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ORIGINAL PAPER

The fractal dimension of a conspicuous ornament varies with mating status and shows assortative mating in wild red-legged partridges (*Alectoris rufa*)

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Abstract

Complex body designs, such as plumage ornaments in birds, can be described by fractal geometry. These complex patterns could have a role as visual signals during courtship and social interactions, but an empirical validation in the wild is currently lacking. Here, we investigated whether the fractal dimension (FD) of a complex plumage pattern displayed by red-legged partridges *Alectoris rufa* could function as a potential sexual signal. We captured wild birds early in the breeding season and tested if mated and unmated birds differed in the FD of their conspicuous melanin-based black bib. We also tested if the FD of the black bib was correlated within the pair, looking for evidence of assortative mating based on the expression of this trait. We simultaneously assessed similar effects in other ornamental traits (black bib size, white throat patch and black flank band surface, redness of the eye rings and bill). Mated birds showed higher black bib FD values than unmated ones. Mated males, but not females, also displayed a larger black bib. Moreover, the black bib FD (but not the trait size) and the white throat patch surface showed assortative mating. Finally, females with higher black bib FD showed smaller black flank band surface, suggesting a trade-off in the expression of the two melanin-pigmented plumage traits. This provides unique and novel indication for the shape complexity of a pigmented trait, here described by its fractal dimension, to be potentially under sexual selection in a wild animal.

Keywords Assortative mating · Complex plumage patterns · Mate choice · Melanin-based coloration · Sexual signaling

Introduction

Plumage ornaments are widespread in birds and often play key roles during courtship and social interactions (Andersson 1994; Andersson and Iwasa 1996). Since Darwin (1871), a wide range of conspicuous color badges or colorful structures have been thought to act as signals of individual quality to conspecifics. Research on the sexual signaling functionality of these traits has been foremost focused on the expression and size of melanins and carotenoid-based ornaments (Alonso-Alvarez and Galván 2011; Cantarero et al. 2017; Galván et al. 2014; Griggio et al. 2009; Griggio et al. 2005), while less attention has been paid to their spatial distribution and shape across the body (but see Endler 1990; Galván et al. 2017; Pérez-Rodríguez et al. 2013). Animal color patterns are used in predation avoidance, individual recognition, and intra- and inter-specific communication (Endler 1980, 1990; Kühl and

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Burghardt 2013). Recently, it has been suggested that these complex and heterogeneous configurations could also act as signals of individual quality (Pérez-Rodríguez et al. 2013, 2017), thus offering new opportunities to study and compare the variation of these patterns among individuals.

Fractal dimension (FD) is a parameter that measures the complexity of patterns as a ratio of the change in detail to the change in scale, and it is influenced by properties that include the number, length, tortuosity, and connectivity of elements within a given object (e.g., Falconer 2005). Many complex designs in the body of living organisms can be described by fractal geometry (e.g., Jovani et al. 2013). Despite color patterns are widespread in the animal kingdom, there are few studies dealing with the potential role of fractal geometry of signaling traits. Moreover, as far as we know, there is an absence of studies testing the role of FD-based ornaments under free-living conditions. Recently, Pérez-Rodríguez et al. (2013) proposed that the FD measurement can be an easy and reliable technique to capture individual variability in the expression of complex ornaments with biological significance. They found that the FD of the black melanin-based bib of red-legged partridges *Alectoris rufa* (Fig. 1) predicted better individual body condition (size-corrected body mass). Moreover, an experimental food restriction during the molt of these birds induced a lower FD expression, confirming that the FD of this trait is condition-dependent (Pérez-Rodríguez et al. 2013). The FD of an ornament could therefore potentially act as a visual signal revealing the quality of its bearer (by following the Zahavi 1977's handicap principle), more specifically, its ability to maintain good physical condition during a short period of high demand of resources, such as molting, or the ability to maintain plumage in good shape during long periods. As far as we know, Pérez-Rodríguez et al. (2013) is the only study linking the FD of a trait to sexual signaling in any animal species. However, we must consider that the cited pioneering work was performed on a captive farm-reared population, which could obviously have been the subject of artificial selective pressures that can potentially affect the development of ornaments as compared with wild birds (García-de Blas et al. 2015).

In the present study, we aimed to address the role of complex plumage patterns described by their FD as potential sexual signals in a wild animal, the red-legged partridge. It expresses many conspicuous traits (Fig. 1) and has served as an animal model to address different evolutionary eco-physiology questions, particularly those related to the signaling role of its colored traits. Both sexes have similar complex plumage patterns and red coloration in the eye rings, bill, and tarsi (Fig. 1), and show similar investment in parental care. Males often help during the incubation and rearing chicks themselves, thus allowing double-nesting events (i.e., one nest per parent; Casas et al. 2009; Cramp and Simmons 1980). Theory predicts that similar reproductive investment in both sexes but high variability among individuals favors the evolution of mutual mate choice on condition-dependent signals (Kokko and Johnstone 2002 and references therein). Mutual mate choice could explain why male and female red-legged partridges only subtly differ in the expression of their colored traits (Cramp and Simmons 1980; García-de Blas et al. 2013; Pérez-Rodriguez and Viñuela 2008), and it could also promote assortative mating based on the level of signal expression (e.g., Britton et al. 2009; Edward and Chapman 2011; Johnstone et al. 1996; Riebel et al. 2010), but it has not been tested in this gallinacean.

Studies on sexual signaling in red-legged partridges have mostly focused on the red carotenoid-based coloration of the head under captivity condition (bill and eye rings; e.g., Alonso-Alvarez and Galván 2011; Blas et al. 2006; García-de Blas et al. 2016; Pérez-Rodríguez et al. 2008). This red color could serve as an honest indicator of individual condition, as shown by the positive association found between individual redness, antioxidant status (Alonso-Alvarez and Galván 2011; Blas et al. 2006), and parasite resistance (Mougeot et al. 2009). Moreover, females produce more eggs when experimentally mated with males whose red coloration was artificially intensified (Alonso-Alvarez et al. 2012), which supports sexual selection on this trait. In contrast, much less is known about the role of melanin-based coloration in this species. Melanin pigments can be readily synthesized by animals and are apparently less costly to produce than carotenoid pigments (Prum 2006). Similarly to carotenoid-based coloration, empirical work on captive partridges has suggested that melanin-based coloration is linked to individual quality and subject to trade-offs (Bortolotti et al. 2006; Galván and Alonso-Alvarez 2008, 2009).

Here, we studied a free-living population of red-legged partridges during pairing in early spring, testing if mated and unmated adults differed in the black bib FD and if the expression of this trait was correlated within the pair, as predicted when assortative mating is taken place due to similar mate choice preferences (e.g., Johnstone et al. 1996). To that end, wild red-legged partridges were captured during the breeding season in central Spain. Furthermore, we analyzed whether black bib FD was correlated with the expression of other conspicuous ornaments of this species in order to explore if it could be involved in a multiple signaling context, for instance, being redundant or not with other traits (Bro-Jorgensen 2010; Candolin 2003; Johnstone et al. 1996; Møller and Pomiankowski 1993a, b). Indeed, some studies have recently shown that the use of multiple signals may reduce quality-assessment errors that might occur when evaluating only one trait (Cantarero et al. 2017; Roulin et al. 2011; Smith and

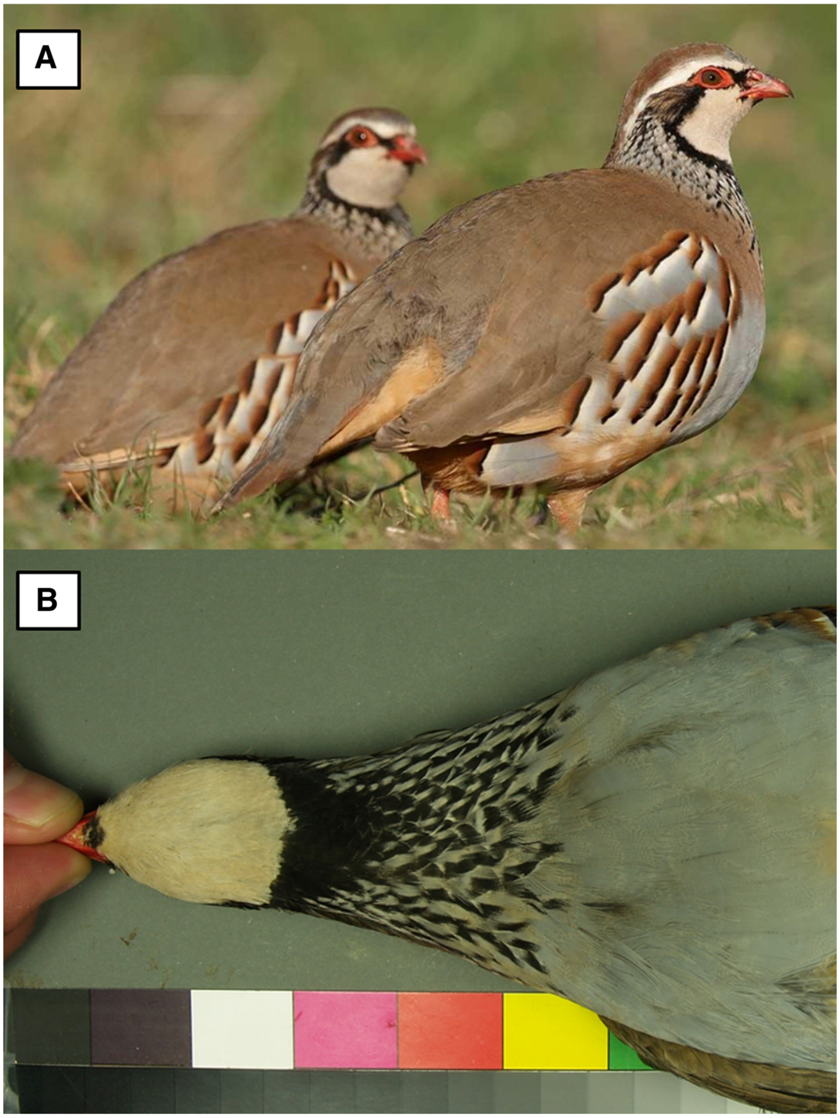

Fig. 1 **a** A couple of red-legged partridges (left female, right male) showing their similar ornamental traits: the red integuments, the white throat patch, the black bib and its complex pattern, and the flank bands (photo credit: Rafael Palomo Santana). **b** Example of a picture used to measure black bib FD and size

Evans 2009). Thus, we also assessed the size of the black bib, white throat, and black flank bands, as well as the redness of the eye rings and bill. Unpigmented feather patch, such as the white bib, although are considered to be cheap to produce (Prum 2006), but may increase conspicuousness towards predators (Dale and Slagsvold 1996). In fact, these patches are particularly exhibited by males while they sing for attracting females during the courtship or defending territories (e.g., Penteriani et al. 2007). If achromatic plumage indicates phenotypic quality, white feather patches could also be used as signals during the breeding and non-breeding seasons (Santos et al. 2011).

Assuming a potential link between ornament expression and individual quality, we predicted (i) that mated individuals should exhibit larger and redder ornaments or a larger fractal dimension compared to unmated ones and (ii) the existence of assortative mating in the level of ornament expression of paired birds.

Material and methods

General field methods

We captured 48 free-living red-legged adult partridges by means of a night-lighting and netting technique (Benítez-Lopez et al. 2011). The birds were caught in Ciudad Real (Central Spain) in three different study areas separated by 40 km (Miguelturra, $n = 24$; Ballesteros de Calatrava, $n = 5$; Santa Cruz de Mudela, $n = 19$). These localities are characterized by Mediterranean scrubland, olive trees, and cereal crops. Restocking with farm-reared birds, which is commonplace in hunting estates, was not used as a management strategy in these areas. The birds were captured throughout 1 month (from March 9th to April 7th of 2010) at the end of the long mating season of this species (from January to April), just before laying time (mostly between mid-April and mid-May; Casas et al. 2009). During this period, partridge pairs are seen together almost constantly (Arias de Reyna Martinez 1975; Braza et al. 1985), so individuals found alone at night are a reliable signal of unmated status. Afterwards, the status was verified by radio-tracking (see below). Accordingly, 35 individuals (17 males and 18 females) were classified as mated individuals, whereas 13 birds were unmated (7 males and 6 females).

The birds were sexed from plumage, biometry, and ornaments (Sáenz de Buruaga et al. 2001). The age of the bird could not be determined reliably due to wing feather wear in most birds. They were ringed and weighed with an electronic balance (± 1 g), and tarsus length was measured with a digital caliper (± 1 mm). Head length (distance from the back of the head to the tip of the bill) was also measured. All captured adult individuals were photographed by following Galván and Alonso-Alvarez (2009) to analyze their ornamentation. We took digital photographs of the breast and of the left flank of birds with a digital camera (Olympus E-510) under standard bird position and light conditions, by using a Kaiser Repro Lighting unit (Kaiser, Germany). For each photo, the same standard gray reference and scale (Kodak Gray Scale, Kodak, New York) was placed next to the bird's neck. The coloration of bill and eye rings of red-legged partridges was measured with a portable battery-driven Minolta spectrophotometer CM-2600d (Tokyo, Japan).

Finally, birds were tagged individually with radio-transmitters endowed with a sensor of mortality (Biotrack, UK, 10 g) and were released at the place of capture. Tagged birds were monitored using a "Sika" receiver (Biotrack, UK) with a hand-held 3-element. Adult partridges were radio-tracked once per day during 3 days after the capture. After that, birds were radio-tracked weekly until the end of the breeding season (July). This allowed us to confirm if birds were indeed mated by determining stable (social) couples.

Color measurements and fractal dimension analysis

In the case of bill and eye ring redness, we determined the hue values from spectrophotometer measurements by following the formula in Saks et al. (2003). Total brightness obtained from our spectrophotometer (360–700 nm) was added as a covariate to models testing the hue (see "Statistical Analyses" and García-de Blas et al. 2016). Reflectance spectra for each trait were obtained as means of three sequential measurements of each trait by changing the position of the trait with respect to the spectrophotometer. Repeatabilities of triplicate measurements were significant for both traits ($r > 0.68$, $P < 0.001$), with mean values for each sample being used.

We analyzed digital photographs using Adobe Photoshop (version 7.0). The surfaces of the black bib, white throat patch, and black and brown flank bands were measured with the "magic wand" tool in Adobe Photoshop. In a previous study, the repeatability of these measurements was very high (see Galván and Alonso-Alvarez 2009). We did not measure these variables for one mated female because the quality of the photographs was poor. Additionally, we calculated the ratio of the black surface as the proportion of the black surface to total melanized (brown and black) surface in flank feathers obtained from digital pictures. Finally, pictures of the chest were processed using the HarFa software to obtain FD for the black bib of each individual. We used the box-counting method because it can evaluate the FD of fractals without self-similarity (Pérez-Rodríguez et al. 2013).

Statistical analyses

Statistical analyses were conducted using SAS v9.3 software (SAS Institute, Carry North Carolina, USA). Generalized mixed models were used to test differences in the expression of the ornaments (black bib FD, FD controlled by black bib surface, black bib surface, white throat surface, black flank band surface, black flank proportion, eye ring hue and bill hue) in terms of mating status and sex. The mating status (mated or unmated), sex, and their interaction were tested in every model. The site where the birds were caught (three different areas; above) and a cluster variable to control for pseudoreplication derived from capturing the two members of a couple were added as random factors. The cluster identity was nested into the site random factor. Body mass and tarsus length were included as covariates to control for potential bias due to variability in individual size. The length of the head was also added as a covariate in the model testing the white throat surface. In the model, testing the red hue of the eye ring and bill, the total brightness of the trait was added as a covariate (above). Overfitting was not an issue according to the large enough sample size ($N/k > 3$; Forstmeier and Schielzeth 2011). Covariates were removed from the models when $P > 0.10$. All the dependent variables were normally distributed, except for the hue values of the eye ring and bill that were log-transformed to reach normality. LSD post hoc tests were used for pairwise comparisons to establish differences within each sex and mating status. Satterthwaite degrees of freedom are shown. Least square means ± SE from the mixed models are provided in Fig. 2. Cohen's d values were provided as effect sizes for pairwise comparisons (Cohen 1992). The random factor in the models provided P values from 0.015 to 0.470. Alternatively, when conventional ANCOVA models were used instead of mixed models, the results did not differ (see Table S1 in ESM). The assortative mating among ornament values was tested using male values as the dependent variable and female values as the independent

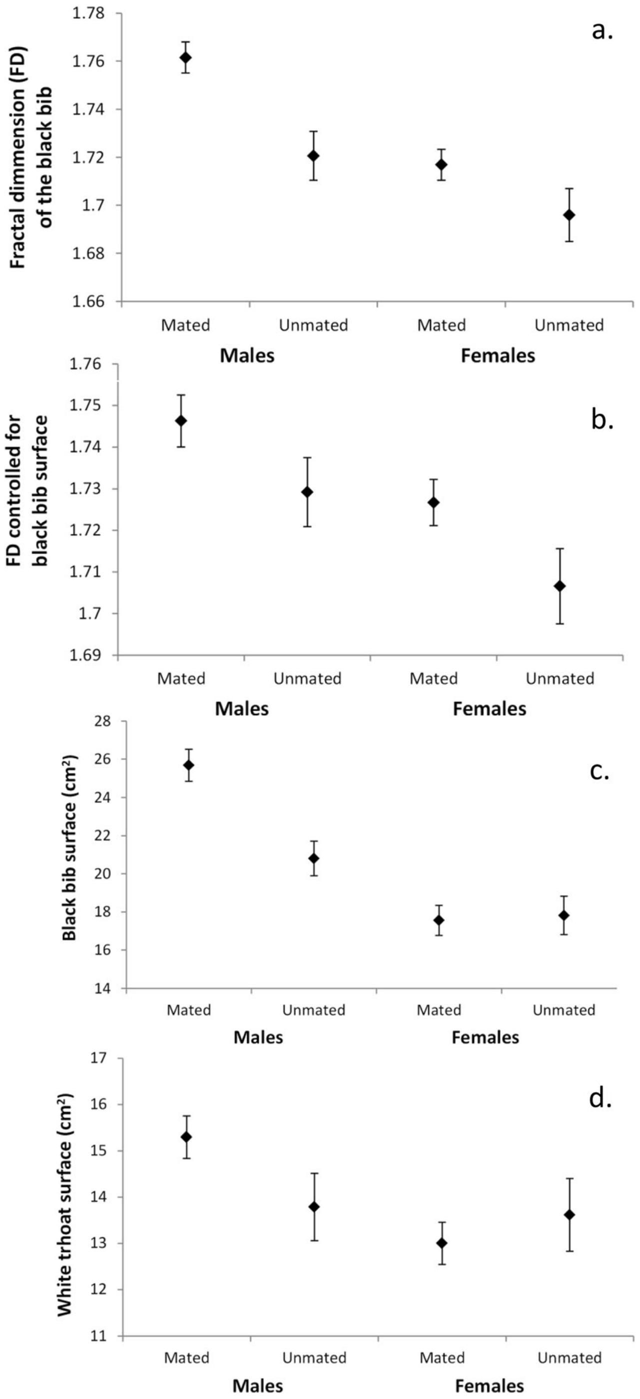

Fig. 2 Differences in ornamentation (mean ± SE) according to mating status and sex (males left; females right) of wild red-legged partridges: fractal dimension (FD) of the black bib (**a**), FD controlled for black bib surface (**b**), black bib surface (cm^2) (**c**), and white throat surface (cm^2) (**d**)

variable, adding the site identity as a random factor (always P value > 0.32). We also tested the trait value of females as residuals of mixed models controlling for the site identity random term, providing the same results. Conventional Pearson's correlation tests are described in the ESM. Figure 3 shows raw data.

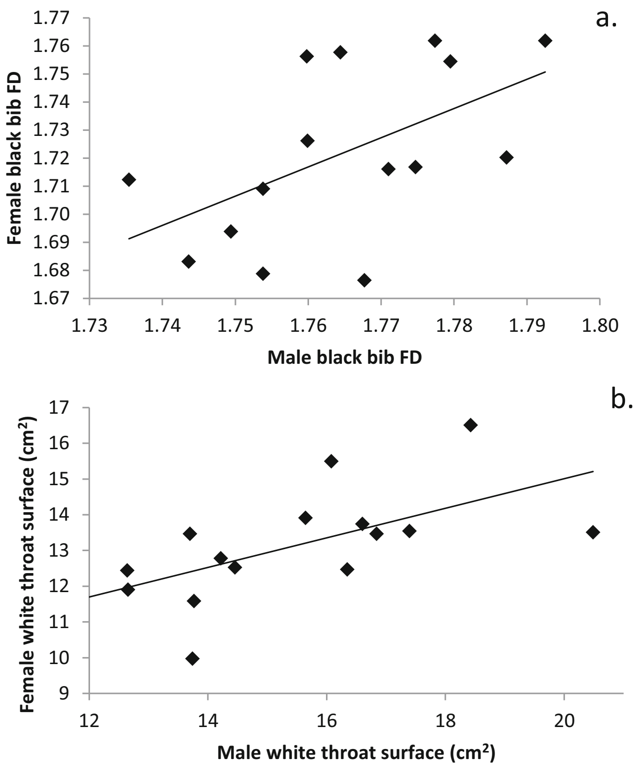

Fig. 3 The relationship among social pairs between the male and female black bib fractal dimension (FD) (**a**) and white throat surface (cm^2) (**b**)

Results

Differences in ornament expression depending on mating status and sex

The FD of the black bib differed between mated and unmated birds and sexes (Fig. 2a). Mated birds and males showed higher FD values, but there was no interaction between these (Table 1). The effects remained significant when the interaction was removed (mating status $F_{1,31.6} = 11.25$, $P = 0.002$, Cohen's $d = 1.09$; mated 1.74 ± 0.01, unmated 1.71 ± 0.01; sex $F_{1,19.4} = 46.26$, $P < 0.001$, $d = 1.98$; males 1.74 ± 0.01, females 1.70 ± 0.01). When the FD was controlled for the black bib surface (slope ± SE 0.006 ± 0.001), the model did not show any substantial change (Table 1 and Fig. 2b).

The mating status and sex interacted in the model testing black bib surface as the dependent variable (Table 1). Mated males showed larger bibs than unmated males ($P < 0.001$; $d = 2.04$; 1.98; Fig. 2c), but females did not show such a difference ($P = 0.813$). Males also showed larger black bibs than females among mated and unmated birds (both $P < 0.046$; $d = 1.15$ and 1.98, respectively). Tarsus length was retained by the model but negatively correlated with black bib size (slope ± SE -0.995 ± 0.275). In any case, removing tarsus length from the black bib model did not change the results (sex x mating status interaction estimate ± SE $= -4.007 \pm 1.693$, $F_{1,43} = 5.60$, $P = 0.023$; the difference between mated and

Table 1 Generalized mixed models showing the effect of mating status (mated vs unmated), sex, and their interaction on the ornaments of wild red-legged partridges. The study area where birds were trapped and a cluster factor for controlling pseudoreplication due to capturing a couple were simultaneously included as random terms (see Statistical Procedures)

Ornament	Terms in the model	Estimate ± SE	*F*	dfs	*P*
Black bib fractal dimension (FD)	Mating status	− 0.0209 ± 0.013	10.98	1, 31	0.0024
	Sex	0.0446 ± 0.007	17.82	1, 42.3	0.0001
	Interaction	− 0.0199 ± 0.016	1.47	1, 42.3	0.2317
FD controlled for black bib surface	Mating status	− 0.0200 ± 0.010	5.97	1, 36.6	0.0195
	Sex	0.0196 ± 0.009	7.91	1, 37.8	0.0078
	Interaction	0.0029 ± 0.015	0.04	1, 37.9	0.8438
	Black bib surface	0.0060 ± 0.001	23.30	1, 36.6	< 0.0001
Black bib surface	Mating status	0.2590 ± 1.084	9.45	1, 39	0.0038
	Sex	8.1190 ± 1.409	21.45	1, 39	< 0.0001
	Interaction	− 5.1291 ± 1.550	10.95	1, 39	0.0020
	Tarsus length	− 0.9950 ± 0.174	13.14	1, 39	0.0008
White throat surface	Mating status	0.6164 ± 0.909	0.45	1, 32.1	0.5090
	Sex	2.2934 ± 0.453	4.49	1, 41.9	0.0401
	Interaction	− 2.1244 ± 1.162	3.34	1, 41.9	0.0747
Black flank band surface	Mating status	0.0342 ± 0.322	0.36	1, 38.9	0.5546
	Sex	0.3518 ± 0230	0.64	1, 39.6	0.4296
	Interaction	− 0.3409 ± 0.454	0.56	1, 39.6	0.4576
Black flank proportion	Mating status	− 0.0319 ± 0.023	1.29	1, 39.5	0.2626
	Sex	− 0.0232 ± 0.017	0.38	1, 39.9	0.5409
	Interaction	0.0261 ± 0.033	0.62	1, 39.9	0.4347
Eye ring hue	Mating status	− 0.0221 ± 0.034	0.41	1, 34.6	0.5277
	Sex	0.0138 ± 0.021	0.75	1, 43	0.3906
	Interaction	0.0128 ± 0.046	0.08	1, 42.9	0.7805
	Total brightness	0.0003 ± 0.001	19.96	1, 41.6	< 0.0001
Bill hue	Mating status	0.0007 ± 0.018	0.37	1, 43	0.5480
	Sex	− 0.0324 ± 0.013	4.27	1, 43	0.0447
	Interaction	0.0137 ± 0.025	0.31	1, 43	0.5808
	Total brightness	0.0005 ± 0.001	28.50	1, 43	< 0.0001

unmated males and females, respectively estimate ± SE = 4.367 ± 0.888, $P < 0.001$ and estimate ± SE = 0.204 ± 1.230, $P = 0.869$).

The model testing variability in white throat patch surface also showed a marginally non-significant interaction ($P = 0.075$; Table 1). Similarly to the black bib surface, the white throat patch tended to be larger in mated males compared to unmated males (estimate ± SE = 1.508 ± 0.860, $P = 0.087$; $d = 0.79$; Fig. 2d), with no such difference in females (estimate ± SE = 0.616 ± 0.909, $P = 0.502$). Males also showed larger white throat patches compared to females among mated ($P < 0.001$; $d = 1.74$) but not unmated ($P = 0.875$) male birds. Other ornaments did not show significant effects (Table 1). A backward stepwise model selection only provided a significant effect (the rest of P values > 0.10): the bill redness, with males displaying redder bills (lower hue) than females ($F_{1,22.6} = 7.03$, $P = 0.011$; $d = 0.77$; males 0.37° ± 0.01, females 0.40° ± 0.01).

Finally, the relationship of black bib FD with the expression of other ornaments was also assessed in those models testing FD as the dependent variable. The other ornaments were alternatively tested as covariates, also analyzing their interactions with fixed factors. With the exception of the black bib size (above), the only other trait significantly linked to FD was the surface of the black flank bands, but only among females (mating status $F_{1,29.1} = 9.59$, $P = 0.004$; sex $F_{1,22.5.} = 4.00$, $P = 0.058$; black flank band $F_{1,23.3} = 0.31$, $P = 0.583$; black flank band x sex $F_{1,22.3} = 10.60$, $P = 0.004$). The black flank band surface was not significantly associated with FD in males ($F_{1,20} = 0.18$, $P = 0.677$; slope ± SE 0.003 ± 0.006), while in females, it was ($F_{1,20} = 5.00$, $P = 0.037$; slope ± SE − 0.026 ± 0.011). Females with greater black bib FD showed smaller black band flank surfaces and vice versa.

Assortative mating according to ornament expression

The black bib FD of the male was positively correlated with the black bib FD of its mate ($F_{1,11} = 6.29$, $P = 0.029$; slope ± SE: 0.295 ± 0.117; see Fig. 3a for a plot of raw data). This association was even stronger when the standardized residuals obtained from a linear regression of FD on black bib surface values ($r = 0.32$ and 0.42 for males and females, respectively) were tested ($F_{1,9.99} = 22.96$, $P = 0.001$; slope ± SE 0.808 ± 0.169). The white throat surface of males and females was also correlated among social pairs ($F_{1,13} = 7.06$, $P = 0.019$; slope ± SE 0.851 ± 0.320; Fig. 3b for a plot of raw data). However, neither the black bib surface ($F_{1,10.6} = 0.35$, $P = 0.568$) nor any other study ornamental or morphometric trait (body mass, tarsus or total head length) showed significant within-pair associations (all P values > 0.10; see also ESM).

Discussion

Our study revealed that the level of complexity in the design of a colored ornament differs between mated and unmated individuals in the wild. Mated red-legged partridges displayed black bibs with a greater fractal dimension value than unmated red-legged partridges. Males with a larger black bib, but not females, were also more likely to be mated. Moreover, the black bib FD (but not its size) was able to predict the probability of being mated, and this trait and the white throat patch surface area showed assortative mating. Other ornaments did not display any of these effects. The results as a whole seem to suggest that, in red-legged partridges, the black bib FD could play a relevant role in terms of animal signaling.

The combination of different colors within or between feathers produces complex pigmentation patterns and additional opportunities to signal an individual's quality, different from other features of the same trait (such as its size or color). This is the type of patterns that can be revealed and measured by means of fractal dimension (FD) analyses. To understand how FD-measured ornaments can reliably reveal individual quality, the proximate physiological mechanisms involved in their production must be briefly mentioned. Firstly, complex patterns in avian plumage are mostly produced by melanins as they are the only pigments under direct cellular control (Galván et al. 2017). Differences in the modulation, presence, arrangement, or differentiation of the cells responsible for the pigmentation (melanocytes) give rise to complex spatial patterns (Lin et al. 2013). The perturbations affecting developmental stability include a range of genetic (e.g., inbreeding), endocrine and environmental factors (e.g., deviant climatic conditions, food deficiency, parasitism) (reviewed in Palmer and Strobeck 1986) which may have short- and long-term fitness consequences (e.g., growth, survival, fecundity) (Birkhead et al. 1999; Møller 1997). Traits such as feathers, which are replaced regularly, are strongly subjected to these factors (Møller 1993), so signals based on plumage arrangements and spatial distribution could be important in signaling contexts (Pérez-Rodríguez et al. 2017). Many of these plumage traits show more complexity than simple bilateral symmetry. Their expression could thus reveal the individual capacity to create bands of certain characteristics and space them throughout the body (Bortolotti et al. 2006). Additionally, Pérez-Rodríguez et al. (2017) also suggests that individual quality can be revealed by the effort made to maintain the complex trait in good condition avoiding damages due to social conflicts or the effect of wearing due to environmental factors. Our results are consistent with a link between complexity and individual quality as we found that paired individuals of both sexes had significantly higher black bib FD and, interestingly, this association was independent of an individual's body size or the size of its bib.

Furthermore, individuals were shown to pair assortatively with respect to the black bib FD and size of the white throat patch, which suggests that these traits could be used in a mutual mate choice context. Mutual mate choice may lead to divergent, state-dependent preferences in both sexes (high-quality individuals choose high-quality mates, while low-quality individuals are left with low-quality mates) or instead uniform, directional preference for high-quality mates in both sexes (Riebel et al. 2010). In the last case, high-quality individuals pair off first, forcing low-quality individuals to mate each other as last resource (Riebel et al. 2010), thus also leading to positive assortative mating. Whatever the selective process, the difference between mated and unmated birds, as well as intra-pair correlations, may suggest that both ornaments have evolved under sexual selection (but see also, e.g., Class et al. 2017 for environmental effects explaining assortative mating).

Achromatic plumage traits such as the white throat patch may evolve as sexual signals (Cantarero et al. 2017; Mennill et al. 2003). The majority of costs proposed to define white plumage patches as individual quality signals are maintenance costs such as higher detectability and predation risk (Götmark and Annika 1995), higher probabilities of suffering conspecific aggression (Penteriani et al. 2007; Qvarnström 1997), ectoparasite infestation (Kose and Møller 1999), and feather fragility (Bonser 1995). Nonetheless, production costs have also been suggested. For instance, in male dark-eyed juncos (*Junco hyemalis*) a poor (low protein) quality diet may reduce the size of white patches in tail feathers (McGlothlin et al. 2007).

The size of the black bib differed between mated and unmated birds, but only among males. This trait is apparently involved in both sexual and/or aggressive behaviors in wild birds (Cramp and Simmons 1980 and references therein). Because individuals risk injury during agonistic encounters, a large bib could be costly to maintain and therefore possibly favored by intra-sexual and/or social selection (Lyon and Montgomerie 2012). In the last case, we must note that if particular ornaments confer social advantages, such as competition for ecological resources other than mates (Tobias et al. 2012; West-Eberhard 1979, 1983), then they may evolve outside the framework of sexual selection. This form of "non-sexual selection" (social selection) may also contribute to explain the evolution of weapons, ornaments, and behavior in both males and females (Cantarero et al. 2015; Kabasakal et al. 2017). On the other hand, in a sexual selection context, it has been hypothesized that selective pressures on secondary sexual characters are more intense in males than in females, presumably because male-male competition for reproductive resources is usually stronger (Tobias et al. 2012). Competition among males could operate to achieve access to preferred females or over resources necessary for breeding like territories (Clutton-Brock 2007). Females choosing males with large bibs could also obtain high-quality males that are more likely to acquire and defend good territories, but also capable to face the production costs of this trait and perhaps invest more in reproduction. In this line, Galván and Alonso-Alvarez (2009) suggested that larger black bibs of red-legged partridges could signal a better capacity to face oxidative stress during trait development (see also Galván and Alonso-Alvarez 2008). The simultaneous effects of intra- and intersexual selection on the black bib size could explain differences between mated and unmated birds. In fact, Hoi and Griggio (2008) showed a dual utility of a melanin-based ornament (the black beard) in the bearded tit *Panurus biarmicus*, namely the best predictor of dominance in male competition contest and a sexually selected ornament by females. The same explanation could apply to the white throat patch expression, although the mating status effect was here weaker (only a marginal significance).

Multiple ornaments may provide multiple messages of quality components or may redundantly signal the overall quality of an individual (Jawor et al. 2003). Different signals may be assessed in an additive way, thus increasing the strength of preferences (Künzler and Bakker 2001). Indeed, some studies have shown that birds may assess multiple signals to minimize errors that might occur if they evaluate just one trait (Candolin 2003; Laucht and Dale 2012). Here, however, the black bib FD independent of the trait size was mostly uncorrelated to other traits, which initially suggests that it may potentially transmit some particular component of individual quality.

Pérez-Rodríguez et al. (2013) experimentally demonstrated that captive red-legged partridges enduring a shortage in food availability during molt produced black bibs with lower FD, suggesting that the quantity or quality of the diet (energy, macro or micronutrients) may affect the trait expression. The black bib FD would, hence, reveal the individual capacity to obtain such hypothetical resources. Here, we found that females, but not males, with higher FD values showed smaller black band flank surfaces. This may suggest some cost in the simultaneous production of both traits, at least for females. Both traits have also been positively correlated to size-corrected body mass ("body condition") in captive partridges in two independent studies (Bortolotti et al. 2006 and Pérez-Rodríguez et al. 2013). Therefore, they could contribute to revealing such a quality component as redundant or "backup signals" (Johnstone et al. 1996; Møller and Pomiankowski 1993b) instead of acting as signals of specific quality components (above), at least in females.

Contrary to our prediction, we found that carotenoid-based traits were unrelated to mating status. Mate choice has been considered as the main force responsible for the evolution of sexual ornaments (Andersson 1994). However, in many species, ornaments are also involved in post-mating sexual selection. Such sexual signals influence the decisions of the mate in how much to invest in common offspring (Burley 1986). In this regard, Alonso-Alvarez et al. (2012) experimentally showed that female red-legged partridges differentially increase their investment in progeny when the redness of carotenoid-based head ornamentation of their mate was experimentally increased during the laying period. Here, we found no association between mating status and carotenoid-based ornaments, which supports the idea that these traits could influence allocation decisions after pair formation. Furthermore, eye ring redness is a trait that may suffer important changes in short-time periods responding quickly in captive birds to changes in food availability (Pérez-Rodriguez and Viñuela 2008), which suggests that this is a trait that could signal current physical condition (as compared to other ornaments with slower or null response to physical condition, such as beak or plumage out of molt period). Finding any effect of this kind of rapidly changing traits on mating success may thus be more difficult.

Finally, we must note that we could not classify birds per age class (see "Methods") due to wing feather wear. This open the possibility that mated birds with higher FD were older than not mated ones. In this context, we must consider that theoretical models predicted that animals should prefer older mates because, merely by surviving, they have proven their high genotypic quality for viability (Brooks and Kemp 2001; Kokko 1997; Manning 1985). Older mates could also provide more resources to reproduction or reduce mating and breeding costs due to their experience (Brooks and Kemp 2001). Hence, age and individual quality could be intrinsically linked and difficult to separate. High FD in our birds could thus be signaling a quality such as age.

In conclusion, we have provided here evidence supporting the idea that the shape complexity of a pigmented trait is potentially under sexual selection in the wild. Our results also highlight the utility of FD measurements (Pérez-Rodríguez et al. 2013, 2017) to capture individual variability in complex ornaments with biological significance. This is a first step in studying the role of FD-based ornaments in free-living conditions. Further experimental work is now needed to understand the physiological mechanism constraining the expression of these traits (e.g., Lin et al. 2013), verifying that animals are indeed able to perceive individual differences in FD and also demonstrating that FD variability is linked to individual fitness.

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Compliance with ethical standards

Conflict of interest Alejandro Cantarero has received a research Juan de la Cierva-formación postdoctoral grant from MINECO. Jesús Carrasco Naranjo, Fabián Casas, Francois Mougeot, Javier Viñuela, and Carlos Alonso-Alvarez declare that they have no conflicts of interest.

Informed consent Informed consent was obtained from all individual participants included in the study.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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