



Original Article

Juvenile plumage whiteness is associated with the evolution of clutch size in passerines

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Received 21 June 2018; revised 22 March 2019; editorial decision 23 March 2019; accepted 2 April 2019; Advance Access publication 30 April 2019.

The offspring of many animals are conspicuous during parental dependence, despite juveniles generally suffering from high predation risk. However, to date, it is unclear whether offspring structural ornaments play a role in intrafamily communication. This is the case of conspicuous plumage in young birds, which is worn unchanged during a long period after fledging, when they still depend on their parents. If plumage color facilitates intrafamily interactions, its role should be more important in large-brooded species, where the strength of intrafamily conflict is potentially stronger. We therefore performed a comparative study in 210 passerine bird species to test whether an offspring structural trait, white plumage, evolves more frequently in lineages with larger clutches. We also explored the number of broods raised per year as another source of intrafamily conflict. First, we found that juvenile whiteness was more frequent in open-nesting species. Moreover, in agreement with our prediction, the presence of juvenile white tail/wing patches was strongly and positively associated with clutch size. This relationship was not due to the strong resemblance between offspring and adult plumage, which was controlled for in the statistical analyses. Moreover, the association remained significant after taking into account predation risk, for which there was information for a subset of species. In contrast, juvenile whiteness was not associated with the number of broods raised per year. These results may suggest that the evolution of juvenile conspicuousness is favored in species with potentially stronger intrabrood sibling conflict.

Key words: clutch size, intrabrood conflict, juvenile signals, parent–offspring conflict, plumage color, predation risk.

INTRODUCTION

Conflicts over limited resources are common in animal societies, including humans. How these conflicts are resolved by interacting individuals usually depends on information exchange and the expression of signals (Danchin et al. 2004; Conrard and List 2009; Arganda et al. 2012; Huck et al. 2017; Chaine et al. 2018). For example, facial patterns in a paper wasp and facial expression in macaques reduce the likelihood of social aggression, especially in large social groups (Tibbetts and Dale 2004; Waller et al. 2016). Indeed, in many taxa, signals of phenotypic quality or fighting ability allow individuals to predict social outcomes and to avoid costly interactions with unrelated opponents (Hurd 1997; reviewed by Maynard-Smith and Harper 2003; Searcy and Nowicki 2005).

Likewise, the expression of signals of quality can play a role in settling conflicts among relatives in species with parental care (Grodzinski and Johnstone 2012; Morales and Velando 2013). Family members constitute a small society with overlapping but not identical interests (Trivers 1974). Given that each offspring is

more closely related to itself than to its parents and siblings, they each should try to take a disproportionate share of resources. Consequently, an intersibling conflict may arise (O'Connor 1978). Moreover, optimal parental investment levels for offspring are greater than for parents, leading to parent–offspring conflict (Trivers 1974). Finally, each parent would profit if the other provided more care, leading to a sexual conflict (Lessells 1999). The resolution of intrafamily conflicts involves continuous behavioral interactions during which offspring may for instance express dynamic begging signals according to their need (like vocal and postural displays, as well as integument coloration); signals that parents use to assign provisioning effort to specific offspring (Godfray 1995; Jourdie et al. 2004; Bize et al. 2006; de Ayala et al. 2007; Wiebe and Slagsvold 2012). However, the young of many animal species also display nondynamic structural signals during the period of parental dependence, whose role in intrafamily interactions is less known. This is the case of conspicuous plumage in young birds, which has received little attention compared to begging displays.

Juvenile plumage is fully developed at the end of the nestling period and is worn unchanged for several weeks until the postfledging molt (on average, during 2 months in passerines; Moreno and Soler 2011), after which an adult-like plumage is acquired (Jenni and

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Winkler 1994). It has been hypothesized that one of the major selective pressures that affect chick plumage color is predation (reviewed by Kilner 2006; see also Graber 1955), which is the main cause of high juvenile mortality after leaving the nest (Naef-Daenzer et al. 2001; Berkeley et al. 2007; Miranda et al. 2007). Thus, plumage conspicuousness in juveniles should have an adaptive value during this phase that compensates enhanced predation risk. For instance, it may allow fledglings to be easily spotted by parents outside the nest (see Penteriani et al. 2007a, although this study was performed in a nocturnal species). Importantly, plumage color is developed at the same time that begging displays and related traits lose intensity or simply disappear. For instance, skin coloration becomes covered by feathers and vocal signals are diminished after leaving the nest, probably because of reduced responsiveness by parents (Middleton et al. 2007). Additionally, contrary to dynamic postural or vocal displays, and even to integument coloration of nestlings (Soler et al. 2007; Martín-Gálvez and Soler 2017), young birds cannot control plumage color to signal need in the short term. Thus, plumage color reflects offspring phenotypic quality in the long term, and can be expressed even prior to fledging and for several weeks thereafter. Accordingly, intraspecific studies have found that condition-dependent plumage color of nestlings affects parental provisioning (Lyon et al. 1994; Griggio et al. 2009; Parejo et al. 2010; Ligon and Hill 2010; Barrios-Miller and Siefferman 2013; Romano et al. 2016) and the competitive interactions among brood mates (Morales and Velando 2018).

For juvenile conspicuousness facilitating social interactions among family members, we should expect a prominent role in avian lineages with large broods. First, social interactions and information exchange are more frequent in large groups (Pacala et al. 1996), and signals (at least, nonmanipulative ones) have evolved to facilitate information exchange and the resolution of social conflicts (for intrafamily conflict see Trivers 1974; Godfray 1995). Second, social networks are probably more complex in large families (Morales and Velando 2013), simply because there is a higher probability of interacting with more individuals. Third, sibling conflict is expected to be stronger in large broods, since the higher the number of young to be fed the stronger the competition for limited parental resources (i.e., intrabrood conflict; Godfray and Parker 1992; Kilner 1999, 2006; Smiseth et al. 2007). Indeed, in the great tit (*Parus major*), interactions among siblings have been found to be stronger and more frequent in large families and also in those with limited food availability (Royle et al. 2012), that is, when resources are potentially more restricted. Interestingly, in Rallidae, chick general conspicuousness (a measure of bill, flesh and plumage coloration combined) shows a weak but positive association with clutch size (Krebs and Putland 2004). However, other comparative studies have mainly focused on begging-related traits. For instance, nestling mouth conspicuousness has been found to be positively associated with different proxies of intrafamily conflict (extrapair paternity: Kilner 1999; brood reduction: Soler and Avilés 2010; Caro et al. 2016; clutch size: Avilés et al. 2008; but see Kilner and Davies 1998). Hitherto, no comparative study has looked for associations of specific plumage signals with clutch size or other proxies of the strength of intrafamily conflict.

We therefore performed a study in 210 passerine bird species to test whether juvenile white plumage evolves more frequently in lineages with larger clutches. Additionally, we explored the number of broods raised per year as another source of intrafamily conflict (i.e., interbrood conflict; Parker and MacNair 1979). Passerines offer an interesting system to test the study question because they are altricial and, thus, several siblings are cared for at the nest, usually by both parents. It is a diverse and well-studied group

representing 50% of all bird species, and juvenile plumage is generally well described (Cramp and Perrins 1998). White plumage increases conspicuousness when combined with melanized feathers, as is usually the case in passerines (Brooke 1998, Beauchamp and Heeb 2001; Galván and Solano 2016). Furthermore, in many bird species, white plumage patches of adult birds signal individual quality to conspecifics (e.g., Weidmann 1990; Gustafsson et al. 1995; Beauchamp and Heeb 2001; Álvarez 2004; Ferns and Hinsley 2004; Osorno et al. 2006; Morales et al. 2007; Penteriani et al. 2007b; Griggio et al. 2011; Crowhurst et al. 2012; Guindre-Parker et al. 2013; Walker et al. 2014; see also reviews by Galván 2008; Penteriani and Delgado 2017). Possibly, white plumage plays a similar role in juveniles too, as suggested by intraspecific studies (Penteriani et al. 2007a; Romano et al. 2016). Moreover, white plumage patches in the tail and wings seem to function as “flash marks” to conspecifics, especially when the birds perform flicking tail and wing movements (Brooke 1998; Beauchamp and Heeb 2001; Stang and McRae 2009), behaviors that are typically displayed by young birds while begging for food (Grim 2008). Thus, white tail and wing feather patches seem particularly good candidates as juvenile signals to other family members.

Unpigmented plumage can be costly to wear, mainly because it attracts predators (e.g., Slagsvold et al. 1995; Martin and Badyaev 1996). Other associated costs of white plumage are dirt removal (see Griggio et al. 2011, and references therein) and higher vulnerability of feathers to physical breakage and degrading bacteria or lice (Kose and Møller 1999; Burt and Ichida 2004; Goldstein et al. 2004; Ruiz-de Castañeda et al. 2012). In this context, developing feathers, and especially tail, wing, and ventral feathers, are continuously in direct contact with the nest material, where debris and feather-degrading micro and macro-organisms are abundant, and will differentially affect white plumage; effects that should be visualized during both the nestling and fledgling periods. Thus, we measured whiteness in these traits, assuming that the costs of wearing these feathers are high. As mentioned above, these potential costs point to an adaptive value in social contexts of wearing white plumage.

Our prediction was that tail, wing, and ventral plumage whiteness of juveniles should be more frequent in species with a higher need to signal quality, namely in those species with a larger clutch size (and, potentially, with more frequent interactions and stronger intrabrood conflict) or with more than one brood per year (i.e., stronger interbrood conflict). To explore this prediction, we collected information from Western Palearctic passerines and, by means of Bayesian phylogenetic mixed models, examined the association between juvenile plumage whiteness and clutch size and number of broods. Since juvenile and adult conspicuousness are positively associated to a large extent in passerines (Moreno and Soler 2011), we also controlled for female conspicuousness in the analyses. Finally, we took into account predation rate in a subset of species for which it was available ($n = 79$), and nest type (cavity vs. open nests) in the whole data set to control for the supposedly high predation risk in open nests (Martin et al. 2017) and for the higher insalubrity of cavity nests (González-Braojos et al. 2012), which may increase the costs of wearing white plumage.

METHODS

Juvenile plumage whiteness

First, we characterized juvenile ventral whiteness from the colored plates of the electronic version of *The Complete Birds of the Western Palearctic on CD-ROM 1.0* (BWP; Cramp and Perrins 1998) by using

Photoshop (ver. 11.0.2; Adobe System Inc., San Jose, CA), and following a similar method to that described by Villafuerte and Negro (1998) and Soler et al. (2005). Specifically, we used the “magnetic lasso”, an edge-detection tool, to select ventral feathers from below the tail to the breast and to the edge of the wing, excluding both the legs and the wing (see Figure A1 in Electronic Supplementary Material for an example of the selected area). We used 16% edge contrast, 5-pixel width, and 80 lines per inch. Then, the program calculated median lightness values for pixels within the selected area (range of lightness: 27.3–228.7). This procedure was repeated twice in 15 randomly chosen species indicating that lightness was highly repeatable ($r = 1.0$; $F_{14,15} = 1312.8$; $P < 0.001$). For simplicity, ventral lightness will be called “ventral whiteness” henceforth. In contrast to the more homogeneous and diffused color pattern of ventral feathers, tail, and wing white feathers are usually present as a thin edge or neat stripe, which cannot be easily measured with an edge-detection tool. Thus, for the tail and the wing, the presence/absence of white feathers was registered as a categorical factor based on the description of juvenile plumage coloration in BWP. Specifically, whiteness was scored as present if the expressions “white” or “off-white” were explicitly mentioned in the description of wing feathers (excluding under coverts and axillaries, which are more concealed from the view of other individuals and, thus, are less likely to function as signals) or tail feathers (excluding under tail coverts, for the same reason). Reference to “pale”, “creamy”, “buff”, or “Isabelline” tail and wing feathers in the text was not considered as presence of white. When the juvenile was described as similar to the adult or to the first adult, we then checked the corresponding description. Written descriptions of plumage coloration allowed us to assess the presence/absence of white patches objectively, since the observation of colored plates is always subjected to potential observers’ bias. In order to register adult female plumage whiteness, we followed the same protocol as for juveniles. The presence of white in tail/wing feathers was obtained in the description of adult female spring/worn plumage.

Ventral whiteness was not significantly associated with the presence/absence of white wing or tail feather (Supplementary Table S2). However, the presence/absence of white wing feathers was strongly and positively correlated with the presence/absence of white tail feathers (Supplementary Table S2). Thus, we scored tail and wing white feathers into a single 3-level categorical variable, hereafter “tail/wing whiteness”: 0 = no white feathers present in either the tail or the wing; 1 = white feathers present in one of the traits but not in the other; 2 = white feathers present in both traits.

Table 1

Relationship between mean clutch size and juvenile whiteness while controlling for body mass, nest type (open vs. cavity or domed), and species predation rate (data available for 79 species)

Dependent variable	Predictor	Post. mean	(Post. mean) 95% CI	z-score 95% CI	Effective sample size	pMCMC
Juv. tail/wing whiteness	(Intercept)	-3.04	-6.37 to 0.31	0.82–1.08	2336.08	0.075
	Clutch size	0.59	0.22–0.96	0.84–1.12	2305.79	0.002
	Nest type (cavity)	-1.26	-2.35 to -0.18	0.87–1.15	2321.32	0.023
	Body mass	0.52	-1.01 to 2.03	0.87–1.15	2342.43	0.51
	Predation rate	0.01	-0.01 to 0.03	0.86–1.14	2351.00	0.59
Juv. ventral whiteness	(Intercept)	249.13	182.15–315.79	0.99–1.31	2339.74	<0.001
	Clutch size	1.26	-5.31 to 7.87	1.20–1.59	2232.75	0.71
	Nest type (cavity)	-16.65	-34.70 to 1.32	0.93–1.23	2326.60	0.074
	Body mass	-50.62	-82.26 to -19.02	0.82–1.09	2350.02	0.003
	Predation rate	-0.18	-0.54 to 0.18	1.02–1.35	2346.23	0.32

We show average values of 100 MCMCglmm models ran on 100 random phylogenetic trees. Significant effects (pMCMC < 0.05) are shown in bold.

Data collection

Mean clutch size was used as a proxy of the number of siblings that can be present at the nest and, thus, of potential sibling competition and number of different social interactions. We obtained information on mean clutch size, and also on the number of broods (one vs. more than one brood per year), nest type (open vs. cavity or domed nests), and female mass (g) from the BWP and, when not available (clutch size for 4 species and number of broods for ten species), we used the *Handbook of the Birds of the World Alive* (HBWA; Del Hoyo et al. 2017). When provided information was clutch size range instead of the mean clutch size, we calculated the average of the maximum and minimum values. Female mass was log₁₀-transformed before the analyses. Predation rates (i.e., percentage of nests lost due to predation) of a subset of species ($n = 79$) were obtained from BWP, 2 reviews (Martin and Clobert 1996; Wesolowski and Tomiałojć 2005) and other bibliographic sources (see Supplementary Table S1). When various values per species were available, predation rates were averaged. Species values for all variables can be found in Supplementary Table S1.

Statistical analyses

We used Bayesian phylogenetic mixed model analyses from the MCMCglmm package (Hadfield 2010), as implemented in R 4.2.5 (R-Core-Team 2017) with the appropriate libraries (“MCMCglmm”, “ape”, and “MASS” (Paradis et al. 2004), and “mvtnorm” (Venables and Ripley 2002)). This analysis enables the inclusion of a phylogeny as a design matrix that is considered as a random effect (Genz and Bretz 2011; Currie and Meade 2014). We performed one MCMCglmm model with juvenile ventral whiteness as a continuous response variable with normal error, and another one that included tail/wing whiteness as a categorical response variable with ordinal distribution. In both models, we entered mean clutch size, nest type (open vs. cavity/domed nests), predation rate, and log-female mass as predictors ($n = 79$ species). Since there was weak evidence for the association between predation rate and juvenile whiteness (Table 1), we ran the models after excluding this variable from the analyses to increase sample size ($n = 210$ species). In addition, we checked whether the results remained qualitatively similar after controlling for adult plumage whiteness. However, due to the high collinearity between juvenile and adult whiteness, we show the models with and without the adult trait. Finally, both models were run again to include the number of broods per year, which was available for a few less species ($n = 201$ species).

Female mass and mean clutch size were significantly associated to each other (pMCMC = 0.044; MCMCglmm model with female mass as a continuous dependent variable with normal distribution, mean clutch size as the only predictor and phylogeny as a random factor). Female mass and nest type were not significantly associated (similar model to the previous one but with nest type as the only predictor; pMCMC = 0.55), and the same was true for mean clutch size and nest type (pMCMC = 0.13; MCMCglmm model with clutch size as dependent variable assuming normal distribution and nest type as the only predictor). Predation rate was not related to the rest of covariates (all pMCMC ≥ 0.84; MCMCglmm model with predation rate as dependent variable and nest type, female mass and clutch size as predictors).

We used the prior [list(G=list(G1=list(V=1, nu=0.02)),R=list(V=1,nu=0.02))] for ventral whiteness. For tail/wing whiteness, we fixed the residual variance to 1 [list(G=list(G1=list(V=1,nu=100,alfa.mu=0,alfa.V=1)),R=list(V=1,fix=1))], as recommended for categorical dependent variables (de Villemereuil et al. 2013). We let the algorithm run for 100,000 iterations, with a burn-in period of 6000 and thinning interval of 40. We used Geweke’s convergence diagnostic for Markov chains (Geweke 1992), which is based on a standard z-score of means of the first (10%) and the last part (50%) of a Markov chain (Table 1). For a converged Markov chain, the absolute value of a Geweke statistic should be smaller than 1.96 at the 0.05 alpha level (Zhang 2016). To account for phylogenetic uncertainty, the models were run on 100 random phylogenetic trees from Birdtree.org with Ericson backbones (all species) (Jetz et al. 2014), and results were then averaged. The random effect of phylogeny was reported as heritability (h²) (Hadfield 2010), which is a measure of the phylogenetic signal analogous to Pagel’s lambda that ranges from zero (nonphylogenetic signal) to 1 (high phylogenetic signal).

RESULTS

As predicted, juvenile tail/wing whiteness was higher in species with larger clutches after controlling for predation rate, nest type and the species body mass (pMCMC ≤ 0.003 in the 100 runs; see average values in Table 1; n = 79 species). Predation rate was relatively high (mean ± SE = 33.82 ± 2.40% of nest lost to predators; range: 0–91%) but was not significantly associated with juvenile tail/wing whiteness in any of the 100 runs (all pMCMC ≥ 0.53). Body mass did not show a significant association with tail/wing whiteness. However, juveniles of open-nesting species showed whiter tail/wings in this reduced data set (Table 1).

When predation rate was excluded from the model and we increased sample size, clutch size was still strongly and positively

related to juvenile tail/wing whiteness (pMCMC ≤ 0.0034 in the 100 runs; see average values in Table 2; n = 210 species; see also Figure 1). In contrast, the effects of body mass and nest type did not reach statistical significance in this model (Table 2). Adult female tail/wing whiteness was also strongly and positively associated with clutch size (Supplementary Table S3). After including female tail/wing whiteness as a covariate in the model of juvenile tail/wing whiteness, we found that the effect of clutch size on juvenile tail/wing whiteness remained highly significant in models that considered either the reduced or the whole data set (Supplementary Tables S4 and S5). This suggests a role for offspring juvenile tail/wing whiteness despite the strong resemblance between adults and juveniles. On the other hand, juvenile tail/wing whiteness was not significantly associated with the number of broods per year (Supplementary Table S6). The phylogenetic signal of juvenile tail/wing whiteness was intermediate (h² = 0.52; 95% CI = 0.45–0.60).

One may argue that tail and wing white feather patches are not the only conspicuous traits present in juvenile plumage. For instance, pure black can be very conspicuous as well. In addition, white small dots combined with beige can serve as camouflage rather than signaling. However, if we exclude species in which juveniles are almost black (n = 11), or in which whiteness in the tail and wing is only present as white-spotted plumage (n = 3), the relationship between tail/wing whiteness and clutch size remains highly significant (Supplementary Table S7).

Ventral whiteness was not significantly associated with mean clutch size, either when controlling for predation rate or when excluding it from the model (Tables 1 and 2). Neither was it related to the number of broods per year (Supplementary Table S6). Nonetheless, juveniles of species with larger body mass had darker ventral plumage (Tables 1 and 2). Juveniles of species that build open nests also showed whiter ventral plumage, although only in the whole data set. The phylogenetic signal of juvenile ventral whiteness was very high (h² = 0.84; 95% CI = 0.65–0.94). Interestingly, adult female ventral whiteness was positively associated with clutch size (Supplementary Table S3). However, after including it as a covariate in the model of juvenile ventral whiteness, the effect of clutch size on juvenile ventral whiteness remained nonsignificant (Supplementary Table S4).

DISCUSSION

To date, it is unclear whether juvenile plumage conspicuousness plays a role in intrafamily communication. Here, we show that the expression of juvenile white patches in the tail and wings is strongly and positively associated with clutch size in 210 passerine species, while controlling for the effect of phylogeny. The relationship

Table 2
Relationship between mean clutch size and juvenile whiteness when excluding predation rate from the model (n = 210 species)

Dependent variable	Predictor	Post. mean	(Post. mean) 95% CI	z-score 95% CI	Effective sample size	pMCMC
Juv. tail/wing whiteness	(Intercept)	-2.09	-4.32 to 0.16	0.82-1.08	2374.79	0.070
	Clutch size	0.38	0.16-0.60	0.86-1.14	2339.20	0.001
	Nest type (cavity)	-0.36	-0.96 to 0.24	0.85-1.12	2350.36	0.24
	Body mass	0.37	-0.55 to 1.29	0.77-1.02	2351.80	0.44
Juv. ventral whiteness	(Intercept)	215.10	157.05-272.25	0.85-1.13	2360.58	<0.001
	Clutch size	3.44	-0.74 to 7.63	0.96-1.28	2371.01	0.11
	Nest type (cavity)	-12.03	-23.05 to -0.90	0.80-1.06	2297.77	0.036
	Body mass	-44.08	-64.02 to -24.02	0.86-1.14	2343.65	<0.001

We show average values of 100 MCMCglmm models ran on 100 random phylogenetic trees. Significant effects (pMCMC < 0.05) are shown in bold.

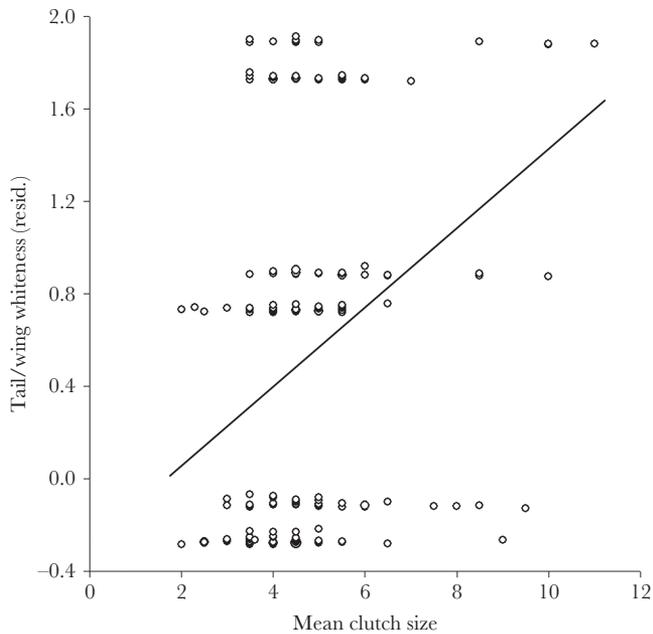


Figure 1

Relationship between juvenile tail/wing whiteness (values close to 0 are species without white in tail or wing feathers; values close to 1 are those showing white in one of the traits; values close to 2 are species with white in both traits) and mean clutch size (number of eggs) across 210 Passerine species. Values of tail/wing whiteness are residuals from a MCMCglmm model that included tail/wing whiteness as dependent variable and nest type (open vs. cavity/domed nest) and body mass as predictors, while controlling for phylogenetic relationships among species. The line is the best fit MCMCglmm model (also controlling for phylogeny).

remains significant when taking into account predation risk in a subset of species, and resemblance between juvenile and adult white plumage in the whole data set. Results also show that juvenile plumage whiteness is more frequent in open-nesting passerines, although this relationship depended on the subset of species included in the analysis.

The detected association between clutch size and feather whiteness suggests that selection maintains offspring conspicuousness in large families, perhaps because offspring signals facilitate information exchange in large groups and the resolution of intrafamily conflicts (Morales and Velando 2013). Similarly, mouth and flange color patterns in juvenile birds are more likely to evolve in larger families (Krebs and Putland 2004; Soler and Avilés 2010; but see Kilner and Davies 1998) and when there is a higher degree of intrabrood conflict, due to extrapair paternity or brood reduction (Kilner 1999; Avilés et al. 2008). Our results support that juvenile whiteness in passerines plays a role in settling the conflict between brood mates. In a wider context, outside the family framework, white plumage patches on the tail and wings are more frequent in social bird species that flock (Beauchamp and Heeb 2001; Stang and McRae 2009), and these signals seem to increase group cohesion (Beauchamp and Heeb 2001). Likewise, juvenile white plumage could function as a signal of phenotypic quality that facilitates social interactions among family members when there is a more complex social network structure in the family. In other words, juvenile plumage whiteness could reduce costs that derive from family conflict, which should result in fitness benefits for parents and offspring and, thus, be favored by selection.

The expected association between plumage whiteness of juveniles and clutch size was not detected for ventral feathers, despite adult female ventral whiteness being positively associated with clutch size. Contrary to white wing and tail patches, which are only conspicuous when the birds move and flick both traits (Grim 2008), white ventral feathers cannot be hidden within cryptic plumage and thus might facilitate juvenile detection by predators, and this should constrain its evolution in scenarios of social communication. However, contrary to this explanation, we found that predation rate was not significantly associated with ventral whiteness in the reduced subset of species, and that juveniles were whiter in open-nesting passerines, which are more exposed to predators (Martin et al. 2017). Thus, it is possible that social interactions at the juvenile stage are more important for open- than for hole-nesters. In fact, due to the stronger predation pressure in open nests, nestlings leave the nest at earlier developmental stages than nestlings of cavity-nesting species (Lack 1954; Naef-Daenzer and Gruebler 2016; Martin et al. 2017) and are often flightless when they leave (reviewed by Naef-Daenzer and Gruebler 2016). Therefore, fledglings of open-nesting species would need enhanced signaling capacity due to higher parental dependency during the first days outside the nest.

Despite previous studies showing that juveniles are more conspicuous immediately before and after leaving the nest (e.g., Baker and Parker 1979, including more than 500 bird species), the function of juvenile plumage color has been scarcely explored in the context of intrafamily communication (although see Moreno and Soler 2011 for general plumage conspicuousness). To date, no comparative study has explored whether specific plumage signals relate to family size or to the strength of intrafamily interactions. This is striking given that young passerines wear their juvenile plumage unchanged for on average 2 months, part of which time they may be still dependent on their parents and remain in family groups, sometimes even until the following breeding event (delayed plumage maturation; Cramp and Perrins 1998). Specifically, white plumage patches in the tail and wing generate very conspicuous traits when the tail and wings are shaken quickly (Brooke 1998; Beauchamp and Heeb 2001; Stang and McRae 2009), as young passerines typically do while begging for food (Grim 2008). In a previous intraspecific study in eagle owls, juveniles with experimentally reduced plumage whiteness showed lower condition, likely because they received less food than their sibs or as the result of sib-sib competitive interactions (Penteriani et al. 2007a). Hence, juvenile white plumage could play a role in intrafamily communication in nonpasserines as well.

Plumage whiteness is probably not a specific trait of juveniles. Therefore, we cannot discard that its association with clutch size is partly due to a role for adult white plumage in intrafamily communication. Yet, this does not explain why offspring plumage whiteness is maintained by selection in the first place, when strong pressures exist against plumage conspicuousness in juveniles due to predation (Graber 1955; Kilner 2006; see values of predation rate in Supplementary Table S1). Moreover, after controlling for adult female conspicuousness, the relationship between juvenile whiteness and clutch size remained highly significant. In addition, juvenile plumage may also evolve to be clearly distinct from adult plumage, so adult and juvenile plumage evolution may be decoupled in many species (Moreno and Soler 2011). Finally, plumage signals could serve other functions outside the family, like acquiring social status among juveniles before the winter (Moreno and Soler 2011) or signaling “immaturity” to reduce aggression from adult conspecifics after fledging (Ligon and Hill 2013). These possibilities are compatible with our findings because signals are observed by multiple

receivers and can function in several social contexts inside and outside families (West-Eberhard 1983; Morales and Velando 2013).

In conclusion, we found that offspring plumage whiteness in the tail and wing is more frequent in lineages with larger broods, suggesting that white plumage plays a role in the communication among family members close to fledging or thereafter. Also, juveniles have whiter plumage in open-nesting species, perhaps because social interactions at the juvenile stage are more important for open-nesters. Although the correlative nature of comparative studies does not allow us to establish causality, we hope that our results encourage future research exploring other potential sources of variation in juvenile plumage and also more experimental studies on specific plumage traits within species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was financed by the Ministerio de Economía, Industria y Competitividad MINECO (CGL2016-79390-P, CGL2017-83103-P, CGL2017-83843-C2-1-P and CGL2013-48193-C3-1-P) and the European Regional Development Fund (FEDER). J. Morales was supported by a Ramón y Cajal contract from MINECO.

We thank Jordi Moya Laraño for help with the R scripts and Emilio García Juárez for the assessment of juvenile whiteness in plates of BWP.

Conflict of interest: The authors declare no conflict of interest.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Morales et al. (2019).

Handling editor: John Fitzpatrick

REFERENCES

- Álvarez F. 2004. Black and white tail markings in Rufous Bush Chats *Cercotrichas galactotes*: size, symmetry and the extent of seasonal abrasion. *Ardeola*. 51:169–175.
- Arganda S, Pérez-Escudero A, de Polavieja GG. 2012. A common rule for decision making in animal collectives across species. *Proc Natl Acad Sci USA*. 109:20508–20513.
- Avilés JM, Pérez-Contreras T, Navarro C, Soler JJ. 2008. Dark nests and conspicuousness in color patterns of nestlings of altricial birds. *Am Nat*. 171:327–338.
- de Ayala RM, Saino N, Möller AP, Anselmi C. 2007. Mouth coloration of nestlings covaries with offspring quality and influences parental feeding behavior. *Behav Ecol*. 18:526–534.
- Baker RR, Parker GA. 1979. The evolution of bird coloration. *Philos Trans R Soc Lond B*. 287:63–130.
- Barrios-Miller NL, Siefferman L. 2013. Evidence that fathers, but not mothers, respond to mate and offspring coloration by favouring high-quality offspring. *Anim Behav*. 85:1377–1383.
- Beauchamp G, Heeb P. 2001. Social foraging and the evolution of white plumage. *Evol Ecol Res*. 3:703–720.
- Berkeley LI, McCarty JP, Wolfenbarger LL. 2007. Postfledging survival and movement in dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk*. 124:396–409.
- Bize P, Piau R, Moureau B, Heeb P. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc Biol Sci*. 273:2063–2068.
- Brooke MD. 1998. Ecological factors influencing the occurrence of ‘flash marks’ in wading birds. *Funct Ecol*. 12:339–346.
- Burt EH, Ichida JM. 2004. Gloger’s rule, feather-degrading bacteria, and color variation among song sparrows. *Condor*. 106:681–686.
- Caro SM, Griffin AS, Hinde CA, West SA. 2016. Unpredictable environments lead to the evolution of parental neglect in birds. *Nat Commun*. 7:10985.
- Chaine AS, Shizuka D, Block TA, Zhang L, Lyon BE. 2018. Manipulating badges of status only fools strangers. *Ecol Lett*. 21:1477–1485.
- Conradt L, List C. 2009. Group decisions in humans and animals: a survey. *Philos Trans R Soc Lond B*. 364:719–742.
- Cramp S, Perrins CM. 1998. The complete birds of the western palearctic on CD-ROM, version 1.0. Oxford (UK): Oxford University Press.
- Crowhurst CJ, Zanollo V, Griggio M, Robertson J, Kleindorfer S. 2012. White flank spots signal feeding dominance in female diamond firetails, *Stagonopleura guttata*. *Ethology*. 118:63–75.
- Currie TE, Meade A. 2014. Keeping yourself updated: Bayesian approaches in phylogenetic comparative methods with a focus on Markov chain models of discrete character evolution. In: Garamszegi LZ, editor. *Modern phylogenetic comparative methods and their application in evolutionary biology: concepts and practice*. Berlin (Heidelberg): Springer-Verlag.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. *Science*. 305:487–491.
- Del Hoyo J, Elliott A, Sargatal J, Christie DA, Juana E. 2017. *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions. <http://www.hbw.com/> on October 2017.
- Ferns PN, Hinsley SA. 2004. Immaculate tits: head plumage pattern as an indicator of quality in birds. *Anim Behav*. 67:261–272.
- Galván I. 2008. The importance of white on black: unmelanized plumage proportion predicts display complexity in birds. *Behav Ecol Sociobiol*. 63:303–311.
- Galván I, Solano F. 2016. Bird Integumentary Melanins: biosynthesis, forms, function and evolution. *Int J Mol Sci*. 17:520.
- Genz A, Bretz F. 2011. *Computation of multivariate normal and t probabilities*. Heidelberg (Germany): Springer-Verlag.
- Geweke J. 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In: Bernardo JM, Berger JO, Dawid AP, Smith AFM, editors. *Bayesian Statistics 4*. Oxford (UK): Oxford University Press. p. 169–193.
- Godfray HC. 1995. Evolutionary theory of parent-offspring conflict. *Nature*. 376:133–138.
- Godfray HCJ, Parker GA. 1992. Sibling competition, parent-offspring conflict and clutch size. *Anim Behav*. 43:473–490.
- Goldstein G, Flory KR, Browne BA, Majid S, Ichida JM, Burt EH. 2004. Bacterial degradation of black and white feathers. *Auk*. 121:656–659.
- González-Braojos S, Vela AI, Ruiz-de Castañeda R, Briones V, Cantarero A, Moreno J. 2012. Is nestling growth affected by nest reuse and skin bacteria in pied flycatchers *Ficedula hypoleuca*? *Acta Ornithol*. 47:119–127.
- Graber RR. 1955. Taxonomic and adaptive features of the juvenal plumage in North American sparrows. PhD thesis, University of Oklahoma, Norman.
- Griggio M, Morosinotto C, Pilastro A. 2009. Nestlings’ carotenoid feather ornament affects parental allocation strategy and reduces maternal survival. *J Evol Biol*. 22:2077–2085.
- Griggio M, Valera F, Casas-Criville A, Hoi H, Barbosa A. 2011. White tail markings are an indicator of quality and affect mate preference in rock sparrows. *Behav Ecol Sociobiol*. 65:655–664.
- Grim T. 2008. Wing-shaking and wing-patch as nestling begging strategies: their importance and evolutionary origins. *J Ethol*. 26:9–15.
- Grodzinski U, Johnstone RA. 2012. Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proc Biol Sci*. 279:109–115.
- Guindre-Parker S, Gilchrist HG, Baldo S, Doucet SM, Love OP. 2013. Multiple achromatic plumage ornaments signal to multiple receiver. *Behav Ecol*. 24:672–682.
- Gustafsson L, Quvarström A, Sheldon BC. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature*. 375:311–313.
- Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw*. 33:1–22.
- Huck S, Leutgeb J, Oprea R. 2017. Payoff information hampers the evolution of cooperation. *Nat Commun*. 8:15147.
- Hurd PL. 1997. Cooperative signalling between opponents in fish fights. *Anim Behav*. 54:1309–1315.
- Jenni L, Winkler R. 1994. *Moult and ageing of European passerines*. London: Academic Press.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Redding D, Mooers AO. 2014. Distribution and conservation of global evolutionary distinctness in birds. *Curr Biol*. 24:1–12.
- Jourdie V, Moureau B, Bennett AT, Heeb P. 2004. Ecology: ultraviolet reflectance by the skin of nestlings. *Nature*. 431:262.

- Kilner R. 1999. Family conflicts and the evolution of nestling mouth colour. *Behaviour*. 136:779–804.
- Kilner R. 2006. Function and evolution of color in young birds. In: Hill GE and McGraw KJ, editors. *Bird coloration: function and evolution*. London (UK): Harvard University Press. p. 201–232.
- Kilner R, Davies NB. 1998. Nestling mouth colour: ecological correlates of a begging signal. *Anim Behav*. 56:705–712.
- Kose M, Møller AP. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (*Hirundo rustica*). *Behav Ecol Sociobiol*. 45:430–436.
- Krebs EA, Putland DA. 2004. Chic chicks: the evolution of chick ornamentation in rails. *Behav Ecol*. 15:946–951.
- Lack D. 1954. *The natural regulation of animal numbers*. Oxford: Oxford University Press. 343 pp.
- Lessells CM. 1999. Sexual conflict in animals. In: Keller L, editor. *Levels of selection in evolution*. Princeton (NJ): Princeton University Press. p. 75–99.
- Ligon RA, Hill GE. 2010. Feeding decisions of eastern bluebirds are situationally influenced by fledgling plumage color. *Behav Ecol*. 21:456–464.
- Ligon RA, Hill GE. 2013. Is the juvenal plumage of altricial songbirds an honest signal of age? Evidence from a comparative study of thrushes (Passeriformes: Turdidae). *J Zool Syst Evol Res*. 51:64–71.
- Lyon BE, Eadie JM, Hamilton LD. 1994. Parental choice selects for ornamental plumage in American coot chicks. *Nature*. 371:240–243.
- Martin TE, Badyaev AV. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution*. 50:2454–2460.
- Martin TE, Boyce AJ, Fierro-Calderon K, Mitchell AE, Armstad CE, Mouton JC, Bin Soudi EE. 2017. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. *Funct Ecol*. 31:1231–1240.
- Martín-Gálvez D, Soler JJ. 2017. Decoding colouration of begging traits by the experimental addition of the appetite enhancer cyproheptadine hydrochloride in magpie *Pica pica* nestlings. *J Avian Biol*. 48:353–361.
- Maynard-Smith J, Harper D. 2003. *Animal signals*. Oxford: Oxford University Press.
- Middleton HA, Green DJ, Krebs EA. 2007. Fledgling begging and parental responsiveness in American dippers (*Cinclus mexicanus*). *Behaviour*. 144:485–501.
- Miranda AP, Alberti GAJD, Iborra GML. 2007. Survival rates of young magpies *Pica pica* in a mountain population of Eastern Spain. *Acta Ornithol*. 42:63–68.
- Morales J, Cuervo JJ, Moreno J, Soler JJ. 2019. Data from: juvenile plumage whiteness is associated with the evolution of clutch size in passerines. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.s88fv55>
- Morales J, Moreno J, Merino S, Sanz JJ, Tomás G, Arriero E, Lobato E, Martínez-de la Puente J. 2007. Female ornaments in the Pied Flycatcher *Ficedula hypoleuca*: associations with age, health and reproductive success. *Ibis*. 149:245–254.
- Morales J, Velando A. 2013. Signals in family conflicts. *Anim Behav*. 86:11–16.
- Morales J, Velando A. Forthcoming 2018. Coloration of chicks modulates costly interactions among family members. *Behav Ecol*.
- Morales J, Velando A. 2018. Coloration of chicks modulates costly interactions among family members. *Behav Ecol*. 29:894–903.
- Naef-Daenzer B, Grübler MU. 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. *J Field Ornithol*. 87:227–250.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J Anim Ecol*. 70:730–738.
- O'Connor RJ. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim Behav*. 26:79–96.
- Osorno JL, Morales J, Moreno J, Merino S, Tomás G, Vásquez RA. 2006. Evidence for differential maternal allocation to eggs in relation to manipulated male attractiveness in the Pied Flycatcher (*Ficedula hypoleuca*). *J Ornithol*. 147:605–611.
- Pacala SW, Gordon DM, Godfray HCJ. 1996. Effects of social group size on information transfer and task allocation. *Evol Ecol*. 10:127–165.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*. 20:289–290.
- Parejo D, Avilés JM, Rodríguez J. 2010. Visual cues and parental favouritism in a nocturnal bird. *Biol Lett*. 6:171–173.
- Parker GA, MacNair MR. 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim Behav*. 27:1210–1235.
- Penteriani V, Delgado MD. 2017. Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. *Phil Trans R Soc B*. 372:20160064.
- Penteriani V, Delgado MD, Alonso-Álvarez C, Sergio F. 2007a. The importance of visual cues for nocturnal species: eagle owl fledglings signal with white mouth feathers. *Ethology*. 10:934–943.
- Penteriani V, Delgado MD, Alonso-Álvarez C, Sergio F. 2007b. The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. *Behav Ecol*. 18:143–147.
- R-Core-Team. 2017. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Romano A, Bazzi G, Caprioli M, Corti M, Costanzo A, Rubolini D, Saino N. 2016. Nestling sex and plumage color predict food allocation by barn swallow parents. *Behav Ecol*. 27:1198–1205.
- Royle NJ, Pike TW, Heeb P, Richner H, Kölliker M. 2012. Offspring social network structure predicts fitness in families. *Proc Biol Sci*. 279:4914–4922.
- Ruiz-de-Castañeda R, Burt EH, González-Braojos S, Moreno J. 2012. Bacterial degradability of an intrafeather unmelanized ornament: a role for feather-degrading bacteria in sexual selection? *Biol J Linn Soc*. 105:409–419.
- Searcy WA, Nowicki S. 2005. *The evolution of animal communication*. Princeton (NJ): Princeton University Press.
- Slagsvold T, Dale S, Kruszewicz A. 1995. Predation favors cryptic coloration in breeding male pied flycatchers. *Anim Behav*. 50:1109–1121.
- Smiseth PT, Lennox L, Moore AJ. 2007. Interaction between parental care and sibling competition: parents enhance offspring growth and exacerbate sibling competition. *Evolution*. 61:2331–2339.
- Soler JJ, Avilés JM. 2010. Sibling competition and conspicuousness of nestling gaps in altricial birds: a comparative study. *PLoS One*. 5:e10509.
- Soler JJ, Avilés JM, Cuervo JJ, Pérez-Contreras T. 2007. Is the relation between colour and immune response mediated by nutritional condition in spotless starling nestlings? *Anim Behav*. 74:1139–1145.
- Soler JJ, Moreno J, Avilés JM, Møller AP. 2005. Blue and green egg-color intensity is associated with parental effort and mating system in passerines: support for the sexual selection hypothesis. *Evolution*. 59:636–644.
- Stang AT, McRae SB. 2009. Why some rails have white tails: the evolution of white undertail plumage and anti-predator signalling. *Evol Ecol*. 23:943–961.
- Tibbetts EA, Dale J. 2004. A socially enforced signal of quality in a paper wasp. *Nature*. 432:218–222.
- Trivers R. 1974. Parent-offspring conflict. *Am Zool*. 14:249–264.
- Venables WN, Ripley BD. 2002. *Modern applied statistics with S*, 4th edn. New York (NY): Springer.
- Villafuerte R, Negro JJ. 1998. Digital imaging for colour measurement in ecological research. *Ecol Lett*. 1:151–154.
- de Villemereuil P, Gimenez O, Doligez B. 2013. Comparing parent-offspring regression with frequentist and Bayesian animal models to estimate heritability in wild populations: a simulation study for Gaussian and binary traits. *Methods Ecol Evol*. 4:260–275.
- Walker LK, Ewen JG, Brekke P, Kilner RM. 2014. Sexually selected dichromatism in the hibi *Notiomystis cincta*: multiple colours for multiple receivers. *J Evol Biol*. 27:1522–1535.
- Waller BM, Whitehouse J, Micheletta J. 2016. Macaques can predict social outcomes from facial expressions. *Anim Cogn*. 19:1031–1036.
- Weidmann U. 1990. Plumage quality and mate choice in mallards (*Anas platyrhynchos*). *Behavior*. 115:127–14.
- West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Quart Rev Biol*. 58:155e183.
- Wesołowski T, Tomiałojć L. 2005. Nest sites, nest predation, and productivity of avian broods in a primeval temperate forest: do the generalisations hold? *J Avian Biol*. 36:361–367.
- Wiebe KL, Slagsvold T. 2012. Parents take both size and conspicuousness into account when feeding nestlings in dark cavity nests. *Anim Behav*. 84:1307–1312.
- Xie W, Lewis PO, Fan Y, Kuo L, Chen MH. 2011. Improving marginal likelihood estimation for Bayesian phylogenetic model selection. *Syst Biol*. 60:150–160.
- Zhang Z. 2016. Modeling error distributions of growth curve models through Bayesian methods. *Behav Res Methods*. 48:427–444.