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# Sexual and natural selection in the evolution of extended phenotypes: the use of green nesting material in starlings

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## Abstract

Although sexual selection is typically considered the predominant force driving the evolution of ritualized sexual behaviours, natural selection may also play an important and often underappreciated role. The use of green aromatic plants among nesting birds has been interpreted as a component of extended phenotype that evolved either via natural selection due to potential sanitary functions or via sexual selection as a signal of male attractiveness. Here, we compared both hypotheses using comparative methods in starlings, a group where this behaviour is widespread. We found that the use of green plants was positively related to male-biased size dimorphism and that it was most likely to occur among cavity-nesting species. These results suggest that this behaviour is likely favoured by sexual selection, but also related to its sanitary use in response to higher parasite loads in cavities. We speculate that the use of green plants in starlings may be facilitated by cavity nesting and was subsequently co-opted as a sexual signal by males. Our results represent an example of how an extended phenotypic component of males becomes sexually selected by females. Thus, both natural selection and sexual selection are necessary to fully understand the evolution of ritualized behaviours involved in courtship.

## Introduction

Individuals exhibit a variety of morphological and behavioural traits in courtship that provide reliable information about the quality of the sender (Borgia & Gore, 1986; Ryan, 1998; Maynard-Smith & Harper, 2003; Emlen *et al.*, 2012), and can even constitute a nonmorphological extension of the individual's phenotype (i.e. extended phenotype, *sensu* Dawkins, 1982). For example, males of several bird species collect materials and build complex structures, perform exaggerated exhibitions of nesting components or incorporate odd materials into their nest structures (Collias & Collias, 1984; Borgia & Gore, 1986; Soler *et al.*, 1998; Hansell, 2000). These behaviours are often used to attract partners, or to incentivize reproductive effort in their partners after mating, through displays of a particular breeding activity related to their condition, breeding status or experience (Hansell, 2000; Veiga *et al.*, 2006; Trnka & Prokop, 2011; Moreno, 2012; Tomás *et al.*, 2013; García-Navas *et al.*, 2015). Although sexual selection for improving mating and fertilization success is generally considered the predominant force driving the evolution of these ritualized behaviours, natural selection may also play an important role in their origin and maintenance (e.g. Candolin & Tukiainen, 2015).

One of the best-studied examples of these extended phenotypic signalling behaviours is the presence of green plants, flowers and fresh aromatic herbs in bird nests, which are incorporated by breeders and do not form part of the nest structure. A variety of naturally and sexually selected nonmutually exclusive hypotheses have been suggested to explain the evolution of the use of green nesting material in birds. First, the volatile compounds of green plants could positively affect

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nestling health, either because they reduce ectoparasite and bacterial loads (the 'nest protection hypothesis') or because they directly favour nestling condition and immune response (the 'drug hypothesis') (Clark, 1991; Gwinner & Berger, 2005; Mennerat *et al.*, 2009a,b). Both of these hypotheses posit that green nesting material improves offspring condition and fitness, and therefore, the behaviour would be favoured by natural selection. Second, the 'sexual selection hypothesis' suggests that the green plant-carrying behaviour is related to male quality, condition or social status, and is therefore favoured by sexual selection (e.g. Fauth *et al.*, 1991; Pinxten *et al.*, 2003; Brouwer & Komdeur, 2004; Veiga *et al.*, 2006; Polo *et al.*, 2015).

Supporting the idea that natural selection favoured the use of green nesting material in birds, a review of the natural history literature on nesting behaviour and composition of nesting material revealed that passerines nesting in cavities, which typically reuse old nest sites, were more likely to incorporate green plants into their nests, whereas passerines nesting in open nests were less likely to use green nesting material (Clark & Mason, 1985; Scott-Baumann & Morgan, 2015). For example, female blue tits, *Cyanistes caeruleus*, incorporate plants in the nest from the end of nest construction until fledgling, favouring nestling condition and immune response (Mennerat *et al.*, 2009b; Tomás *et al.*, 2013). In contrast, most studies of starlings suggest that males carry green plants to nests to attract females during courtship, rather than to control ectoparasite and bacterial loads during the nesting period (Dubiec *et al.*, 2013; Scott-Baumann & Morgan, 2015). Moreover, male starlings generally incorporate green plants only during the beginning of the breeding period (European starling, *Sturnus vulgaris*, Fauth *et al.*, 1991; and spotless starling, *Sturnus unicolor*, Veiga *et al.*, 2006), and then, females remove green plants from nests after beginning egg laying (Veiga & Polo, 2012). These observations contradict what would be expected if these plants provided a beneficial function to their offspring (Polo *et al.*, 2015; Scott-Baumann & Morgan, 2015). Moreover, males carry more plants when females are close to the nest box (Brouwer & Komdeur, 2004), and polygynous males incorporate more green plants to each of their nests than monogamous males (Veiga *et al.*, 2006), both of which further support a sexually selected function for the use of green plants.

Here, we attempt to understand the relative importance of natural and sexual selection in modulating the evolution of an extended phenotypic trait involved in sexual signalling, the presence of green nesting material among starling species. Based upon the assumption that sexual size dimorphism reflects the intensity of sexual selection and sex-specific selective pressures (Moore, 1990; Dunn *et al.*, 2001; Cotton *et al.*, 2004; Ford, 1994; Bonduriansky & Rowe, 2005; Rubenstein & Lovette, 2009) and that cavity nests are more prone to be infested with ectoparasites and bacteria (Collias & Collias, 1984; Marshall, 1981; see also Clark & Mason, 1985; Scott-Baumann & Morgan, 2015), we tested the predictions that (i) the use of nonstructural green nesting material is more frequent among sexually dimorphic species and (ii) green nesting material evolved as a sanitary behaviour, thus being more prevalent among cavity-nesting species, group-living species and/or species living in humid habitats, which typically are more susceptible to contagion and transmission of parasites (Rózsa *et al.*, 1996; Piersma, 1997; Heeb *et al.*, 2000; Moyer *et al.*, 2002; Tella, 2002).

## Material and methods

### Comparative data

We collected information on nesting materials, other life-history traits (i.e. nest type, social system and habitat type; Urban *et al.*, 1997; Feare & Craig, 1999 and Craig *et al.*, 2009); and adult morphology (Feare & Craig, 1999; Lislevand *et al.*, 2007; Dunning, 2007) for up to 47 starling species, roughly half of the Sturnidae in the world. A species was considered to use green nesting material ($n$ = 28 species) only when one of the sources explicitly reported the presence of nonstructural green leaves, flowers, fresh aromatic plants or small green branches. We only categorized a species as not using green plants when there was no mention of the presence of these materials, but there was information about other nesting components (e.g. dry grass and twigs, feathers, hairs, snakeskin or plastic). Species with incomplete descriptions of nesting materials were excluded, as well as those where information was reported from only a single nest. Life-history variables were considered as discrete characters: nest type (open or cavity), social behaviour (group-living or solitary) and habitat type (grassland, scrubland or closed forest).

Sexual dimorphism was determined as the standardized residuals of the phylogenetically controlled linear regression of male over female morphological measurements (log-transformed) for the following traits: body mass ($n$ = 31 species), wing length ($n$ = 47 species), tail length ($n$ = 46 species) and tarsus length ($n$ = 45 species). Considering all of the available information, we obtained complete morphological data for 29 species. When dimorphism in body mass was excluded, the number of species with complete data increased to 44.

### Statistical analyses

We controlled for relatedness among starling species using a subset of the phylogenetic reconstruction of Maia *et al.* (2013). The phylogeny was initially built for all 113 starling species and five out-groups using sequences from up to five mitochondrial coding genes and four nuclear introns (Lovette & Rubenstein, 2007;

Lovette *et al.*, 2008). The topology and branch lengths were inferred using Bayesian methods in BEAST (Drummond & Rambaut, 2007; see details in Maia *et al.*, 2013).

Sexual dimorphism was characterized as the linear combination of the morphological traits outlined above using phylogenetic principal component analyses (pPCA, Revell, 2009). In a first pPCA we conducted, all four traits (body mass, wing, tail and tarsus lengths) were considered (pPCA1; $n = 29$ species). However, to increase the sample size, we performed a second pPCA excluding body mass (pPCA2; $n = 44$ species). The pPCA1 described 75% of total variance through its first two components (PC1.1, 46% and PC1.2, 29%), and the pPCA2 described 86% of variance (PC2.1, 62% and PC2.2, 24%). Both first components (PC1.1 and PC2.1) had positive and high loadings for the dimorphism in wing length and tarsus length (and, in the case of PC1.1, also body mass; Table 1), whereas the second components (PC1.2 and PC2.2) were mostly defined by dimorphism in tail length (Table 1). Thus, the first principal components were interpreted as general descriptors of dimorphism in body size, whereas the second principal components described dimorphism in tail length relative to body size.

We first explored the use of green nesting material in relation to each morphological trait (body mass, wing, tail and tarsus length) using phylogenetic logistic regressions. We then analysed the use of green plants in relation to the components of dimorphism, with the presence or absence of green nesting material as the response variable and the first two principal components as predictor variables. We also analysed the phylogenetic principal components in relation to life-history traits (nest type, social system, habitat type, use of green nesting material and use of other odd nesting material) to identify potential confusing covariations between sexual dimorphism and other predictor variables. Analyses were conducted using the packages phylolm (Ho & Ané, 2014) and phytools (Revell, 2012) in R v3.2.2 (R Core Team, 2015).

**Table 1** Phylogenetic principal component analysis for morphological variables of sexual dimorphism: The phylogenetic signal (lambda), standard deviation, proportion of variance and factor loadings are presented for pPCA1 (with body mass, wing length, tail length and tarsus length dimorphism; $n = 29$ species) and pPCA2 (in which body mass was excluded to increase the sample size; $n = 44$ species).

| | pPCA1 | | | pPCA2 | | |
|---|---|---|---|---|---|---|
| | lambda = 6.67e–5 | | | lambda = 0.26 | | |
| | PC1.1 | PC1.2 | PC1.3 | PC2.1 | PC2.2 | PC2.3 |
| Phylogenetic PCA | | | | | | |
| Standard deviation | 1.361 | 1.076 | 0.818 | 1.363 | 0.847 | 0.651 |
| Proportion of variance | 0.463 | 0.289 | 0.167 | 0.619 | 0.239 | 0.141 |
| Factor loadings | | | | | | |
| MassD | 0.649 | −0.465 | 0.579 | – | – | – |
| WingD | 0.873 | 0.259 | 0.012 | 0.856 | 0.154 | 0.493 |
| TailD | 0.087 | 0.935 | 0.281 | 0.696 | −0.703 | −0.146 |
| TarsusD | 0.813 | −0.007 | −0.505 | 0.800 | 0.446 | −0.400 |

To explore the evolution of green plant use in relation to nest type (open or cavity), social behaviour (group-living or solitary) and habitat type (grassland, scrubland or closed forest), we examined the transition rates between states of green plant use conditioned on each of those traits in separate models of ancestral state reconstruction (Pagel & Meade, 2006). In a first model, rates of gain of the behaviour were considered to be the same in (i.e. not influenced by) the presence or absence of the other trait, and therefore four transitions were estimated (gains and losses of adding greenery and gains and losses of the ecological trait examined). This model was then compared with a full model in which transitions in the same direction (i.e. all gains or all losses) were allowed to have different rates when occurring in the presence or absence of the conditional trait. This model therefore describes a scenario in which transition rates for the evolution of adding green nesting material are conditional on the ecological trait being examined, and was described by eight parameters (gains and losses of greenery in the presence and in the absence of the secondary trait, as well as gains and losses of the secondary trait in the presence and in the absence of greenery addition). We compared the maximum likelihood of both models and considered the evolution of adding nest greenery to be associated with the ecological trait in question when the 8-parameter model was preferred over the 4-parameter model (i.e. when different transition rates for gain and loss of greenery depending on the state of the secondary trait improved model fit). The relationship between the use of plants and habitat type (with three states corresponding to the three classes of habitat) was analysed as a multistate character, and therefore, an eight-parameter model of independent evolution was compared with the full 18-parameter model in which transition rates were allowed to vary among types of habitat. Model parameters were estimated using BAYESTRAITS v2 (Pagel & Meade, 2006).

## Results

### Sexual selection

The use of green leaves, flowers and aromatic plants in nests occurred more frequently among sexually dimorphic starlings (Fig. 1). In particular, species that carry green plants were more dimorphic in body mass (phylogenetic logistic regression: $t = 2.42$, df = 29, $P = 0.02$) and wing length dimorphism ($t = 2.86$, df = 45,

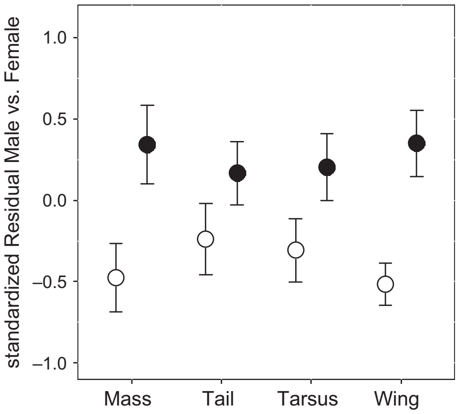

**Fig. 1** Differences in sexual dimorphism (mean standardized residuals ± SE) between starling species that use green nesting material (black circles) and those with no evidence of the use of green plants (white circles).

$P = 0.01$). There were similar but nonsignificant trends in tail length dimorphism ($t = 1.07$, df = 44, $P = 0.29$) and tarsus length dimorphism ($t = 1.62$, df = 43, $P = 0.11$) (Fig. 1). The probability of using green nesting material increased with the degree of male-biased size dimorphism (Fig. 2). Specifically, the use of green plants was positively and significantly associated with both first components PC1.1 and PC2.1, which described dimorphism in body mass, wing length, and tarsus length (Table 2). However, there were no significant relationships with the second components (describing tail length dimorphism, Table 2). Sexual size dimorphism (PC2.1) was not related to habitat type ($t = 1.07$, $P = 0.29$), nest type ($t = -1.01$, $P = 0.32$), social system ($t = -1.21$, $P = 0.23$) nor to other odd types of nesting materials (green plants: $t = 2.39$, $P = 0.02$; other odd materials: $t = -1.39$, $P = 0.17$). When all of these variables were considered together in a logistic model, the use of green nesting material maintained a positive and significant relationship with sexual size dimorphism (PC2.1) and nest type, but there was no relationship with habitat type or social system (Table 3).

### Natural selection

The model that considered independent transition rates for the evolution of the use of green nesting material when in cavities and open nests was preferred over the model with equal rates (LRT = 13.37, df = 4, $P = 0.01$; Fig. 3). This model suggests that gains in the use of green plants are about nine times more likely in cavity-nesting species, whereas loss of the behaviour is about four times more likely in open-nesting species. Transitions to the use of green nesting material were not correlated with transitions in social system ($\chi^2 = 3.15$, df = 4, $P = 0.53$) nor in habitat type ($\chi^2 = 4.12$, df = 10, $P = 0.94$).

## Discussion

We found that the use of green plants, leaves, flowers and aromatic herbs in nests is positively related to both sexual size dimorphism and cavity nesting in starlings. The use of green nesting material among sexually dimorphic species supports the idea that this behaviour is involved in sexual selection (Moore, 1990; Dunn *et al.*, 2001; Cotton *et al.*, 2004; Ford, 1994; Bonduriansky & Rowe, 2005; Emlen *et al.*, 2012). This result is consistent with experimental studies in two species of starlings showing that the amount of plants carried by males plays a role in mate attraction (Brouwer & Komdeur, 2004) and is positively related to male mating status (Veiga *et al.*, 2006). Female preference for males that carry more green plants to nests may have exaggerated this trait, especially in species under stronger and more asymmetric sexual selection (i.e. those with marked size dimorphism) (Fig 2). Thus, this result is consistent with the hypothesis that green nesting material played a major role in sexual signalling within the Sturnidae (Fauth *et al.*, 1991; Pinxten *et al.*, 2003; Brouwer & Komdeur, 2004; Veiga *et al.*, 2006).

Our results also show that the use of green plants was more likely to evolve among cavity-nesting species. That is, gains in the use of green plants were more common in cavity-nesting species whereas losses were more common in open-nesting species. It is worth noting, however, that nest type distribution in this group is unbalanced (with 39 cavity-nesting species and only eight open-nesting species) and that both traits were evolutionarily labile, which made it difficult to determine their ancestral states. However, this result is consistent across two different types of comparative analyses (i.e. PGLS and analysis of transition rates) and also with previous studies (Clark & Mason, 1985). Because cavities might be more susceptible to be colonized by parasites (Collias & Collias, 1984; Marshall, 1981), the use of green plants in cavity-nesting species suggests that this behaviour likely has a sanitary function in this group (Scott-Baumann & Morgan, 2015). In support of this idea, Gwinner & Berger (2005) found fewer bacteria in nests treated with green plants in the European starling. However, most experiments with starlings have not found that green nesting material reduces ectoparasite loads in nests (Fauth *et al.*, 1991; Gwinner *et al.*, 2000; Brouwer & Komdeur, 2004; reviewed in Scott-Baumann & Morgan, 2015). Furthermore, males did not carry more green plants when nests were experimentally contaminated with ectoparasites (Brouwer & Komdeur, 2004). This mixed evidence on the sanitary function of green nesting material in starlings could be attributed to the fact that most experimental studies have focused on only specific best-studied groups of ectoparasites. Our results are consistent with the hypothesis that green plants in nests may play a sanitary function, likely affecting some groups of

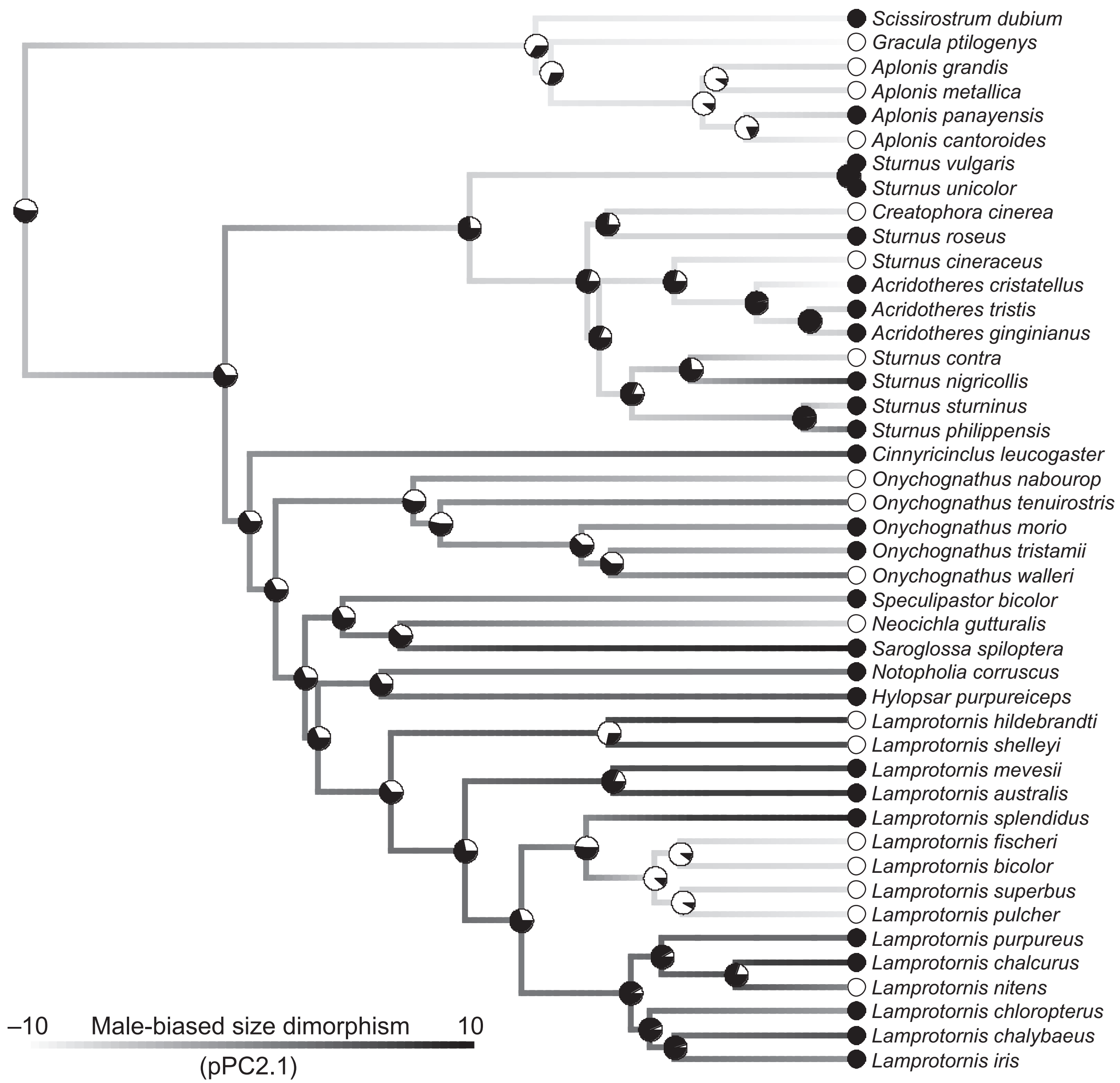

**Fig. 2** Relationship between the use of green plants in nests and sexual dimorphism in starlings. The colour of the branches represents the first component of variation in the pPCA2 ($n$ = 44 species) (white: low dimorphism, black: male-biased size dimorphism). Terminal points represent the use green nesting material (black: yes, white: no). The points at nodes represent ancestral character estimation for the green plants-adding behaviour.

parasites or inducing particular changes in microbial communities of cavity nests. However, the antiparasitic effects of green plants in starling nests remain unclear (Dubiec *et al.*, 2013; Scott-Baumann & Morgan, 2015), suggesting this original function might have been lost, at least in the extant species in which it has been experimentally tested.

Experimental studies have shown that the use of green nesting material affects female breeding activity and can have negative effects upon reproductive success, as opposed to what would be expected if only antiparasitic functions are invoked (Polo *et al.*, 2010, 2015; Veiga & Polo, 2012). Thus, the experimental addition of green plants to nests attracted competing females (Polo *et al.*, 2010) and reduced offspring recruitment rates (Polo *et al.*, 2015). Female owners also remove green nesting material from nests (Veiga & Polo, 2012), and therefore, recent reviews have argued that this male extended phenotype likely evolved via sexual selection in starlings (Scott-Baumann & Morgan,

**Table 2** Use of green nesting material in relation to the principal components of sexual dimorphism. Results are from the phylogenetic logistic regressions. Bold indicates significant predictor variables.

| | α | Estimate | SE | *z* | *P-value* |
|---|---|---|---|---|---|
| pPCA1 (*n* = 29 spp) | | | | | |
| PC1.1 | 0.104 | **0.250** | **0.108** | **2.326** | **0.020** |
| PC1.2 | | 0.069 | 0.095 | −0.731 | 0.465 |
| pPCA2 (*n* = 44 spp) | | | | | |
| PC2.1 | 0.137 | **0.158** | **0.069** | **2.277** | **0.023** |
| PC2.2 | | 0.065 | 0.118 | 0.547 | 0.584 |

**Table 3** Relationship between the use of green nesting material and predictor variables of sexual selection (sexual size dimorphism) and natural selection (habitat type, nest type and social system): Results from the phylogenetic logistic regression (α = 0.26). Bold indicates significant predictor variables.

| | *β* | SE | *z* | *P-value* |
|---|---|---|---|---|
| Habitat type | −0.24 | 0.57 | −0.43 | 0.667 |
| Social system | 1.35 | 0.97 | 1.38 | 0.164 |
| **Nest type** | **3.04** | **1.39** | **2.19** | **0.028** |
| **Sexual dimorphism (PC2.1)** | **0.16** | **0.08** | **2.15** | **0.031** |

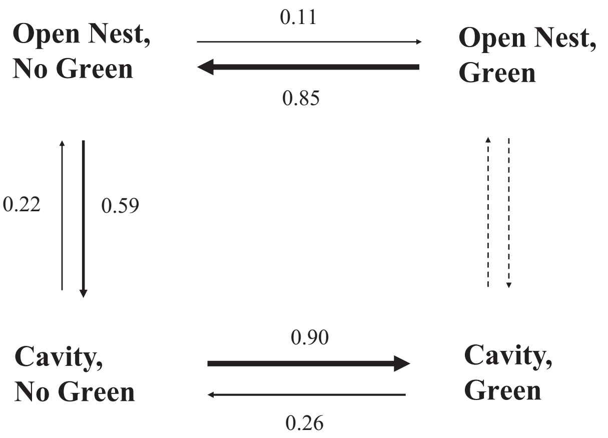

**Fig. 3** Flow diagram for the most probable transitions between the use of green plants in nest and the type of nest (i.e. cavity vs. open nest) in starlings. Parameters refer to the state transitions estimated via Bayesian procedures using a uniform prior between 0 and 1. Decreasing robustness of arrows indicates decreasing magnitude of transition rates; dashed lines represent the transition rates estimated in zero.

2015). Therefore, green plants may have originally provided a sanitary function in cavity nests and had a positive effect on nestlings' health (Gwinner, 2013), becoming a reliable signal to females, which could have favoured the exaggeration of this trait via sexual selection (Veiga *et al.*, 2006). In species with high rates of polygyny and marked size dimorphism like the spotless starling, where polygynous males carry more plants to attract partners (Veiga *et al.*, 2006), the ornamental function of this behaviour may have been exaggerated to the point where it actually incurs fitness costs on the female (Polo *et al.*, 2015), and its sanitary function may have been lost entirely. Hence, in some cases, green nesting material may be involved in sexual conflict, where the potential positive effects on nestling health might be exceeded by the costs that this male behaviour imposes upon the female during the breeding period (Polo *et al.*, 2015). Thus, we speculate that the maintenance of this trait might depend upon experienced and high-quality females being capable of coping with the increased rates of intrasexual competition when paired with attractive males (Polo & Veiga, 2006). Future studies in other species within this clade should elucidate how pervasive are sanitary functions, or loss thereof, among extant starling species.

Finally, the use of green plants at nests had multiple gains and losses across the starling phylogeny (Fig. 2). The disappearance of this behaviour is particularly interesting given that they are more likely among species with open nests and lower sexual dimorphism, and could be related to the fitness costs associated with nest greenery. One possibility is that these costs are incurred through competitive interactions among breeding females (Polo *et al.*, 2010, 2015). In other words, the use of plants may be lost at the same time that sexual size dimorphism decreases, as this secondary reduction of sexual dimorphism has also been observed in highly social, cooperatively breeding species of African starlings (Rubenstein & Lovette, 2009). The strength of sexual selection in cooperatively breeding species is similar in males and females, which may have eroded differences between the sexes in traits used for competition for mates and/or breeding resources (Rubenstein & Lovette, 2009). The loss of the use of green nesting material in some species was likely related to this reduction in sexual size dimorphism in highly social species that experience intense female–female competition. Although we did not find a relationship between the use of greenery and social system (Table 3), sexual dimorphism was significantly lower in cooperatively breeding species, consistent with other studies in this group (Rubenstein & Lovette, 2009; Maia *et al.*, 2016). Another possibility is that these fitness costs are higher for species that have open nests, potentially because the presence of aromatic plants in open nests increase their detectability by predators (see Cresswell, 1997; Weidinger, 2002, for predation as a selective force acting on nesting behaviour of birds). This would explain why the loss of green plant-adding behaviour is many times more likely for open nesters than for cavity nesters. Additional research is required to understand the potential costs associated with the evolution of these extended phenotypes.

In summary, this is the first comparative study exploring the function of green plants in nests of different bird species. Experimental and observational studies have provided detailed, but often conflicting, information on the function of plants in some avian species. Our results suggest that both natural selection and sexual selection were involved in the evolution of this behaviour in starlings. Our results also show that the evolution of this extended phenotype is favoured by cavity nesting and is associated with sexual selection. In the light of previous experiments and observational studies, we speculate that the green plant-carrying behaviour originated in cavity nests with a sanitary function and was subsequently favoured by females via sexual selection. This hypothesis provides an evolutionary framework to explain previous mixed experimental results in some starling species, and the rapid and complex evolution of this behaviour highlights the need for studies on its functional role across species. Our study adds to the growing literature suggesting that that both natural and sexual selection may be necessary to provide a complete picture of the evolution of sexual signals in animals. Although sexual selection is typically considered the predominant force driving the evolution of ritualized behaviours and exaggerated phenotypic traits involved in courtship, natural selection may also play an important and often underappreciated role.

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