and mating system. Univariate non-parametric statistical tests (i.e. chi-square, binomial test, Fisher's exact test, Wilcoxon test, Mann–Whitney and Kruskal–Wallis tests) were used to assess differences in coloration and their relationship with sex and mating system. As a result of the small sample size (fewer than five cases), individuals of the white morph were excluded from the univariate analyses and were pooled with pale morphs in multivariate analyses.

Average productivity (fledged chicks/year) was calculated for each RU across the period 2008–2019 (origin of the data: Gobierno de Aragón/Fundación para la Conservación del Quebrantahuesos; annual synthesis of M. Razin/Ligue pour la Protection des Oiseaux). RUs with less than 6 years of breeding information ($n = 8$) were excluded from the analyses in order to retain only reliable productivity means, which also included those territories established in the latest 5 years ($n = 4$) because inexperienced breeders usually show a lower

Figure 2. Different degrees of coloration of Bearded Vultures in the Pyrenees (Spain and France). From left to right, white, pale, medium and dark morphs, respectively (see Methods). Pictures: J. A. Sesé.

productivity (Margalida et al. 2003, Arroyo et al. 2021). Likewise, breeding seasons without clear information of territory occupation and/or in which clutches were extracted for captive breeding and reintroduction projects (Ferrer et al. 2014, Gil et al. 2019) were also excluded from the analyses. To test the relationship between breeding performance and degree of coloration, average productivity values were analysed grouping by morph of each sex and mating system, both together and separately. In addition, we fitted general linear models with all potential combinations of predictive variables (i.e. female and dominant male morph, mating system and number of years of territory occupation) to test their effects on average productivity. In the case of trios, only the colour of the alpha male was considered in general linear models. Models were adjusted with a Gaussian function and identity link, and were compared and ranked according to Akaike information criterion (AIC) values (Burnham et al. 2011). All computations were done in R version 3.6.3. (R Core Team 2020) and statistical significance was set at $P < 0.05$.

RESULTS

We performed a total of 159 observation bouts involving 70 RUs (48 pairs and 22 trios), which represents 40.7% of the current Pyrenean Bearded Vulture population (Gil et al. 2019). Overall, 162 individuals (92 males and 70 females) were classified in the RUs (Table 1). We were able to assign each individual to a given morph.

Proportion of colour morphs

The majority of Pyrenean Bearded Vultures were classified as the medium colour morph, representing 67.3% of individuals, followed by the pale morph with 22.2% of individuals and dark morph with 8.6%. The white morph (1.8%) was observed in only three individuals, two females and one male (Table 1). Colour morph distribution showed a large overlap between sexes (Fig. 3). The most common morph combination was medium–medium both in pairs (69.4%, $n = 25$) and in trios (54.5%, $n = 12$), followed by the pale–pale combination, both in pairs (11.1%, $n = 4$) and in trios (13.6%, $n = 3$).

Using all data, but excluding white individuals, the proportions of each morph showed statistically significant differences between the sexes ($\chi^2 = 9.554$, df = 2, $P = 0.008$), with more males belonging to the pale morph, and more females belonging to the dark morph. These differences in morph proportions were also observed when data of trios were examined separately (pooled alpha and beta males; Fisher's exact test: $P = 0.027$), but not in the case of pairs (Fisher's exact test: $P = 0.213$).

Comparing the proportion of males and females with the theoretical sex ratio (50:50) within each type of coloration, statistically significant differences were observed for the pale morph using all data, with fewer females than expected (binomial test: $P = 0.004$). On the other hand, no differences were observed between sexes with respect to the theoretical proportion for either the medium morph (binomial test: $P = 0.338$) or the dark morph (binomial test: $P = 0.180$).

Table 1. Colour morphs of adult breeding Bearded Vultures in the central-western Pyrenees according to sex and mating system.

Morph	All data			Pairs		Trios		
	Females	Males	All	Females	Males	Females	Alpha males	Beta males
White	2 (3%)	1 (1%)	3 (2%)	2 (4%)	0 (0%)	0 (0%)	0 (0%)	1 (4.5%)
Pale	9 (13%)	27 (29%)	36 (22%)	6 (13%)	9 (19%)	3 (14%)	7 (32%)	11 (50%)
Medium	49 (70%)	60 (65%)	109 (67%)	35 (73%)	38 (79%)	14 (64%)	13 (59%)	9 (41%)
Dark	10 (14%)	4 (4%)	14 (9%)	5 (10%)	1 (2%)	5 (23%)	2 (9%)	1 (4.5%)
Total	70	92	162	48	48	22	22	22

The percentage over total values in columns are shown in parentheses.
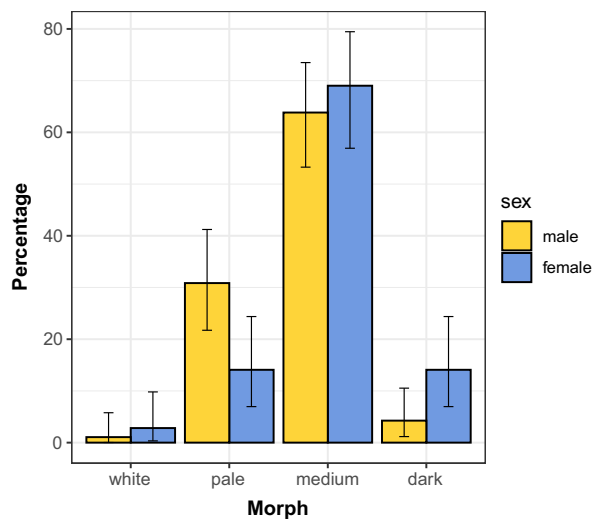
Figure 3. Colour morph proportions (%) of adult breeding Bearded Vultures in the Pyrenees according to sex. Error bars show 95% confidence intervals.
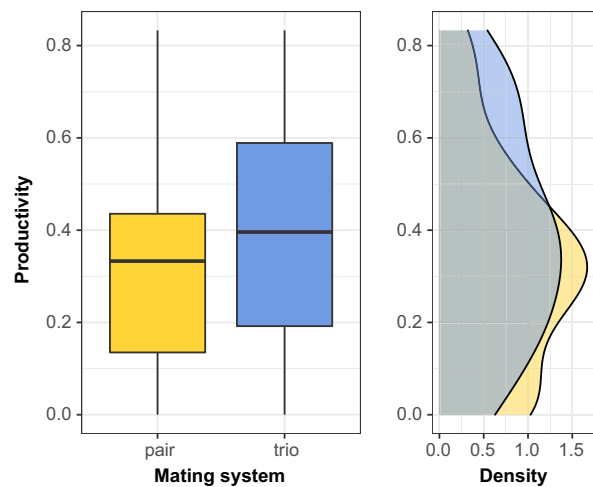

Figure 4. Productivity of Bearded Vultures recorded in 59 territories in the Pyrenees (Spain and France) in relation to the mating system (pairs, $n = 36$ vs. trios, $n = 23$) (left). The density plot (right) shows the high degree of overlap among mating systems. Interestingly, whereas the productivity of trios is quite symmetrical, the productivity of pairs seems negatively skewed. Lines show the median, and 25% and 75% quartiles. The boxplot length shows the interquartile range (IQR). The upper and lower whiskers extend from the hinge to the largest and to the smallest value no further than 1.5 * IQR from the hinge, respectively.

Within pairs, females showed a darker coloration than males in 31.2% of cases ($n = 15$), the same morph as males in 60.4% of cases ($n = 29$), and were lighter than males in only 8.3% of cases ($n = 4$; binomial test: $P < 0.001$). Within trios, the proportion of morphs did not statistically differ between alpha and beta males (Fisher's exact test: $P = 0.442$). Alpha males showed a darker coloration than beta males in 27.3% of cases ($n = 6$), the same morph in 68.2% of cases ($n = 15$), and were lighter than the beta males in only 4.5% of cases ($n = 1$; binomial test: $P = 0.001$).

No statistically significant differences were observed in the proportion of morphs for females in pairs ($n = 48$) and trios ($n = 22$; Fisher's exact test: $P = 0.454$). By contrast, the proportion of morphs differed statistically between males in pairs ($n = 48$) and in trios (alpha and beta pooled together, $n = 43$), because the latter tended to be of lower intensity of coloration (Fisher's exact test: $P = 0.013$). The difference was more evident in the beta males (Fisher's exact test for males in pairs vs. beta males in trios: $P = 0.006$), but not between males in pairs and alpha males in trios (Fisher's exact test: $P = 0.105$).

Productivity

No statistically significant differences in productivity were observed in relation to the mating system (means of 0.31 chicks/year for pairs and 0.39 chicks/year for trios; Wilcoxon test: $W = 320.5$, $P = 0.227$) (Fig. 4). Likewise, no statistically significant differences in average productivity were observed in relation to females' morph (Kruskal–Wallis test, $H = 0.913$, df = 2, $P = 0.633$) and males' morph of pairs or alpha male in trios (Kruskal–Wallis test, $H = 1.604$, df = 2, $P = 0.448$). There were no statistically significant differences in average productivity in relation to the colour morph combination of the individuals in the RU (females' morph in pairs: Kruskal–Wallis, $H = 0.736$, df = 2, $P = 0.692$; males' morph in pairs: Kruskal–Wallis, $H = 0.419$, df = 2, $P = 0.811$; females' morph in trios: Kruskal–Wallis, $H = 2.725$, df = 2, $P = 0.256$; alpha males' morph in trios: Kruskal–Wallis, $H = 2.045$, df = 2, $P = 0.360$; beta males' morph in trios: Kruskal–Wallis, $H = 0.473$, df = 2, $P = 0.789$) (Fig. 5).

A multimodel comparison of 28 different general linear models including all potential combinations of independent variables (i.e. female and dominant male morph, mating system and number of years of territory occupation) showed that the best predictors of average productivity were the
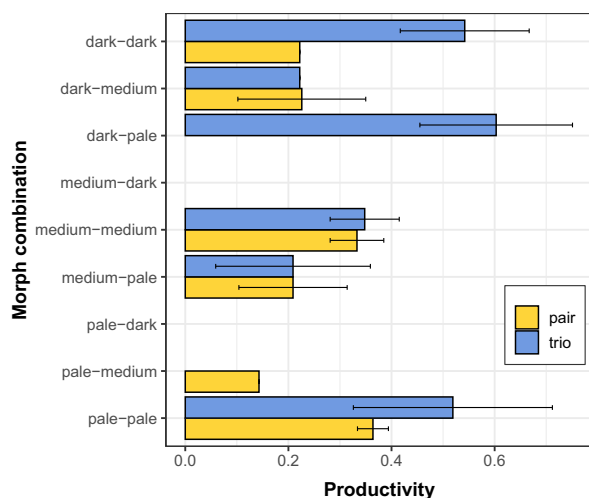
Figure 5. Productivity of Bearded Vultures according to the colour combination of territory holders (female–male) and mating system. In the case of trios, only alpha males were included in this plot. Error bars show mean ± standard error.

number of years of territory occupation, mating system and its interaction (model ranked first), and the number of years of territory occupation (model ranked second; Table 2). Models including all other potential combinations of variables showed ΔAIC > 2 units (Table 2, see Supplementary Materials Table S3). In these two top-ranked models, a detailed analysis of variance showed that the combination of mating system per number of years of territory occupation ($\chi^2 = 3.947$,

$P = 0.047$) in the first case, and the number of years of territory occupation ($\chi^2 = 4.466$, $P = 0.035$) in the second model, were statistically significant predictors of average productivity. Interestingly, no model including mates' coloration had a statistically significant effect on average productivity (detailed results of the two top-ranked models are available in the Supplementary Materials, Tables S1 and S2).

DISCUSSION

Individual colour variations according to sex and mating system within the studied population of Bearded Vultures proved to be quite subtle. The medium morph was the most common in both sexes. Overall, females showed darker coloration than males, but with a large overlap. In the polyandrous trios, dominant males showed a tendency to exhibit darker coloration than subordinate males, but this was not statistically significant. Finally, no differences in average productivity were found in relation to territory holders' coloration. Indeed, these results do not fully match with any of our original assumptions associated with a visual signal function of cosmetic coloration in this species.

General coloration pattern

The Bearded Vulture shows geographical variation in the degree of coloration throughout its range

Table 2. Multi-model comparison of general linear models with average productivity as the dependent variable and all combinations of the independent variables female and alpha male morph, mating system and number of years of territory occupation.

Model	df	logLik	AIC	ΔAIC	AIC$_w$
n_years + mating system + n_years*mating system	5	5.5677	−1.1354	0.0000	0.3108
n_years	3	3.1747	−0.3495	0.7859	0.2098
n_years + mating system	4	3.5220	0.9561	2.0915	0.1092
n_years + female colour morph	5	3.8378	2.3243	3.4597	0.0551
mating system	3	1.7532	2.4935	3.6289	0.0506
n_years + male colour morph	5	3.4841	3.0318	4.1672	0.0387
n_years + mating system + female colour morph	6	4.0866	3.8268	4.9622	0.0260
n_years + mating system + male colour morph	6	3.7217	4.5566	5.6920	0.0181
male colour morph	4	1.5738	4.8523	5.9877	0.0156
female colour morph	4	1.3544	5.2911	6.4265	0.0125
n_years + male colour morph + female colour morph + male colour morph*female colour morph	9	6.2418	5.5163	6.6517	0.0112
male colour morph + mating system	5	2.1136	5.7728	6.9082	0.0098
female colour morph + mating system	5	2.0682	5.8637	6.9991	0.0094

Models were ranked according to AIC values. For simplicity, only the top-ranked models are shown ($n = 28$ models). Abbreviations: AIC, Akaike information criterion; AIC$_w$, Akaike weight; df, degrees of freedom; logLik, log likelihood.

(Delibes *et al.* 1984, Margalida *et al.* 2008). The degree of coloration of the species in the Pyrenees was quite similar to that reported in South Africa, where 10% of the individuals belonged to the pale morph, 84% to the medium morph and 6% to the dark morph (n = 465 field observations of adult individuals throughout the year, without distinction of sex or reproductive status; Brown & Bruton, 1991). In Crete (Greece) the intensity of the coloration varied from pure white to deep orange according to Xirouchakis (1998). In Corsica (France), Thiollay (1968) showed that at least 10–12 adult Bearded Vultures observed were white, whereas Fasce *et al.* (1989) commented that all the individuals of the nine RUs monitored were white, except for two orange females. Geographical variation in the coloration typologies of individuals may be related to the availability of places for taking baths and the type of mud used (Houston *et al.* 1993). There is evidence that Bearded Vultures can bathe not only in the mud from ferruginous springs, but also in other more or less humid substrates rich in iron oxides (Xirouchakis, 1998, Duchateau 2019). Interestingly, although colour acquisition by bathing is an innate behaviour (Frey & Roth-Callies 1994), pure white Bearded Vultures not only exist in populations in Corsica and Crete, where the species seems to have little chance of accessing ferruginous substrates, but have also been observed in the Alps (Novarese 2018) and in the Pyrenees, where there are numerous ferruginous springs (Duchateau & Tellechea 2019, S. Duchateau, pers. obs.). In the Pyrenees, the adult population was estimated in 748 individuals (range 677–826) in 2016 (Margalida *et al.* 2020). According to the results obtained in our work, if the proportion of morphs were extrapolated to the total population, there should be no more than a dozen specimens of the pure white morph in the Pyrenees. Although it is anecdotal, some Bearded Vultures gradually lose the intensity of the coloration after settling in a territory (Fasce *et al.* 1989). In the Pyrenees, a few cases are known of wild individuals of pure white type acquiring coloration later (J. A. Sesé, pers. comm.). These few Bearded Vultures that do not develop feather coloration behaviour represent individuals of great interest in the context of understanding the mechanisms and biological significance of cosmetic coloration in this species.

Between-sex colour variation

Overall, our results showed that there were statistically significant differences in the proportion of morphs between sexes, with males being in general lighter than females. However, it should be emphasized that the degree of coloration cannot constitute a criterion for sex differentiation in the species. According to our results, the majority of birds exhibited the medium morph, and the most common combination of morphs was medium–medium both in pairs and in trios. Curiously, although this topic of coloration in the Bearded Vulture has long caught the attention of naturalists and researchers, there is very little information about sexual differences in coloration in the literature. Frey and Roth-Callies (1994) observed that females had more colour intensity than males in captive birds; however, their results were not statistically significant. Sesé (2019) observed that females had more colour intensity after recording 117 marked adults of known sex (without differentiation of their reproductive status) at a supplementary feeding station for Bearded Vultures located in the central Pyrenees (Aragón), but no statistical analysis was provided. In the eastern Pyrenees (Catalonia), Negro *et al.* (1999) reported that in 142 out of 143 copulations, females were more coloured than males, although their limited number of monitored territories (n = 8) precludes making generalizations.

Within-sex colour variation and its relationship with mating system

In relation to the mating system (i.e. pair or trio), our results showed no differences in the proportion of morphs of females in pairs and females in trios. However, there were statistically significant differences in the proportion of morphs of males in pairs and males in trios. Males in trios tended to be lighter than males in pairs, particularly when beta males were taken into account. When data were analysed separately, alpha males in trios were not significantly darker than beta males. Hence, the statistically significant higher proportion of the pale morph of males in trios than in pairs was mainly due to the contribution of beta males involved in trios. The latter result indicates that, in general terms, beta males have a less marked coloration than other breeding males.

Productivity and coloration intensity

We did not find a relationship between average productivity of the RU and the intensity of coloration of the individuals, whatever their sex or the mating system. Our results showed that average productivity increased with time of occupation of each territory, mating system and their interaction. Indeed, it can be expected that long-term occupied territories are those of better quality. This is also in agreement with Margalida *et al.* (2019) who did not find a relationship between individuals' coloration and breeding success either. In contrast to Carrete *et al.* (2006), trios showed similar productivity to pairs. Our results suggest that other factors such as breeders' experience, weather, human disturbance or intraspecific competition could account for breeding performance, masking the effect of territory quality that we hypothesized to be related to individuals' coloration.

Different hypotheses on coloration

Interpretation of our results with respect to the hypothesis of a visual signalling function of cosmetic coloration in the Bearded Vulture is difficult. Although females were on average darker than males, the gender signalling hypothesis does not hold sufficient support given that colour morph distribution proved to be unimodal, with a large overlap between sexes: the degree of coloration is clearly of little use for a Bearded Vulture to identify the sex of a conspecific.

Although the colouring patterns of alpha and beta males within trios were not statistically different in our results, the latter were confirmed to be, on average, of lighter coloration when compared with males in pairs. Hence the reproductive strategy signalling hypothesis, with beta males of paler coloration signalling their subordination with the aim of being tolerated within RUs holding high-quality territories, could not be discarded. Among Palaearctic raptors, a coloration polymorphism related to different strategies between males is observed in the Western Marsh Harrier *Circus aeruginosus* (Sternalski 2008) and Eleonora's Falcon *Falco eleonorae* (Gangoso *et al.* 2015), but in both species plumage colours are genetically determined. To our knowledge, such a reproductive strategy signalling function has not been highlighted to date in a bird species exhibiting cosmetic coloration (Delhey *et al.* 2007).

The status signalling hypothesis seems to be supported by the fact that females, supposed to be dominant over males due to their usually larger size (López-López *et al.* 2011), were on average darker than their mates. Status signalling to demonstrate fighting ability is mostly expected to work within sexes in a context of intrasexual selection, but can also occur between sexes (Senar 1999). A status signalling function of plumage coloration has been shown in various bird species (Senar 2006), but the Bearded Vulture is the only one among those using cosmetic coloration for which this function is suspected (Delhey *et al.* 2007). Nevertheless, we found no relationship between territory productivity and the degree of coloration for both males and females, which would imply that darker 'potentially dominant' individuals did not monopolize the best territories across our population. With respect to the existence of a hierarchy between individuals of the species, the only data available are, in fact, those referring to alpha and beta males in trios (Bertran *et al.* 2009) and a recent study stating that juvenile birds are dominant over adults and subadults when interacting at feeding stations (Moreno-Opo *et al.* 2020). Evidence linking fighting ability to the degree of coloration of adult individuals is still missing. The fact that not only adult but also immature Bearded Vultures take mud baths (Brown & Bruton 1991, Frey & Roth-Callies 1994) could at first view discredit the status signalling hypothesis. Nevertheless, this behaviour is certainly genetically determined, given that in captivity 90-day-old nestlings already perform it (Vulture Conservation Foundation, 2015), as well as adult individuals from the first time that a bathtub filled with ferruginous mud is offered to them (Frey & Roth-Callies 1994). The essentially brownish immature plumage of the species does not appear suitable to make conspicuous the orange coloration of iron oxide-rich mud. Moreover, there is evidence that in the wild, the colouring behaviour becomes regular for most individuals from the age of 4 years (Sesé 2019), when they become sexually mature but do not yet exhibit the adult plumage.

Because our results confirm that females are on average darker than males, we consider that quality signalling is not the best explanation for cosmetic coloration in the Bearded Vulture, or at least that it is unlikely that this represents the sole function of this behaviour. Testing this

hypothesis more accurately would require long-term monitoring of each RU, involving across-years individual recognition and follow up of the colour intensity for each bird linked to its productivity. Regarding other bird species performing cosmetic coloration, it has been shown that colour intensity signals individual quality in Greater Flamingos (Amat *et al.* 2018) where more coloured individuals are preferred as mates (Freeman *et al.* 2016); this is also the case in Crested Ibises *Nipponia nippon* where females select males whose darker plumage signals greater genetic diversity (Sun *et al.* 2019). On the one hand, it could be expected that coloration intensity may also play this role – the main being status signalling – in Bearded Vultures, as dominant status is often associated with high-quality individuals (e.g. Arcese & Smith 1985). On the other hand, it can be argued that in such a long-lived species where pair bonds are believed to be rather stable across years (Terrasse, 2004, Arroyo *et al.* 2021, S. Duchateau, G. Chéliz, J. A. Gil & P. López-López, pers. obs.), there would be little need to signal individual quality given that pair or trio members generally already 'know' each other when they initiate a new breeding season.

Finally, an additive function of cosmetic coloration in the Bearded Vulture would refer to enhanced territory signalling, with the birds' rufous coloration increasing their conspicuousness when perched on spots overlooking the nesting site and acting as beacons in order to signal territory occupancy (Margalida & Bertran, 2005, S. Duchateau, G. Chéliz, J. A. Gil & P. López-López, pers. obs.). Testing this hypothesis was not possible as part of our study.

CONCLUSIONS

After decades of study and multiple hypotheses put forward, more studies are still needed in order to better understand the role of the cosmetic coloration of Bearded Vultures. Our results are compatible with the hypothesis that the degree of coloration of a given individual might be used as a visual signal reflecting its fighting ability (status signalling hypothesis; Negro *et al.* 1999, 2002). Nevertheless, non-mutually exclusive hypotheses of coloration intensity signalling reproductive strategy or individual quality cannot be excluded. With both sexes performing cosmetic coloration and females being on average darker than males, the Bearded Vulture could represent an interesting case of mutual ornamentation (Kraaijeveld *et al.* 2007) combined with reversed sexual dichromatism (Amat *et al.* 2018). Future studies should focus on analysis of the relationship between the degree of coloration of adult individuals, their hierarchical position and their reproductive status, including territorial and non-territorial birds' coloration in the comparisons. The presence of a significant number of marked Bearded Vultures of known sex, age and reproductive status in the Pyrenees, together with regular observations of individuals at supplementary feeding stations, offer unique possibilities to employ powerful methods for estimating dominance hierarchies (Sánchez-Tojar *et al.* 2018b). This would help to deepen our knowledge about cosmetic coloration as a visual signal in this species and in large vertebrates in general.

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AUTHOR CONTRIBUTIONS

Stéphane Duchateau: Conceptualization (equal); methodology (lead); data collecting (supporting); formal analysis (supporting); writing – original draft (lead), writing – review and editing (equal). **Gonzalo Chéliz:** Data collecting (lead). **Juan Antonio Gil:** Conceptualization (equal); methodology (supporting); data collecting (supporting); writing – original draft (supporting). **Pascual López-López:** Formal

analysis (lead); writing – original draft (supporting); writing – review and editing (equal).

ETHICAL NOTE

None.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary results of the best general linear model.

Table S2. Summary results of the second top-ranked general linear model.

Table S3. Multi-model comparison of Gaussian general linear models with average productivity as the dependent variable and all combinations of the independent variables female and alpha male morph, mating system, and number of years of territory occupation. Models were ranked according to Akaike information criteria values.