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Abstract

In most animals, nests primarily aim to protect offspring, and are presumably shaped by nat- ural selection. In some species, however, nests are conspicuous and elaborate, thereby visible to predators. One hypothesis to explain this apparent paradox is that nests could also evolve through sexual selection. Here, we tested this hypothesis by studying nest weaves across the weaver family (Aves: Ploceidae). We hypothesized that scale-invariance, a measure of vi- sual regularity of the weave, reflects the quality of the nest builder or activates pre-existing preferences exploiting a sensory bias in the receiver. We predicted a link between weave scale- invariance and two proxies of the intensity of sexual selection: mating system and sexual size dimorphism. Our results reveal that species under stronger sexual selection produce more scale-invariant weaves. These results suggest a previously unnoticed sexually selected signal associated with the evolution of some of the most spectacular constructions observed in the animal kingdom.

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C. Doutrelant, R. Covas, J. P. Renoult, E. Harscouet-Commecy conceived the study with the input of D. Oschadleus and S. Andersson. E. Harscouet-Commecy, D. Oschadleus, C. Doutrelant, R. Covas, P. Colençon and M. Pelte collected the data. E. Harscouet-Commecy performed statistical analysis with advice from C. Doutrelant, R. Covas and J. P. Renoult and input from P. Dufour. E. Harscouet-Commecy wrote the first draft of the manuscript with advice from C. Doutrelant, R. Covas and J. P. Renoult. All authors read and revised the manuscript.

Data availability

The dataset and R scripts used to produce the analyses presented in this paper are available at: (a Dryad and Github link will be provided upon acceptance for publication).

Abstract

In most animals, nests primarily aim to protect offspring, and are presumably shaped by natural selection. In some species, however, nests are conspicuous and elaborate, thereby visible to predators. One hypothesis to explain this apparent paradox is that nests could also evolve through sexual selection. Here, we tested this hypothesis by studying nest weaves across the weaver family (Aves: Ploceidae). We hypothesized that scale-invariance, a measure of visual regularity of the weave, reflects the quality of the nest builder or activates pre-existing preferences exploiting a sensory bias in the receiver. We predicted a link between weave scale-invariance and two proxies of the intensity of sexual selection: mating system and sexual size dimorphism. Our results reveal that species under stronger sexual selection produce more scale-invariant weaves. These results suggest a previously unnoticed sexually selected signal associated with the evolution of some of the most spectacular constructions observed in the animal kingdom.

Introduction

Extended phenotypes are traits produced outside the body of the individual carrying the genes coding for their expression (Dawkins, 1982). Examples from a wide diversity of taxa include spider webs, beaver dams, armour of caddisfly larvae, bowerbirds' display arenas, animal nests or burrows and human houses. The concept of extended phenotypes was introduced almost four decades ago (Dawkins, 1982), but few studies have investigated their adaptive functions, diversification and associated life histories. As a consequence, the evolutionary mechanisms underlying the striking diversity of these traits are still poorly understood. While it is likely that many extended phenotypes were initially selected for their protective or resource-gathering function (Hansell, 2005), some may have evolved additional functions, such as sexual signalling (Schaedelin and Taborsky, 2009). To date, this hypothesis has remained poorly investigated.

Nests are prominent examples of extended phenotypes that may serve multiple functions. Their primary function is to ensure the protection of offspring during development (Hansell, 2000). However, in some species, nests are associated with ostentatious signals and thus they can draw predators' or competitors' attention. For instance, in some fishes like sticklebacks (Östlund-Nilsson and Holmlund, 2003), or birds like starlings (Rubalcaba et al., 2016) and kites (Sergio et al., 2011), males decorate nests with coloured algae, green aromatic material and white plastic, respectively. These observations seem at odds with the primary protective function of nests. The current explanation to this paradox proposes that these conspicuous nests could secondarily act as sexual signals (Schaedelin and Taborsky, 2009). This is further supported by evidence that some quantitative or qualitative aspects of nest architecture contribute to determine mating success (Jordan et al., 2016).

Among birds, weaverbirds (Ploceidae) are famous for the highly visible and intricately elaborate nests they construct (Crook, 1964). They have developed a weaving technique in which strands of material are inserted, recovered and reinserted repeatedly in several ways

leading to impressive woven nests (del Hoyo et al., 2011) (Fig. S1A). The nests can take various forms such as ball, mass, retort, or sock, and are made from different plant materials. In many weaver species, nests are built almost entirely by males, with females adding only the inner lining to the bottom of the egg chamber. Weaverbirds are a diverse family containing 121 species organized in 15 genera distributed across Sub-Saharan Africa, Indo-Malayan region and Indian Ocean islands (De Silva et al., 2017). They present various mating strategies, some species being polygamous and others monogamous. Weaverbirds also show between-species variation in sexual dimorphism (del Hoyo et al., 2011; Song et al., 2022). Finally, in some species, the nest seems to be part of the male courtship display, while in others, the males display far from the nest, sometimes even before its construction (Crook, 1964). This family thus presents a large variation in both nest design, intensity of sexual selection and association with the nest while displaying, and therefore represents a unique setup in which to investigate the influence of sexual selection on the evolution of elaborate nests.

Several intraspecific studies have linked weaverbirds' nest characteristics to mate choice, thus suggesting that they can act as a sexual signal. For instance, in red bishops (*Euplectes orix*), village weavers (*Ploceus cucullatus*) and baya weavers (*Ploceus philippinus*), duration, strength of materials and location of the nest influenced female choice (Metz et al., 2009; Collias and Victoria, 1978; Quader, 2006). In addition, in southern masked weavers (*Ploceus velatus*), nest dimensions were partially repeatable, suggesting a possible heritability which would allow this trait to evolve (Walsh et al., 2009). A notable component of weavers' nests is the elaborate weave, which creates a striking visual pattern. In village weavers, nests showed an individual signature in the weave pattern (Bailey et al., 2015). However, whether and how the weave pattern and its visual appearance differ between species, and whether it could evolve through sexual selection has never been investigated.

Two main types of explanations are proposed for the origin of preferences for visual patterns. First, some patterns can be preferred if they are quality indicators (Pérez-Rodríguez et al., 2017), correlating with the value or quality of the signaller, and hence affecting also the fitness of the receiver that chooses those patterns (Cotton et al., 2004; Smith and Harper, 2003). For example, in paper wasps the patterning of the black facial patch is related to survival and dominance (Tibbetts et al., 2015). Another example is the bib of red-legged partridges, where the scale-invariance of the patterning is correlated to immune response and body weight (Pérez-Rodríguez et al., 2013). Scale-invariance describes the regularity of a pattern, or the degree to which a pattern looks similar at a close or distant range (similar when 'zooming' in and out). The well-studied fractals are a particular case of scale-invariant patterns. In medical research, scale-invariance has been shown to correlate with the healthy functioning of many physiological systems (Korolj et al., 2019), suggesting that developmental homeostasis might explain how scale-invariant patterns could be used as quality indicators in animal communication (Pérez-Rodríguez et al., 2017).

Second, a pattern preference might arise from a pre-existing preference. This occurs when a preference has first evolved in a context unrelated to mate choice, and sexual signals have then aligned with the pre-existing preference (Ryan and Rand, 1990). For example, experimental and comparative works suggest that the breast spots of Estrildid finches have been selected because they mimic seeds to which conspecifics are attracted (Mizuno and Soma, 2021, 2022). A particular case of exploitation of pre-existing preferences is the sensory drive, in which pre-existing preferences are determined by the physical characteristics of the habitats through their effect on sensory systems (Endler and Basolo, 1998). The sensory drive hypothesis is supported by several studies on sexual colour signals (Seehausen et al., 2008; Fleishman et al., 2022). Recently, this hypothesis was applied to patterns by using two main findings in human psychology and neuroscience (Renoult and Mendelson, 2019). First, research in humans shows

that stimuli that are efficiently processed (detected more quickly, memorized for longer and more accurately) tend to be perceived as attractive (Endler and Basolo, 1998), a phenomenon known as 'a processing bias' (Renoult and Mendelson, 2019). For example, scale-invariant patterns such as fractals would be visually attractive because their spatial regularity makes them efficiently processed in the visual system (Graf and Landwehr, 2015; Reber et al., 1998). Second, what determines the efficiency of information processing is the sensitivity of neurons. A number of studies, both in humans and non-human animals, have documented that the sensitivity of many neurons in the visual system is tuned to the spatial statistics that are dominant in visual natural environments (Barlow, 2012). Integrating these findings in psychology and neuroscience into the sensory drive hypothesis, it was thus predicted that stimuli mimicking the spatial statistics of natural habitats are efficiently processed, and thus are visually attractive (Renoult and Mendelson, 2019).

In this study, we investigate whether the scale-invariance of weaverbirds' nests is linked to proxies of sexual selection across the weaver family. Scale-invariance is typically measured using the slope of the Fourier power spectrum (hereafter 'Fourier slope') (Winkielman et al., 2006; Hyvärinen et al., 2009; Pérez-Rodríguez et al., 2017). In humans, for both abstract and representational images, there is a preference for Fourier slopes close to -2 (Spehar et al., 2015; Juricevic et al., 2010; Taylor and Spehar, 2016). This value of -2 describes the maximum possible scale-invariance, as reached by perfect fractals (Graham and Redies, 2010; Pouli et al., 2013). But -2 is also the expected average Fourier slope of images of natural habitats or landscapes (Redies et al., 2008). Therefore, signals with a Fourier slope close to -2 could be preferred either because (i) scale-invariance indicates higher qualities of the signaler ('quality indicator hypothesis'), (ii) scale-invariant nests are intrinsically efficiently processed ('universal preference hypothesis', caused by a processing bias independent of natural habitats) or (iii) they are more similar to the average scale-invariance of natural habitats (to which visual systems

have adapted, 'sensory drive hypothesis'). However, beyond the average expected value of -2, there may be some variation in the Fourier slope among different natural habitats. Under the hypothesis of sensory drive, this variation could result in variation in preferences and therefore in the design of sexual signals, which are expected to co-vary with habitats (Hulse et al., 2020). Hence, it is important to calculate the scale-invariance of the habitat in which species live and not to consider by default that all natural habitats have a scale-invariance of -2 when testing the sensory drive hypothesis.

Here, we first measured the Fourier slope in images of nests and of different natural habitats. Then, we calculated (i) the difference between the nests' Fourier slope and -2 (the deviation to perfect scale-invariance) and (ii) the difference between the nests' Fourier slope and the Fourier slope of the surrounding habitat in which the nests were found. Finally, we used comparative methods to relate these differences to two main proxies of sexual selection: mating system (Shuster, 2009) and dimorphism (Szekely et al., 2007). We tested two predictions. First (P1), if the weave is sexually selected because it indicates builder's quality or it matches a universal preference bias for efficient processing, then species under strong sexual selection (polygamous and dimorphic species) should exhibit a nest Fourier slope close to -2. Second (P2), if nest weave is sexually selected by sensory drive, then species under strong sexual selection should exhibit a nest Fourier slope close to the Fourier slope of the corresponding surrounding habitat. The validation of either of these predictions would support the hypothesis of sexual selection on the weave of weaverbird nests.

Methods

Digital photos collection

We gathered a total of 2,829 digital photos of weaver nests (Fig. S1A) from various sources:

the Natural History Museum of Tring virtual database (https://data.nhm.ac.uk/dataset/, 438 images), the Photos of Weaver Nests (PHOWN) virtual database (http://weavers.adu.org.za/, 514 images), photos taken by us in South Africa in January 2021 (1,048 images), and images from birdwatchers contacted individually (928 images). From this raw data collection, we kept 1,291 images of high quality (sharp image with good exposure, displaying a nest of size > 250 pixels) for the analyses, corresponding to 873 nests belonging to 61 species (mean = 14.3 nests per species, s.d. = 26.1).

For the habitats, we first identified all habitats occupied by at least one species of weavers (del Hoyo et al., 2011). We listed a series of keywords: grassland, forest, woodland, wetland, scrub and savannah corresponding to the primary natural habitat of these species. We added two habitat keywords that do not appear in (del Hoyo et al., 2011), agricultural and city, resulting in eight categories of 'surrounding habitats' (weaver habitat). Then we identified four categories of 'foreign habitats': sandy desert, mountain, glacier and coral reef, which are not occupied by weavers (Fig. S2).

For the surrounding' and foreign habitats we gathered images from the internet by searching keywords corresponding to the twelve habitat categories in Google image and using free databases when available. We associated an image to a category based on the type and distribution of the vegetation. We selected images according to their quality (no blur, correct illumination) and angle of view (wide-angle photos depicting a landscape view of habitats as could be seen by birds in flight) (Fig. S2). The number of photos per habitat category varied from 166 to 381 (mean = 257).

Fourier slope

From each nest image, we segmented the nest out using VGG annotator (Dutta and Zisserman, 2019), replacing the original background with a white background. Each image was then cropped to make it square and resized to 1,024 x 1,024 pixels (Fig. S1B). The Fourier slope was

calculated using standard methods in empirical aesthetics (Redies et al., 2007; Graham and Redies, 2010), with Matlab 2021a (Higham and Higham, 2016). Because we are interested in the weave pattern specifically, we excluded variation in the Fourier slope caused by the global shape of the nests (see (Fig. S1) for details). For nests with more than one image (different viewing angles), we used the mean slope value. For habitats, images were also cropped to make them square, and the Fourier slope was calculated from resized images following the same procedure as for nest images. We calculated one slope value per habitat category as the mode of the distribution of slope values of all images of that category.

Fixed predictor variables

To explore the potential role of sexual selection in the evolution of nest weave in Ploceidae, we collected data on mating system and tarsus-based sexual size dimorphism as proxies of sexual selection intensity, these were included in separate models since they are not independent. In addition, we tested the effects of nest visibility and display location and their interactions with the two proxies of sexual selection. We also included two control variables: the origin of data and the size of the image. Detailed information on the predictors is given in (Table 1).

Response variables

Deviation from the presumed selection optima

The response variables describe the deviation of each nest Fourier slope to the predicted selection optima and are calculated as the absolute difference between the nest Fourier slope and the optimum. To test the quality indicator/universal preference prediction (P1), we used a selection optimum of -2, which is the slope value corresponding to maximal scale-invariance (Graham and Redies, 2010; Pouli et al., 2013). The response variable is then the distance of each nest Fourier slope to -2. For the sensory drive prediction (P2), the selection optimum varies for each nest because it corresponds to the modal Fourier slope of the habitat where the

nest was found. Using the GPS coordinates of each photographed nest, we identified which weaver habitat category (grassland, forest, woodland, wetland, scrub, savannah, agricultural and city (see del Hoyo et al., 2011)) surrounded the nest based on the landscape structure as observed on Google Earth satellite images. Each individual nest was thus associated with the modal slope value of its habitat category. We associated individual nests to habitats rather than attributing a species to a habitat because most weaver species are generalists (del Hoyo et al., 2011).

With these response variables we performed four models. Models 1.1 and 1.2 fitted the distance between the nests' Fourier slope and -2 as a response variable (P1). Model 1.1 included mating system, display location, nest visibility, image size and data origin as fixed predictors with interaction terms between mating system and display location and nest visibility. Model 1.2 was similar but used tarsus dimorphism instead of mating system. Models 2.1 and 2.2 fitted as a response variable the distance between the Fourier slope of the nest and the slope of the habitat surrounding the nest (P2). Model 2.1 and 2.2. included mating system and tarsus dimorphism, respectively.

Deviation from alternative selection optima

Any significant association between proxies of sexual selection and the nest weave deviation from presumed selection optima (of either P1 or P2) would suggest selection for matching nest weave to one of these optima. Yet to provide even stronger evidence of selection, it is necessary to show that similar associations are not found when considering alternative optima. We therefore re-fitted the four models using different selection optima. For models 1.1 and 1.2 (P1), the response variable was the deviation of the nest Fourier slope from a range of optima located between -1.5 and -2.5 (with 0.05 step, leading to 21 models with mating system as predictor and 21 with dimorphism). For models 2.1 and 2.2 (P2), the response variable was the deviation of the nest Fourier slope from the distribution mode of the surrounding habitat and

one of the four following foreign habitats: desert, mountain, glacier or coral reef (leading to a total of 10 models, five with mating system and five with dimorphism as predictors). We then examined how the model estimates of the predictors vary in each of these new models simulating alternative selection optima. Observing that the estimates of proxies of sexual selection are the highest for the optimum predicted for P1 (-2) or P2 (surrounding habitat) would thus represent additional support for a stabilizing sexual selection on the weave of weaverbird nests around this optimum.

Statistical models

For all the analyses described above, we fitted Bayesian phylogenetic generalized linear mixed models using the R-package "MCMCglmm" (Hadfield, 2010). To account for phylogenetic relatedness and allow multiple data entries per species, we included the inverse of the variance–covariance matrix and species as random effects in each model. The variance–covariance matrix was built from the recently published Ploceidae phylogenetic tree (De Silva et al., 2017). Model equations are detailed in supplementary material (Eqs S1-S4). We assumed that our response variables follow a Brownian model of evolution. Weak informative inverse-Wishart priors' distribution (V = 1 and nu = 0,002) were set for both random and fixed effects. We let the MCMC algorithm run for 5,000,000 iterations, with a burn-in period of 500,000 and a sampling interval of 5,000. Statistical significance of the posterior mean estimate was inferred when the 95% credible interval (CI) did not cross zero.

Sensory drive permutation tests

To further test the sensory drive hypothesis, we determined a null distribution of estimates by randomly permutating (500 times) the surrounding habitat associated to each nest and fitted models 2.1 and 2.2 described above on each permutated dataset. We then compared the real estimates to the null distributions of estimates. A predictor has a statistically significant effect

on the deviation of the nest Fourier slope to the Fourier slope of the surrounding habitat if its real estimate is outside the 95% interval of the null distribution.

Results

Fourier slope of nests and habitats

All nests and habitats had a Fourier slope within the range [-1.3; -2.4] (Fig. 1). The mean Fourier slope of nests was -1.99. For habitats, the mean Fourier slope was -1.80 when considering all categories of weaver habitats (surrounding habitats), and -1.89 for habitats not occupied by weavers (foreign habitats). Mean slopes differed between surrounding and foreign habitats (t test, t = -17.4, $P < 10^{-3}$), across categories of foreign habitats (ANOVA test, F = 83.5, $P < 10^{-3}$)) and across categories of weaver surrounding habitats (ANOVA test, F = 55.5, $P < 10^{-3}$)).

Presumed selection optima

When testing the quality indicator/universal preference prediction (P1), we found significant associations between the deviation of the nest weave pattern from the maximum scale-invariance (slope -2) and both proxies of sexual selection (Fig. 2) (Fig. 3). This implies that polygamous and sexually dimorphic species build more scale-invariant nests than monogamous and monomorphic species do. Display location had a significant effect in model 1.2 (tarsus dimorphism) but not in model 1.1 (mating system) (Fig. 3). None of the other predictors were significant (Fig. S3A).

Regarding the prediction of the sensory drive hypothesis (P2), we did not find any effect of the two proxies of sexual selection (Fig. 3). Thus, polygamous and sexually dimorphic species build nests whose scale-invariance does not match that of the surrounding habitat better than the nests of monogamous and monomorphic species do. Nest visibility had a significant effect

in model 2.2 (tarsus dimorphism) but not in model 2.1 (mating system) (Fig. 3). None of the other predictors were significant (Fig. S4A).

Alternative selection optima

We observed important variation in the estimates of all the tested predictors when varying the Fourier slope optimum (the reference slope to which the distance of each nest slope is calculated, Fig. 4).

Regarding the quality indicator/universal preference hypothesis (P1), for all three predictors that were significant in the previous regressions (models 1), the estimates were the largest with a response variable describing a deviation from -2 (exactly -2 for mating system and display location, close to -2 for tarsus dimorphism, Fig. 4A-C). These results strongly suggest that the maximal possible scale-invariance corresponds to an optimum and that weaverbird nests are under sexual selection to stabilize their weave scale-invariance around this optimum. In contrast, the estimate of nest visibility which was significant in model 1.1 (but not 1.2) does not peak around -2 (Fig. 4D), which is also not the case for the other predictors (Fig. S3B).

Regarding the sensory drive hypothesis (P2), we first considered nest visibility, the only predictor significantly associated to the deviation of nest slope to the surrounding habitat slope. Fig. 4H shows that, as for the surrounding habitat, some foreign habitats, when set as an optimum, also yielded significant estimates. For the other predictors, the estimates obtained using the deviation from the surrounding habitat as a response variable were always lower than at least one estimate obtained when using the deviation from a foreign habitat (Fig. S4B). These results confirm that the weave of weaverbird nests has probably not been selected to match the scale-invariance of the surrounding habitat.

Permutation test of sensory drive

For both mating system and tarsus size dimorphism, the observed estimates fell within the 95%

limits of the distribution of estimates expected according to a random association between a nest and its habitat. All other predictors were also non-significant, except display location for model 2.1 (Fig.S5).

Discussion

Weaverbirds are widely known for their exceptional nests and intricate weave patterns. We used comparative analyses to investigate whether sexual selection contributes to explain the striking regularity of the weave pattern. We found that the Fourier slope of weaves, a measure of scale-invariance and thus pattern regularity, varies across species within the family. More precisely, weave scale-invariance is closer to its maximal possible value (reflecting perfect regularity) for the nests built by polygamous and more dimorphic species. Using simulations of selection optima, we further showed that sexual selection is likely stabilizing the weave pattern close to the maximal possible scale-invariance. In contrast, we did not find any evidence that the scale invariance of nests covaries with that of their surrounding habitat, neither in monogamous and weakly dimorphic species, not in polygamous and highly dimorphic species. We discuss below the mechanisms that could explain these results and their implications.

Sexual selection for maximizing scale-invariance

The link documented here between the spatial regularity of the weave and mating system and dimorphism supports an effect of sexual selection on the evolution of weave pattern. Several non-mutually exclusive hypotheses can explain this sexual selection.

First, the scale-invariance of traits could indicate the quality of individuals. A link between scale-invariance and condition has been revealed in body trait (Pérez-Rodríguez et al., 2013) but also movements (Hausdorff et al., 1996; Stergiou and Decker, 2011; Peng et al., 2000). In sheep, goats and hens, the fractality of foraging behaviour is used to monitor welfare (Burgunder et

al., 2018; Alados et al., 1996; Maria et al., 2004) while in chimpanzees, individuals with more intense parasite infections exhibit less scale-invariant feeding patterns (Burgunder et al., 2017). The link between scale-invariant behaviour and condition suggests a mechanism explaining how pattern regularities in extended phenotypes, such as weaver nests, could be used as indicators of quality.

Second, a link between scale-invariance of weave and male quality could arise from more scale-invariant nests indicating male dexterity or cognitive capacities. In bowerbirds (Ptilonorhynchidae), and in manakins (Pipridae), brain size (which has been suggested to be an indicator of quality (Sayol et al, 2018)) is positively correlated to the complexity of the bower (Day et al.,2005) and to the gestural complexity of the courtship display (Lindsay et al., 2015), respectively. In weaverbirds, it is not known whether scale-invariance in weave pattern is associated with cognitive capacities, but inter-individual differences in the ability to construct nests have been previously shown, most notably between young, non-experienced males and older, experienced males (Collias and Collias, 1964). Measuring the scale invariance of the nests from birds falling in these different categories would be an important step to evaluate this hypothesis.

Third, more scale-invariant nests could be more resistant, have better thermal insulation or be more waterproof. The link between scale-invariance and these properties has never been studied in bird nests, but is well established in materials physics (Carpinteri, 1994; Guo et al., 2021; Kong et al., 2014). In textile industry, for example, scale-invariance is frequently monitored to detect defective fabrics (Conci and Proença, 1998), and fractal structures have been recently shown to increase abrasion resistance, hydrophobic properties and moisture permeability (Zhang et al., 2021). If it confers resistance and isolation to nests, scale-invariance would be under both natural and sexual selection for direct (nestling protection) and indirect (parental genes) benefits.

Finally, species under strong sexual selection could build more scale-invariant nests if there

is a universal preference bias for efficiently processed visual patterns. Such a preference has been evidenced in both humans (Winkielman et al., 2006; Reber et al., 2004) and other animals (Halberstadt, 2006; Fantz, 1957), and is qualified as bias because it is expressed toward stimuli which species have not co-evolved with (Renoult and Mendelson, 2019). Regarding scale-invariance, in particular, humans have a universal attraction to highly scale-invariant patterns in various inanimate (architectures (Joye, 2007) or paintings (Taylor et al., 2011)) and animate (faces (Menzel et al., 2015)) stimuli. Stimuli with low scale-invariance also cause visual discomfort (Penacchio and Wilkins, 2015). Because high scale-invariance is intrinsically efficiently processed (Spehar et al., 2015), these preferences are generally explained by the universal preference bias for efficient processing. Nevertheless, the application of this preference bias to scale-invariance still needs to be tested empirically in non-human animals.

Nest scale-invariance and sensory drive

In human psychology and neuroscience, a common explanation for the preference for a Fourier slope of -2 is that this value describes the level of scale-invariance that is dominant in natural environments. Because the brain is tuned to efficiently process images of the natural environment, any stimulus with a Fourier slope of -2 also happens to be efficiently processed, and thus to be attractive (Redies et al., 2008; Spehar and Taylor, 2013). In this study, however, we found that the mode Fourier slope of natural landscape peaks around -1.8, not around -2. When simulating a selection optimum at -1.8, none of the two main proxies of sexual selection intensity could significantly explain variation in the match between nest and habitat scale-invariance. Additionally, we found that the Fourier slope varies across natural habitats (see also (Hulse et al., 2020)). Given the observed inter-habitat variation in scale-invariance, to test the sensory drive hypothesis we also compared the statistics of nest weaves to that of their surrounding habitat. Again, we found no evidence that species with more intense sexual selection construct nests that match the visual properties of the surrounding habitat better than species with less

intense selection. Hence, the sensory drive hypothesis does not seem to explain the variability in weave pattern observed in this study. However, we cannot dismiss the possibility that, in our study, the spatial scale considered (the whole landscape around each nest) was too large, and that sensory drive operates at the scale of the immediate nest background (for an example of background influences attractiveness in human faces, (see Menzel et al., 2015)). Finally, and in contrast to the previous explanation, sensory drive could operate on an evolutionary time scale, and thus the hypothesis should be tested while considering the general environment in which species have evolved rather than the surrounding habitats of each nest. Given that sensory drive relies on the tuning of neuronal sensitivities to the physical properties of habitats (Endler and Basolo, 1998), and that this tuning is both shaped by plastic mechanisms during development and by adaptation during evolution (Sengpiel et al., 1999), an exhaustive investigation of the sensory drive hypothesis should ideally consider all temporal and spatial interactions that have occurred between the environment and the sensory system. Such an investigation is, however, outside the scope of this study.

Display location, nest visibility and other factors in relation to weave pattern

Males of more sexually selected species did not build more scale-invariant nests when they display closer to their nest or when their nest is highly visible. This may be because nests function as extended signalling phenotypes even when they are not associated with males displaying at the nests and when hidden. This is the case notably in most species of *Euplectes sp.* weavers, which are highly polygamous and dimorphic and build highly scale-invariant nests despite usually displaying far from the nest and building nests hidden in the vegetation. As single predictors, display location and nest visibility were each found to be significant in only one of the two models, and given this inconsistency, we cannot confirm their association with scale-invariance.

Finally, it is important to note that our proxies of sexual selection did not explain all the

observed variation in scale-invariance. For instance, the species that construct the more fractal nests, *Ploceus pelzelni* and *P. xanthops*, are socially monogamous and present a moderate level of sexual dimorphism. Conversely, among *Euplectes* species, *E. capensis* and *E. aureus* are exceptions in that they construct low fractal nests despite being polygamous and sexually dimorphic. Additional factors not included in our models thus certainly influence weave pattern in weaverbirds. One of these factors could be the material used to weave the nest, which is known to vary between species (del Hoyo et al., 2011) and that could be constrained by the availability of plant species in the nesting habitat. Another factor may be predation by birds and snakes, which is known to influence the general architecture of weaverbird nests (Street et al., 2022) and thus also possibly the weave.

Conclusion

Our comparative analysis revealed a general association between two common proxies of sexual selection, mating system and tarsus dimorphism, and the scale-invariance of the weave pattern of nests at the level of the whole weaverbird family. These results indicate that sexual selection likely influences the regularity of weave pattern in these nests. They also highlight the potential importance of scale-invariance in animal communication. If high scale-invariance provides simultaneous benefits in terms of physical properties of materials and visual attractiveness, then natural and sexual selection likely share similar optima for this trait and a pervasive use of scale-invariance in animal communication can be predicted in extended phenotypes, such as structures built by organisms.

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Competing interests

The authors declare no competing interests.

Tables

Table 1: Summary of the models' fixed predictors, predictions and rational to include theses predictors in the models. All continuous variable were Z-transformed before inclusion in the models. The sample sizes for each level of categorical variable are in brakets. Source might come from HWB: Handbook of the Birds of the World (del Hoyo et al., 2011) and/or from an "expert": when collected during field observations and through literature survey by D. Oschadleus. The literature used is included in the dataset available online. The sexual dimorphism index was calculated for each species as 1-(mean tarsus length of the larger sex/mean tarsus length of the smaller sex) (Lovich and Gibbons, 1992). Because in weavers, males are always larger than females (all values were less than or equal to 0) we multiplied this index by -1 to make it positive and facilitate interpretation. Predictions are formulated for either P1: nest weave is sexually selected because it indicates builder's quality or it matches a universal preference bias for efficient processing, or P2: nest weave is sexually selected by sensory drive.

Category	Fixed predictor	Source	Variable (n)	Prediction	Rational
Proxies of sexual selection intensity	Mating system	HBW	Categorical nominal Two levels: “polygamous” (36), “monogamous” (25)	Negative association: compared to monogamous species, polygamous species construct nests with a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2)	Polygamous species are more likely to be under strong sexual selection than monogamous species (Shuster, 2009)
	Tarsus size dimorphism	HBW or/and Expert	Quantitative continuous (index) (mean = -0.061, s.d. = 0.034)	Negative association: more dimorphic species construct nests with a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2)	More sexually selected species are more dimorphic (Szekely et al., 2007; Dale et al., 2007)
Nest specific predictors	Display location	Expert	Categorical nominal Two levels: “at nest” (28), “elsewhere” (33)	Negative association: species displaying “at nest” construct nests with a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2) compared to species displaying “eslwhere”	Males displaying in front of their nest use it as an ornament and thus are more likely to be selected to weave attractive nests
	Nest visibility	Expert	Categorical nominal Two levels: “visible” (36), “hidden” (25)	Negative association: “visible” nests should have a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2) compared to “hidden” nests	Males construct a visible nest to attract female attention and thus species with more visible nests might weave more attractive nests
Interaction terms	Mating system : Display location & Dimorphism : Display location			Negative interaction: polygamous and dimorphic species construct nests with a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2) compared to monogamous and monomorphic species and this difference is even smaller when the species display at the nest	Polygamous/dimorphic species may put additional effort to weave their nests when the male displays at the nest using the nest in multi-signal courtship
	Mating system : Nest visibility & Dimorphism : Nest visibility			Negative interaction: polygamous and dimorphic species construct nests that with a Fourier slope closer to -2 (P1) or to that of their surrounding habitat (P2) compared to monogamous and monomorphic species and this difference is even more smaller when the species construct visible nest	Polygamous/dimorphic species may put additional effort to weave their nest when the male constructs exposed nests using the nest in a multi-signal courtship
Control	Image size		Quantitative continuous (pixels) (mean = 1.719, s.d. = 907)	None	The Fourier slope is slightly related to image quality
	Origin of data		Categorical nominal Two levels: "museum" and "wild"	None	Photo parameters change depending on how the data were collected

Figures

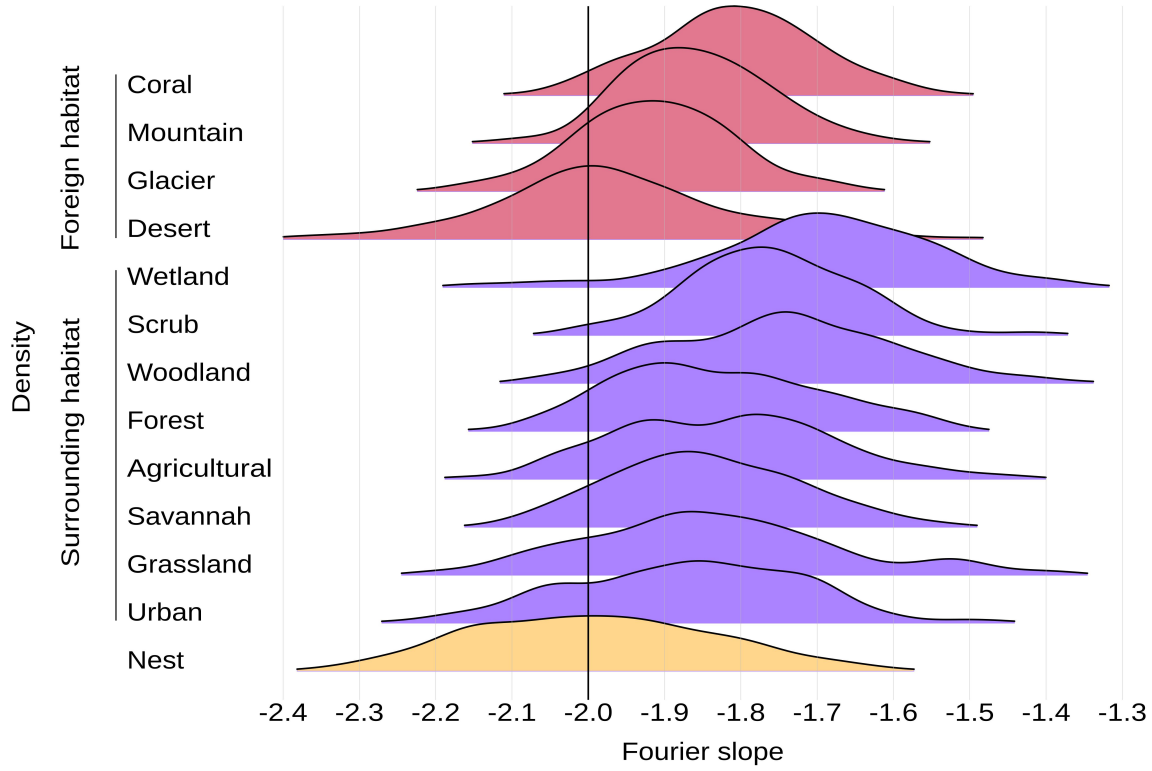

Figure 1: Fourier slopes of nests and habitats. Density distributions of the Fourier slopes are displayed separately for the nests (orange) and the different categories of habitats: surrounding habitats (purple) and foreign habitats (red).

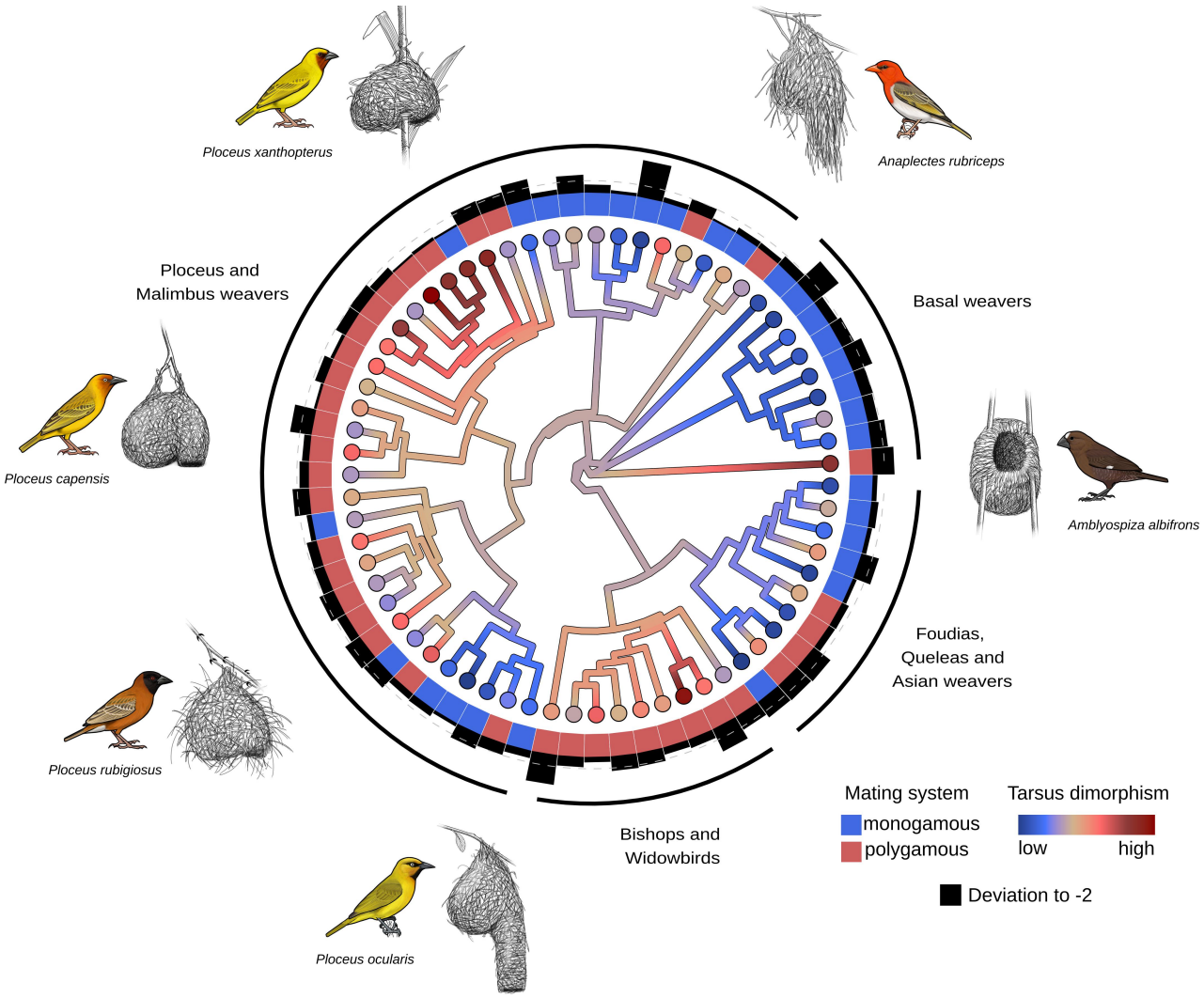

Figure 2: Phylogenetic distribution of the two proxies of sexual selection and association to the scale-invariance of the nests. The colours of circles at branch tips represent the variation in tarsus dimorphism (blue and red corresponding to low and high sexual dimorphism, respectively). The colour gradient within the tree branches indicates the predicted ancestral state for that variable. Coloured squares above branch tips indicate mating system. Black bars give the deviation of nest Fourier slope to the maximal scale-invariance (slope -2): small bars indicate species whose nest weave has an average Fourier slope close to -2 (highly scale-invariant). The scale-invariance of the nest was corrected for its form, its origin and the dimension of the image before calculating the deviation to -2. The fine dotted line around the phylogeny corresponds to the mean deviation to -2. This graph includes six species that were

not included in our models due to missing data for other predictors.

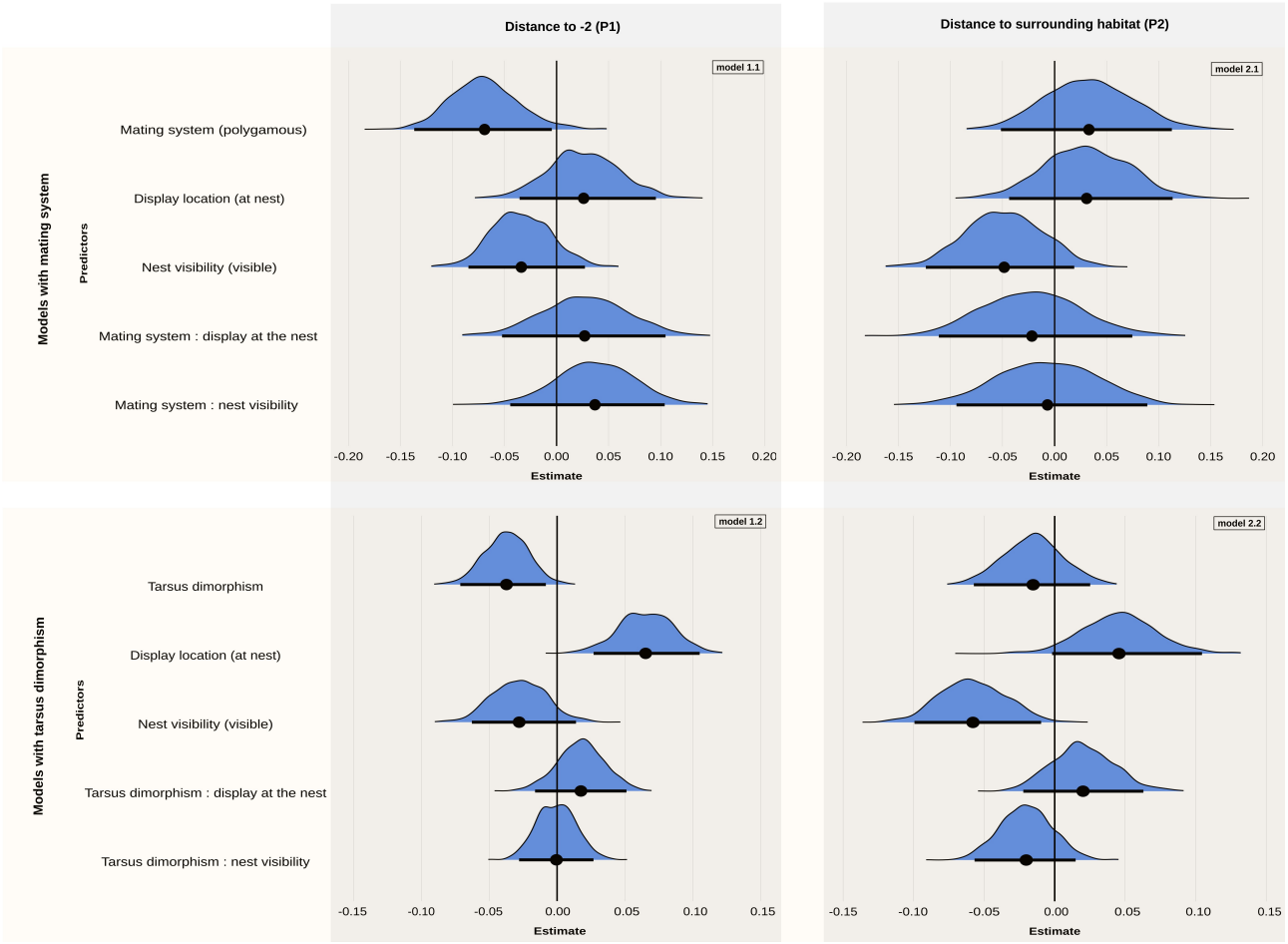

Figure 3: Estimates of the predictors tested in the four models. The posterior distribution of the estimates of each of the tested predictors are shown with horizontal bars representing 95% of the distribution and the points indicating the means. The first column (models 1) represents the effects of the tested predictors on the deviation of the nest Fourier slope to a slope of -2. Those models (one with mating system (model 1.1) and the other with dimorphism (model 1.2)) test P1: species under stronger sexual selection construct more scale-invariant nests. The second column (models 2: 2.1 and 2.2) represents the effects of the tested predictors on the deviation of nest Fourier slope to the mode of the Fourier slope of its surrounding habitat. Those models test P2: through the effect of sensory drive, sexual selection leads nests to match the scale-invariance of their surrounding habitat.

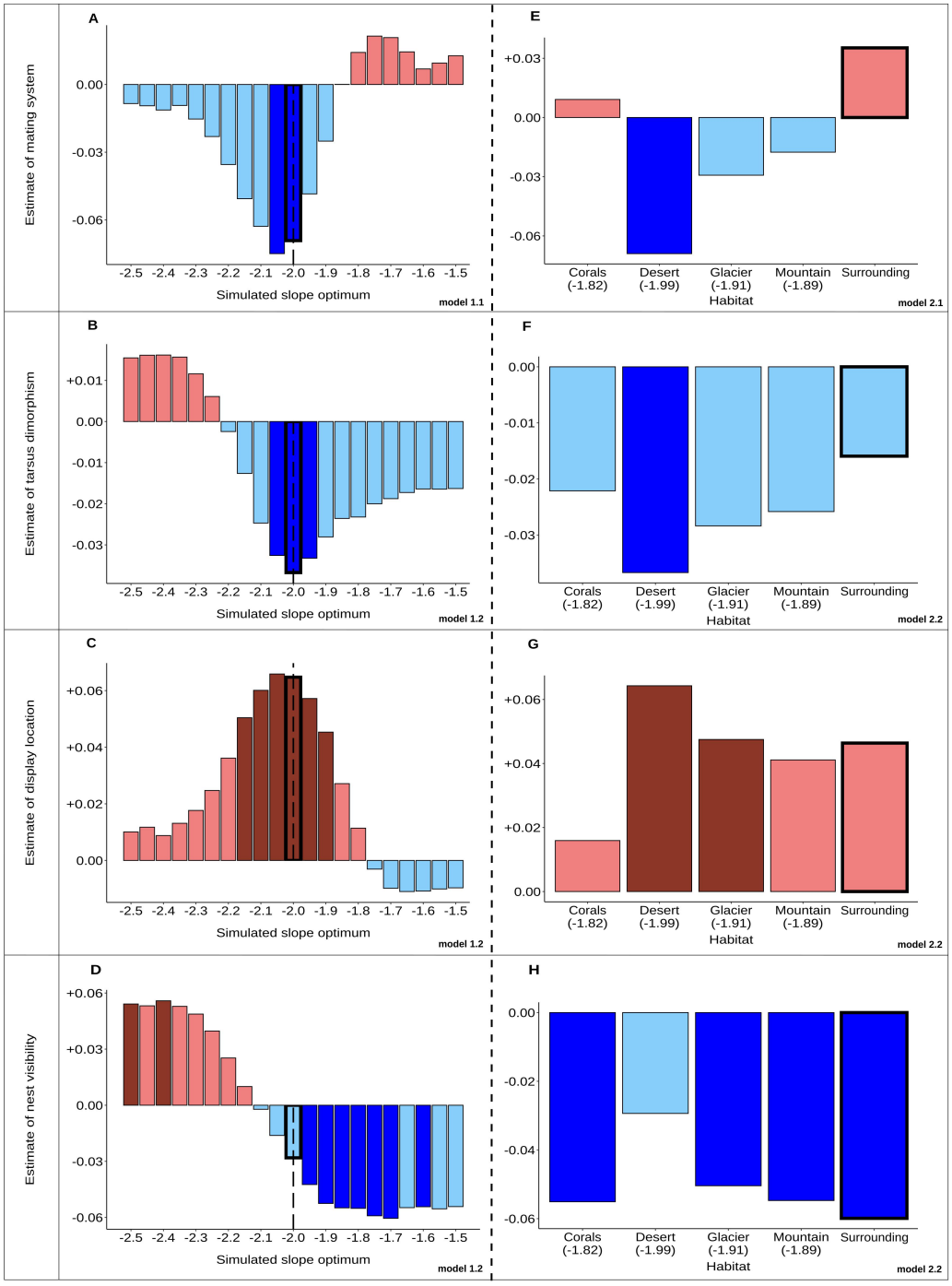

Figure 4: Variation of model estimates when simulating different slope optima. (A-D) The response variable is the distance between the nest Fourier slope and a Fourier slope reference value, named simulated slope optimum, within the range [-2.5; -1.5]. These barplots allow to compare estimates when the reference value is -2 and when it is others values around -2. (E-H) The response variable is the distance between the nest Fourier slope and one reference value corresponding to the Fourier slope of the surrounding habitat or other habitats in which

weaver species never lived and are totally naive (foreign habitats). Red bars correspond to positive estimates and blue bars to negative estimates. Darker bars correspond to significant effects (when lower and upper confident intervals do not cross 0). Bars with a thick outline correspond to the estimates shown in Figure 3. Dotted lines correspond to the presumed selection optima. The names of the models are written at the bottom right of each panel. In models 1, the response variable is the deviation of the nest Fourier slope to -2, while models 2, it is the deviation of the nest Fourier slope to its surrounding habitat. Models 1.1 and 2.1 include mating system as a predictor while models 1.2 and 2.2 include tarsus dimorphism.

Supplementary materials

$$y_{i,j} = \beta_0 + \beta_1 m_i + \beta_2 l_i + \beta_3 v_i + \beta_4 d_i l_i + \beta_5 d_i v_i + \beta_6 o_{i,j} + \beta_7 n_{i,j} + s_i + p_i + \epsilon_{i,j} \quad \text{(S1)}$$

$$y_{i,j} = \beta_0 + \beta_1 d_i + \beta_2 l_i + \beta_3 v_i + \beta_4 d_i l_i + \beta_5 d_i v_i + \beta_6 o_{i,j} + \beta_7 n_{i,j} + s_i + p_i + \epsilon_{i,j} \quad \text{(S2)}$$

$$z_{i,j} = \beta_0 + \beta_1 m_i + \beta_2 l_i + \beta_3 v_i + \beta_4 d_i l_i + \beta_5 d_i v_i + \beta_6 o_{i,j} + \beta_7 n_{i,j} + s_i + p_i + \epsilon_{i,j} \quad \text{(S3)}$$

$$z_{i,j} = \beta_0 + \beta_1 d_i + \beta_2 l_i + \beta_3 v_i + \beta_4 d_i l_i + \beta_5 d_i v_i + \beta_6 o_{i,j} + \beta_7 n_{i,j} + s_i + p_i + \epsilon_{i,j} \quad \text{(S4)}$$

$$s \sim \mathcal{N}(0, \sigma_S^2 \mathbf{I})$$

$$p \sim \mathcal{N}(0, \sigma_P^2 \mathbf{C})$$

$$\epsilon \sim \mathcal{N}(0, \sigma_R^2 \mathbf{I})$$

equation	S1	S2	S3	S4
model	1.1	1.2	1.3	1.4

Equations S1-S4: The four modeled equations. We modeled the distance of the nest slope to (i) -2, here y, and to (ii) the surrounding habitat mode slope, here z, of species i and individual j explained by several fixed predictors: tarsus size dimorphism d and mating system m used as proxies for sexual selection intensity, display location l, nest visibility v, tarsus dimorphism or mating system in interaction with display location and nest visibility respectively dl and dv or ml and mv. Note that $m_i = 0$ when i is monogamous and 1 when i is polygamous, $l_i = 0$ when i do not display at the nest and 1 when i display at the nest, $v_i = 0$ when i construct hidden nest and 1 when i construct visible nest. We also include two additionally fixed predictors to control for the origin of the data o ($o_j = 0$ when the nest of j was photographed in museums and 1 when the nest of j was photographed in the wild) and the dimension of the nest image n. To account for the non-independence of data collected on the same species, the multiple measurement effect, we included species identity s as random effect. Aslo, to account for the non-independence between species we add p the phylogenetic effect as random effect. The final term ϵ correspond to the residual error term. The three last terms are assumed to be normally distributed where $\mathbf{I}$ correspond to the identity matrix and $\mathbf{C}$ the phylogenetic correlation matrix where element $C_{i,i'}$ is the amount of time that elapsed

(since the common ancestor of all sampled taxa) before the speciation event that resulted in taxa i and i'. Our model is also estimating three variances: σ^2_S the intraspecific variance caused by the species contingent characteristics and σ^2_P the intraspecific variance caused by evolutionary history (the phylogenetic effect). Together σ^2_S and σ^2_P accounts for the between-species variability. Finally σ^2_R is the residual error corresponding to the within-species variance of the trait (but also including measurement error and environment effect).

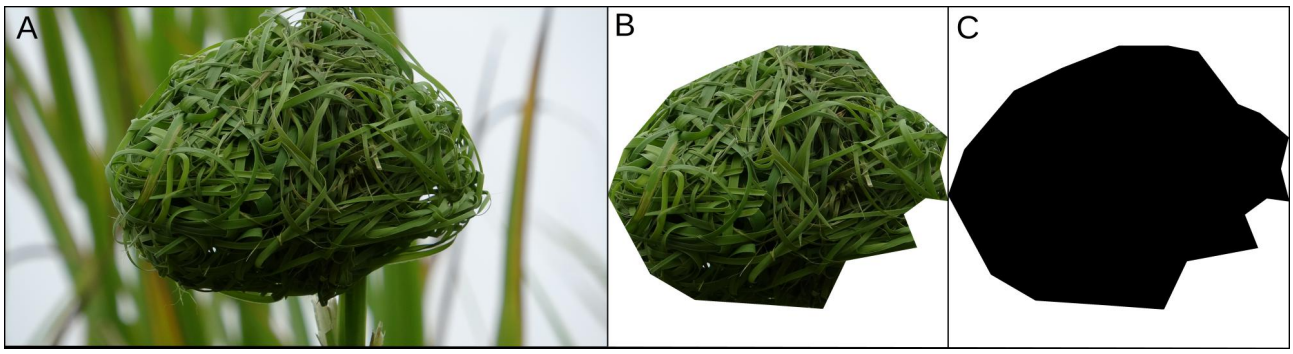

Figure S1: Fourier analysis pipeline. Photos of a nest of Eastern golden weaver (*Ploceus subaureus*) (A) original photo, (B) cropped nest, (C) cropped silhouette. The Fourier slope describes scale-invariance in the whole image, and thus is influenced both by the weave pattern weave and the overall shape of the nest. Because we were interested in analyzing the weave pattern only, we excluded variations caused by nest shape. To do so, for each cropped nest image (B) we created a corresponding binary silhouette image in which pixels within the nest were all set to 0 (black) (C). The Fourier slope was calculated both for the nest image (B) and the silhouette image (C). We then performed a linear regression analysis with the nest Fourier slope as a response variable and the silhouette Fourier slope as predictor, and used the residuals as new values of Fourier slope for the subsequent analyses. An alternative could have been to analyse square images randomly sampled from within the nest; however, in preliminary analyses we found that such images were too small and thus had a Fourier slope strongly influenced by artefacts (aliasing). To calculate the Fourier slope, we transformed each image into the frequency domain using a Fast Fourier Transform and we computed the rotational average of the power spectrum for each frequency. Power spectrum and frequency were analysed in the log–log plane. We performed a least squares fit of a regression line to the log–log power spectrum, fitting data points binned at regular intervals. Only the frequency range between 10 and 256 cycles per image was used for fitting. The Fourier slope corresponds to the slope of the fitted regression line.

Figure S2: Photos of habitats. (A) Habitats surrounding weaver nests (left to right): agricultural, grassland, city, wetland, savannah, forest, scrub, woodland. (B) Foreign habitats, where the weavers do not live (left to right): coral reef, sandy desert, mountain, glacier.

A

Parameter	Estimate	95% CI lower	95% CI upper
Intercept	0.199	0.135	0.255
Mating system (polygamous)	-0.069	-0.141	-0.01
Display location (at nest)	0.027	-0.042	0.084
Nest visibility (visible)	-0.034	-0.087	0.024
Collected (wild)	-0.025	-0.048	-0.003
Image size	-0.011	-0.018	-0.003
Mating system (polygamous) : display location (at nest)	0.026	-0.052	0.106
Mating system (polygamous) : nest visibility (visible)	0.037	-0.034	0.112
Phylogenetic variance	0.001	0	0.004
Between species variance	0.001	0	0.002
Within species variance	0.009	0.008	0.009

Parameter	Estimate	95% CI lower	95% CI upper
Intercept	0.152	0.095	0.206
Tarsus dimorphism	-0.037	-0.068	-0.005
Display location (at nest)	0.065	0.024	0.101
Nest visibility (visible)	-0.028	-0.065	0.009
Collected (wild)	-0.021	-0.044	0
Image size	-0.011	-0.019	-0.004
Tarsus dimorphism : display location (at nest)	0.018	-0.014	0.051
Tarsus dimorphism : nest visibility (visible)	-0.001	-0.031	0.023
Phylogenetic variance	0.002	0	0.004
Between species variance	0.001	0	0.002
Within species variance	0.009	0.008	0.009

B

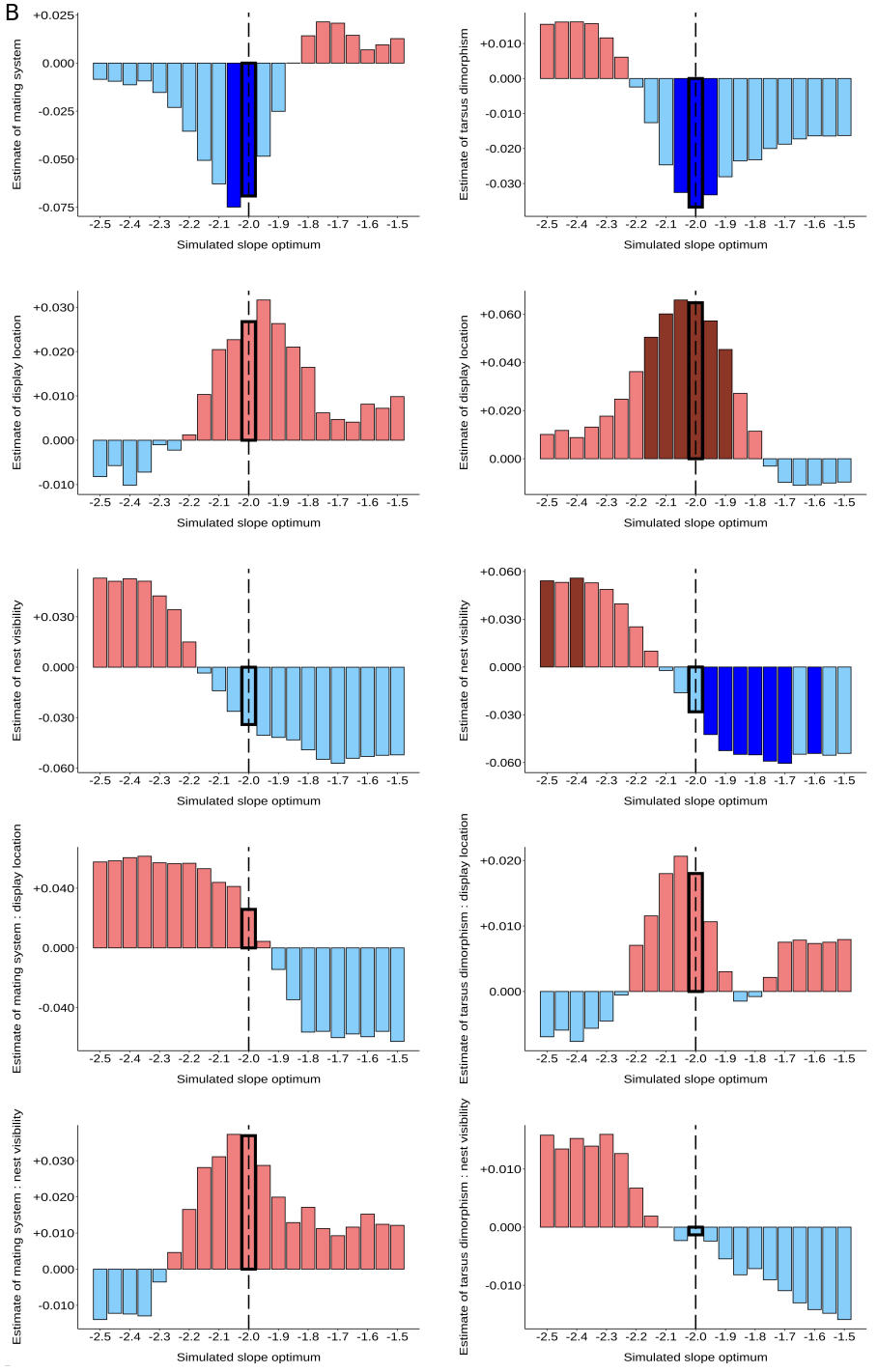

Figure S3: Relationship between the deviation of the nest Fourier slope to a Fourier slope of -2/other values and predictors. (A) Complete models' summaries (model 1.1 left table and model 1.2 right table). (B) Comparison of predictors' estimate obtained when

computing as response the nests Fourier slope deviation to the maximal scale-invariance (Fourier slope of -2, the predicted selective optima) and to other values of Fourier slope between -2.5 and -1.5, the simulated slopes optimum. Red bars correspond to positive estimates and blue bars to negative estimates. Bars that are darker correspond to significant effects (when lower and upper CI do not cross 0). Bars with a thick outline correspond to the estimates shown in the models' summaries (A). Dotted lines correspond to the presumed selection optima.

A

Parameter	Estimate	95% CI lower	95% CI upper
Intercept	0.116	0.029	0.183
Mating system (polygamous)	0.035	-0.043	0.117
Display location (at nest)	0.03	-0.046	0.105
Nest visibility (visible)	-0.045	-0.112	0.031
Collected (wild)	0.145	0.111	0.177
Image size	-0.053	-0.063	-0.043
Mating system (polygamous) : display location (at nest)	-0.023	-0.113	0.067
Mating system (polygamous) : nest visibility (visible)	-0.01	-0.109	0.071
Phylogenetic variance	0.002	0	0.005
Between species variance	0.002	0	0.003
Within species variance	0.017	0.015	0.018

Parameter	Estimate	95% CI lower	95% CI upper
Intercept	0.118	0.052	0.182
Tarsus dimorphism	-0.016	-0.056	0.024
Display location (at nest)	0.046	-0.007	0.094
Nest visibility (visible)	-0.06	-0.11	-0.016
Collected (wild)	0.144	0.113	0.175
Image size	-0.054	-0.064	-0.043
Tarsus dimorphism : display location (at nest)	0.021	-0.021	0.062
Tarsus dimorphism : nest visibility (visible)	-0.02	-0.053	0.009
Phylogenetic variance	0.002	0	0.006
Between species variance	0.001	0	0.003
Within species variance	0.017	0.015	0.018

B

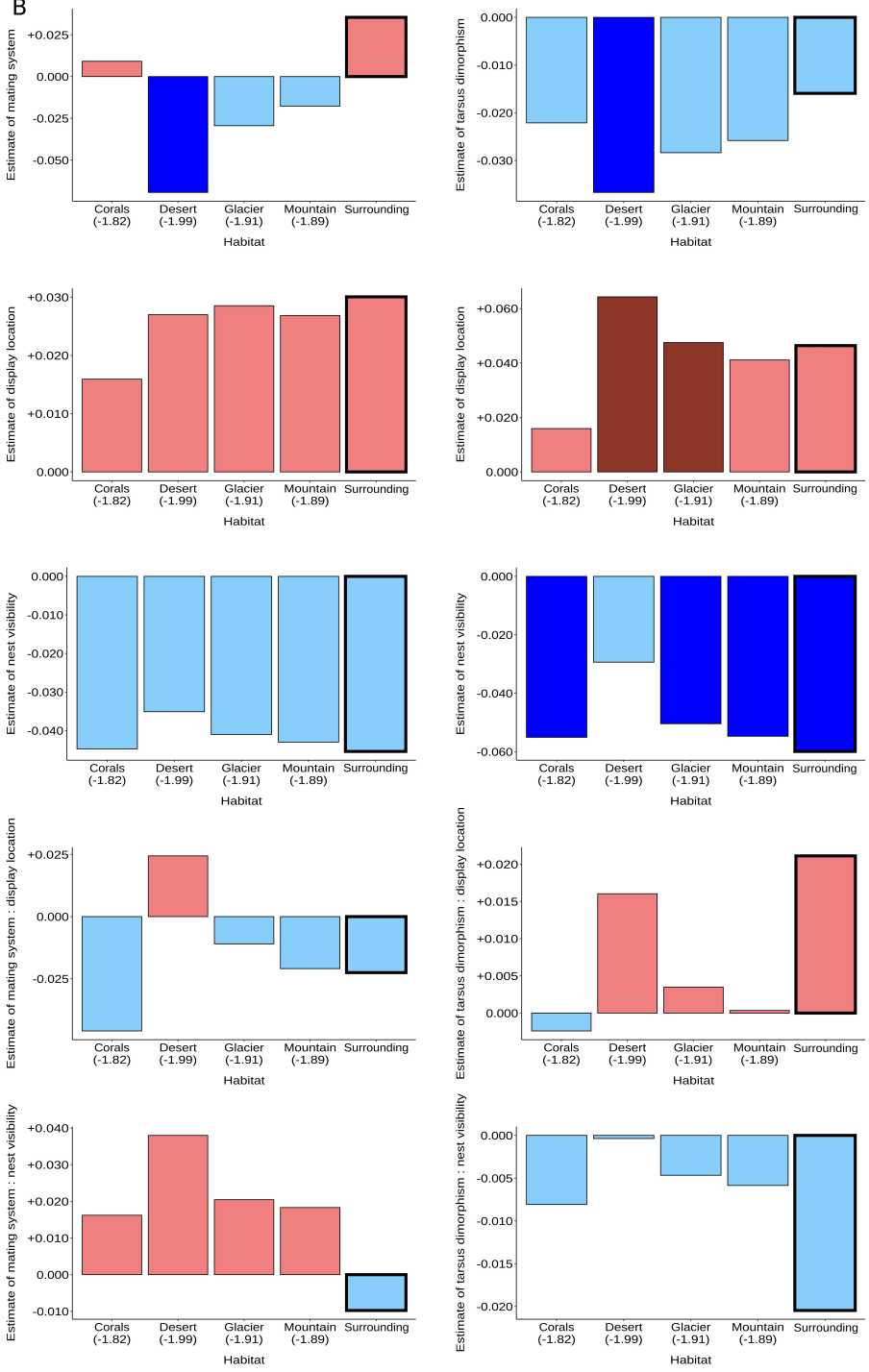

Figure S4: Relationship between the deviation of the nest Fourier slope to the surrounding/foreign habitats and predictors. (A) Complete models' summaries (model 2.1 left table and model 2.2 right table). (B) Comparison of predictors' estimates obtained when computing as response the nests Fourier slope deviation to the Fourier slope of the nest

surrounding habitat and to the foreign habitats. Red bars correspond to positive estimates and blue bars to negative estimates. Bars that are darker correspond to significant effects (when lower and upper CI do not cross 0). Bars with a thick outline correspond to the estimates shown in the models' summaries (A) and also represent the presumed selection optima.

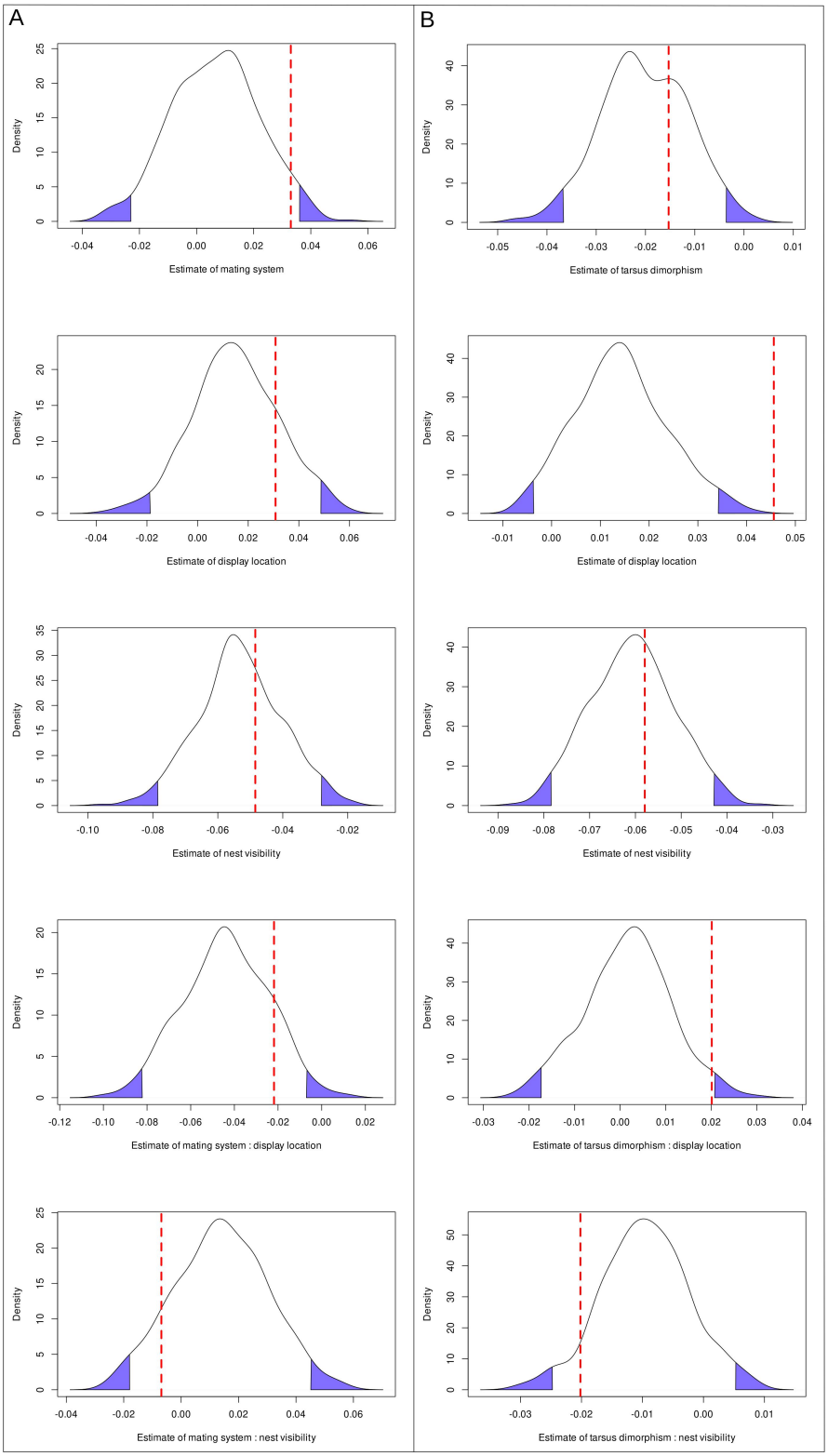

Figure S5: Density distribution of the permutation test. Density distribution of the model estimates after 500 permutations of the nests and their surrounding habitats for the model's predictors to test the sensory drive prediction for (A) model 2.1 and (B) model 2.2. The blue surface under the curve represents 5% of the distribution. The red dotted line represents

the estimate obtained with the original dataset (without permutation).