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ORIGINAL ARTICLE

# Does the tie fit the female? Melanin-based colouration, aggressive personality and reproductive investment in female great tits (*Parus major*)

**Bert Thys**[1] · **Rianne Pinxten**[1,2] · **Marcel Eens**[1]

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## Abstract

The evolution and function of female trait exaggeration in species with traditional sex roles are poorly understood. Competition for social and ecological resources, rather than mating opportunities, may be a key selection pressure in females of socially monogamous species. Moreover, such pre-existing resource competition-selected traits (armaments) may become the object of mating preferences (ornaments); however, the benefits that males may gain in choosing more ornamented females remain unclear. Here, using observational data on free-living female great tits (*Parus major*), we explore whether tie size, a well-known melanin-pigmented plumage trait, covaries with intrasexual aggressiveness during the breeding season and the investment in current reproduction (fledgling number and mass). We found consistent individual differences (i.e. personality variation) in most of the aggressiveness parameters studied. Moreover, we found support for a signalling role of tie size with respects to how close females approached intruders. Interestingly, this relationship was only evident in older females, not first-year breeding females, suggesting age-related changes in the information content of tie size in the context of same-sex aggressiveness. Additionally, although first-year breeding females, on average, produced fledglings with lower body mass compared to older females, tie size was positively associated with fledgling mass, suggesting that males could potentially gain benefits by choosing females with larger tie size. Experimental studies are now necessary to confirm whether females with larger tie size have a selective advantage in female competition (i.e. armament), as well as whether males base their mate choice on female tie size (i.e. ornament).

## Significance statement

Why females of many species with traditional sex roles often have exaggerated traits very similar to those found in males remains poorly understood. We explored the functional significance of a well-known melanin-based plumage trait (tie size) in females of a socially monogamous passerine bird, the great tit. Female tie size positively covaried with consistent individual differences in aggressiveness during female-female interactions, but only so in older females and not first-year breeding females. In addition, females with larger tie size produced fledglings with higher body mass, suggesting that it could potentially be used by males in mate choice. Our study emphasizes that greater attention should be paid to female trait exaggeration in socially monogamous species in the context of female-female competition and male mate choice, as well as to potential age-related changes in the information they convey.

**Keywords** Melanin-based plumage · Female-female aggressiveness · Personality · Age-dependent signalling · Armament-ornament · Dual utility

## Introduction

The evolution of elaborate, decorative and conspicuous traits (e.g. colouration, weaponry, overt aggressiveness) has traditionally received a lot of attention (Andersson 1994). In males, the evolution of such traits has been almost universally ascribed to intrasexual competition for mating opportunities and female mate choice, i.e. the central mechanisms of sexual selection (Andersson 1994; Clutton-Brock 2007). In females,

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✉ Bert Thys
bert.thys@uantwerpen.be

[1] Department of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp, Campus Drie Eiken, Building D, Universiteitsplein 1, 2610 Antwerp, Wilrijk, Belgium

[2] Faculty of Social Sciences, Antwerp School of Education, University of Antwerp, Antwerp, Belgium

the specific selection pressures acting on exaggerated traits are less well understood, apart from the classic case of sex-role-reversed species (Amundsen 2000; Clutton-Brock 2009; Tobias et al. 2012). However, female trait exaggeration is also widespread in species with traditional sex roles, raising questions about their evolution and functional significance (Amundsen and Pärn 2006; Tobias et al. 2012).

In socially monogamous bird species, at least three evolutionary mechanisms have been put forward to explain exaggerated traits in females (Amundsen and Pärn 2006). First, female trait exaggeration can arise as a genetically correlated (non-functional) by-product of selection on males (Lande 1980). Second, mutual mate choice (i.e. mutual sexual selection) can lead to the evolution of ornamentation in both sexes as they signal an individual's quality in terms of good genes and parenting abilities (Kraaijeveld et al. 2007; Clutton-Brock 2009). In this case, female ornaments, like male ornaments, are expected to give information about aspects of fitness, such as fecundity, viability or survival. Third and finally, female trait exaggeration may have evolved to signal competitive ability during intrasexual competition over resources necessary for successful reproduction, such as territories, nest sites and paternal care (i.e. social selection; West-Eberhard 1983; Tobias et al. 2012). Under this latter scenario, females are expected to signal their prospective investment in competitive behaviours towards same-sex conspecifics to avoid conflicts from escalating (Maynard Smith and Parker 1976; Johnstone and Norris 1993). Importantly, these different processes are not mutually exclusive and a growing number of studies, predominantly focusing on males, have indicated that the same trait can be selected by both intrasexual competition and mate choice (e.g. Tarof et al. 2005; Hoi and Griggio 2008; review in Wong and Candolin 2005). These findings are in support of the armament-ornament (or dual utility) hypothesis, stating that traits used in intrasexual competition become the objects of mating preferences due to their pre-existing association with qualities preferred in mates (Berglund et al. 1996; Stern and Servedio 2017). Although the existence of traits with dual utility is well documented in males, only a few studies have assessed this possibility in females of socially monogamous species (e.g. Kraaijeveld et al. 2004; Griggio et al. 2010).

Melanin-based traits in particular are good candidates to evaluate relationships between colouration and competitive trait expression. The deposition of melanin pigments is largely under genetic control, varies greatly among individuals of the same species and is heritable (Ducrest et al. 2008). Moreover, melanin-based traits are presumably costly to produce and maintain (Roulin 2016), they can be involved in mate choice (Kraaijeveld et al. 2007; Roulin 2016) and they likely signal individual differences in competitive, reproductive and life history strategies (Ducrest et al. 2008). Indeed, increasing evidence indicates that melanin-based colouration covaries with suites of other phenotypic traits, with darker individuals for instance often being bigger, having higher metabolic rates and being more sexually active and aggressive compared to lighter individuals (Ducrest et al. 2008). Nonetheless, in females, only a few studies have directly assessed whether melanin-based colouration covaries with consistent individual differences (i.e. personality variation) in risk-taking behaviours (e.g. Da Silva et al. 2013; Nicolaus et al. 2016; Costanzo et al. 2018) or intrasexual aggressiveness (e.g. Morales et al. 2014; López-Idiáquez et al. 2016). This is surprising since, especially in species where both sexes display aggressive or territorial behaviour, intrasexual competition for reproductive resources may be a key selection pressure on female trait exaggeration (West-Eberhard 1983; Tobias et al. 2012). Likewise, although numerous studies have revealed male preference for females with larger (melanin-based) ornaments (see Kraaijeveld et al. 2007; Clutton-Brock 2009), only a few studies have investigated the potential fitness benefits males may obtain in choosing such females (e.g. Clutton-Brock 2009). As a consequence, evidence for a relationship between female melanin-based traits and the investment in current reproduction, as predicted by the mutual mate choice hypothesis, remains scarce (but see Roulin 2004; Remeš and Matysioková 2013).

Here, we use observational data on great tits (*Parus major*), a socially monogamous passerine with biparental care, to explore whether the size of a melanin-based plumage trait (tie) covaries with female-female aggressiveness and the investment in current reproduction. Female great tits are known to respond aggressively towards same-sex intruders during the breeding season to prevent the intruder from taking over the territory, nest site or mate (Slagsvold 1993), i.e. key resources for reproductive success (Dhondt and Schillemans 1983; Both et al. 1999). We recently demonstrated that females in our population consistently adopt different behavioural strategies during same-sex territorial intrusions, both within a breeding season (Thys et al. 2017) and across breeding seasons (BT, unpublished data). Specifically, aggressive behavioural types approach an intruder closely, spent a lot of time on the caged intruder, potentially attacking it, while less aggressive behavioural types stay further away from the intruder and produce alarm calls (Thys et al. 2017). In addition, great tits are slightly sexually dimorphic with females having a smaller melanin-based black breast stripe (or tie) than males (Hegyi et al. 2007; Nicolaus et al. 2016). Importantly, tie size is repeatable and heritable in both sexes (e.g. Norris 1993; Kölliker et al. 1999; Nicolaus et al. 2016), often considered to honestly signal an individual's reproductive potential (Norris 1993; Remeš and Matysioková 2013) and therefore likely to covary with individual differences in behavioural and life history strategies. Previous work has shown that tie size correlates with dominance, aggressiveness and nest defence in males (Järvi and Bakken 1984; Poysa 1988; Quesada and Senar 2007) and exploratory behavioural type in both sexes

(Nicolaus et al. 2016). Female tie size has recently also been linked to offspring quality, thereby suggesting that direct selection by male mate choice might play a role in the evolution of female tie size (Remeš and Matysioková 2013). However, it remains to be determined whether female tie size is used as a signal during female-female competition over reproductive resources. To address this research question, we assessed whether female tie size relates to consistent individual differences in female-female aggressiveness during the breeding season, where females with larger tie size are expected to respond consistently more aggressive compared to females with smaller tie size. Additionally, we examined whether female tie size gives information about the investment in current reproduction. Specifically, we explored whether females with larger tie size produced more offspring (i.e. higher fecundity) or offspring with higher mass at fledging (i.e. higher viability; cf. Remeš and Matysioková 2013).

## Methods

### Study population

Data were collected in a resident semi-urban population of great tits in the surroundings of Antwerp, Belgium (51°09′44″N–4°24′15″E). This population has been monitored since 1997, with at present approximately 150 nest boxes for great tits (e.g. Van Duyse et al. 2000; Rivera-Gutierrez et al. 2010; Raap et al. 2015; Thys et al. 2019). Birds in the population are provided with a metal leg ring as nestlings, or upon first capture, and adults are fitted with a unique combination of colour rings. Age of birds is determined using either hatching records (resident birds) or plumage characteristics upon first capture (first-year vs. older breeders; Svensson 1992). Reproductive activities of breeding pairs are monitored to determine lay date, clutch size, hatch date and fledgling number. When 15 days old, nestlings are ringed and weighed to the nearest 0.1 g, providing a proxy for fledgling mass (Both et al. 1999).

### Measurement of tie size

In three consecutive years (2017–2019), individuals were captured when roosting in nest boxes between half January and early March, as part of ongoing research on novel environment exploration behaviour (see, e.g. Thys et al. 2017). The morning after capture, morphometric measurements and photographs of the breast were taken following general procedures described in Nicolaus et al. (2016). In short, females were placed on their back on top of a millimetric grid in an extended position. Belly feathers were gently smoothed and pictures of the breast were taken from a fixed distance with a Nikon Coolpix S6500 camera (Nikon, Nikon Instruments Europe BV, Amsterdam, The Netherlands). Photographs were analysed using ImageJ (National Institutes of Health, Bethesda, MD, USA) and tie size was calculated as the area of black surface within a 4-cm-long rectangle starting at the lowest point of yellow on the chest and as broad as the width of the shoulders. For a random set of 40 females, we quantified tie size three times, based on three different photographs taken on the same day. Within-day repeatability was high ($R = 0.96$ [0.95–0.97]), indicating the reliability of our method. In total, 190 photographs were taken on 144 females, with 34 females photographed across 2 years and 6 females across 3 years. Tie size was not correlated with structural size (i.e. tarsus length; $r = 0.07$; $P = 0.32$; $N = 190$ observations) and since absolute tie size and tie size corrected for structural size (i.e. proportional to tarsus length) were strongly positively correlated ($r = 0.99$; $P < 0.001$; $N = 190$ observations), we only used absolute tie size for further analyses.

Since male tie size has been found to give information about an individual's reproductive potential (Norris 1993), we wanted to assess whether potential relationships between female tie size and reproductive investment were driven by male tie size. Hence, available photographs of males ($N = 34$) that were found breeding together with females in the dataset were also analysed following the methods described above.

Asymmetry in ornament size between responding and intruding birds may influence the outcome of aggressive interactions (e.g. Järvi and Bakken 1984; Garamszegi et al. 2006; Hegyi et al. 2008; López-Idiáquez et al. 2016), so we also quantified the tie of the stuffed decoy females used during simulated territorial intrusions (see below). The posture of mounted decoys prevented quantification of tie size in the same way as for live individuals, so for decoy birds, we measured the width of the breast stripe to the nearest mm, at the base of the sternum, using a digital calliper (Järvi and Bakken 1984). Although this method does not enable a direct comparison of tie size between responding birds and decoys, it does allow us to assess whether tie width of decoy birds affects the behaviour of responding birds.

### Female-female aggressiveness

Aggressiveness in females was assessed using simulated territorial intrusion, following procedures described in Thys et al. (2017). In short, a taxidermic mount of a female great tit (decoy; one out of five) inside a protective wired mesh was placed on top of the focal female's nest box, at days 2 and 5 of the egg-laying period (with day 1 referring to the day the first egg was laid). From a distance of approximately 15 m, the observer (one out of nine) scored the following aggression parameters during a 5-min observation period: number of alarm calls produced, the minimum distance to the decoy (approach distance, in meters), the time spent on the decoy (in seconds), occurrence of attacks (yes versus no) and entering nest box (yes versus no; Thys et al. 2017). Over the course of

2017–2019, a total of 226 aggression tests were successfully performed on 102 females that were also photographed for tie size in the winter preceding the respective breeding season. When carrying out behavioural assays, information on tie size and reproductive success of the focal individual was unknown for the observer indicating that criteria for blind experimentation were met. Since relatively few females ($N = 26$) were assessed across more than 1 year for both aggressiveness and tie size, we included only data from the first year in which both aggressiveness and tie size measurements were available. This resulted in a sample size of 174 aggression tests on 102 females for further analyses.

## Statistical analyses

### Sources of variation in female tie size

We modelled variation in female tie size using a univariate mixed model with Gaussian errors, including data of all females for which tie size measurements were available ($N =$ 144). The model included random intercepts for ID (i.e. 34 females measured across 2 years, 6 females across 3 years). Age is known to affect tie size (Hegyi et al. 2007; Nicolaus et al. 2016), and given the repeated measurements of tie size on the same individuals, this effect can exist both at the among- and within-individual level (cf. Nicolaus et al. 2016). Hence, using within-individual centering, we partitioned age into its among-individual (mean age per individual) and within-individual effects (age deviation, i.e. the deviation of each observation from an individuals' mean age) and included both variables in the model. We did not include year or maximum age in the model since the former variable was highly correlated with the within-individual age effect ($r = 0.54$; $P < 0.001$; $N = 190$ observations) and the latter with the among-individual age effect ($r = 0.93$; $P < 0.001$; $N = 190$ observations; cf. Nicolaus et al. 2016). The adjusted (cross-year) repeatability of female tie size was calculated from this model as the among-individual variance divided by the sum of the among-individual and residual variance (Nakagawa and Schielzeth 2010).

### Female aggressiveness and tie size

A set of univariate mixed models was used to model variation in different aggression parameters (relationships between different aggression parameters are given in Table S1). Each model included random intercepts for female ID ($N = 102$) and the following fixed effects: female tie size, age (first-year vs. older), decoy tie width and two-way interactions of tie size with age and decoy tie width. Random intercepts for observer identity ($N = 9$) were not included since this resulted in model convergence failures. However, our previous work has shown that observer differences explain little to no variation in aggression parameters (Thys et al. 2017). Similarly, we did not include other fixed effects (e.g. clutch size, Julian date, time of testing) as they have been found to have little effect on female aggressiveness (Thys et al. 2017). Prior to analysis, approach distance was multiplied by $-1$ so that higher values corresponded to more aggressive responses. The different aggression parameters were modelled with the following error distribution: approach distance (square-root transformed) with Gaussian errors, the number of alarm calls and time on the decoy (untransformed) with Poisson errors, and occurrence of attack and entering nest box with binomial errors. The adjusted (within-year) repeatability of aggression parameters was calculated from these models with different error distributions following formulas presented in Nakagawa and Schielzeth (2010).

### Tie size and reproductive investment

Preliminary analysis revealed that nest success (i.e. whether or not at least one nestling fledged) was not predicted by lay date, female tie size, age (first-year vs. older) or the two-way interaction between tie size and age (Table S2). Subsequent analyses focused on successful nests ($N = 83$), for which detailed data on fledgling number and mass (i.e. nestling body mass on day 15) were available. Linear models with Gaussian error distribution, including the fixed effects described above for nest success, were used to model variation in fledgling number and mass, respectively. Since fledgling number and mass differed among years, we centered and standardized both to unit variance within years. The same standardization was applied to lay date, as to control for potential year-specific seasonal effects on fledgling number and mass. Additionally, for the subset of successful nests for which tie size measurements of both sexes were available ($N = 30$), linear models were used to model variation in fledgling number and mass in relation to female tie size, male tie size and their two-way interaction.

All analyses were performed in R 3.6.1 (R Core Team 2019). Continuous response and explanatory variables were centered and standardized to unit variance in all analyses, unless stated otherwise. Individuals with single measurements were included in all mixed models as they contribute in estimating among-individual variances (Nakagawa and Schielzeth 2010). The *sim* function (package *arm*; Gelman et al. 2015) was used throughout to simulate values from the posterior distributions of the model parameters. Based on 2000 simulations, we extracted 95% credible intervals around the mean. Fixed effect estimates were considered to find strong support if the 95% credible intervals (CrI) did not overlap with zero. However, since variance components are bound to be positive, we assessed their support using permutation tests (see, e.g. Araya-Ajoy and Dingemanse 2016; Thys et al. 2019). In short, each permutation we randomly reshuffled data (either tie size or aggression parameters) across observations and performed mixed modelling analysis as described above on the new dataset to obtain a posterior mean estimate for the among-individual variance. This procedure was repeated 1000 times, resulting in a "null" distribution of mean estimates for the among-individual variance. Next, we calculated to probability (permutation.*p*) that the observed mean variance was greater than any mean value based on the "null" distribution.

## Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

## Results

### Variation in female tie size

We found strong support for among-individual differences in female tie size ($\sigma^2$ [95% CrI] = 0.41 [0.32; 0.52]; permutation.$p = 0.005$; Table 1), with tie size being moderately repeatable across years (*r* [95% CrI] = 0.40 [0.32; 0.49]). In addition, tie size increased with age within females (age deviation) and tended to decrease with age among females (mean age; Table 1).

### Female aggressiveness and tie size

We found strong support for among-individual differences in most aggression parameters (i.e. approach distance, number of calls produced, time spent on the decoy and occurrence of attack; all permutation.$p < 0.02$), with the exception of entering the nest box (permutation.$p = 0.106$; Table 2). This indicates that females consistently differed in their aggressive response towards same-sex intruders. In addition, there was support for age effects on aggressiveness, with first-year females on average approaching closer, spending more time on the decoy and being more likely to enter the nest box compared to older females (Table 2). Interestingly, for approach distance, we found support for an interaction-effect between female tie size and age (Table 2), indicating that the relationship between approach distance and tie size differed between age classes. Specifically, in first-year breeding females, there was no support for a relationship between approach distance and tie size ($\beta$ [95% CrI] = − 0.12 [− 0.33; 0.09]), while in older females, there was strong support that females with larger tie size approached the decoy closer compared to those with smaller tie size ($\beta$ [95% CrI] = 0.27 [0.03; 0.52]; Fig. 1; Table 2). For the other aggression parameters, we found no support for an effect of female tie size, or the interaction between tie size and age. In addition, no support was found for an effect of the ornament size of the intruding female (decoy tie width), or an interaction-effect between decoy tie width and tie size of the responding female, on any of the aggression parameters (Table 2).

**Table 1** Sources of variation in female great tit ($N = 144$) tie size. Mean estimates for fixed ($\beta$) and random ($\sigma^2$) effects are given with their associated 95% credible intervals (CrI). Fixed effects that found strong support are denoted in italics. Significance of the among-individual variance was assessed using a permutation test (see text for details; [#]permutation.$p = 0.005$). The adjusted repeatability (*r*), with associated 95% CrI, represents the cross-year repeatability of female tie size

| | Tie size |
|---|---|
| Fixed effects | $\beta$ (95% CrI) |
| Intercept | 0.16 (− 0.15; 0.49) |
| Mean age | − 0.09 (− 0.23; 0.06) |
| Age deviation | *0.31 (0.05; 0.59)* |
| Random effects | $\sigma^2$ (95% CrI) |
| ID | 0.41 (0.32; 0.52)[#] |
| Residual | 0.59 (0.49; 0.72) |
| | *r* (95% CrI) |
| Repeatability | 0.40 (0.32; 0.49) |

### Tie size and reproductive investment

Average fledgling mass was positively related to female tie size (Fig. 2; Table 3) and differed between age classes, with first-year breeding females, on average, producing fledglings with lower mass compared to older females. However, we found no support for an interaction-effect between tie size and age, indicating that the relationship between fledgling mass and tie size did not differ across age classes (Fig. 2; Table 3). On the other hand, fledgling number was not related to female tie size, age or the interaction between tie size and age (Table 3). Also, no support was found for an effect of lay date on either fledgling number or fledgling mass (Table 3).

Since the correlation between female and male tie size within breeding pairs was non-significantly positive ($r = 0.17$; $P = 0.33$; $N = 34$ pairs), we assessed whether the above-mentioned relationship between female tie size and fledgling mass was potentially driven by male tie size. The analysis revealed that this was not the case, since within this subset of pairs ($N = 30$), only female tie size tended to predict fledgling mass ($\beta$ [95% CrI] = 0.33 [− 0.03; 0.69]; Table S3), while male tie size, or the interaction between female and male tie size, did not (see Table S3).

## Discussion

We assessed whether a well-known melanin-based plumage trait (tie size) was associated with consistent individual differences in same-sex aggressiveness during the breeding season

**Table 2** Sources of variation in female great tit ($N = 102$) aggression parameters. Mean estimates for fixed ($\beta$) and random ($\sigma^2$) effects are given with their associated 95% credible intervals (CrI). Fixed effects that found strong support are denoted in italics. Significance of among-individual variances was assessed using permutation tests (see text for details; permutation.*p* values: $^{\#}$0.003; $^{*}$< 0.001; $^{\$}$0.006; $^{\S}$0.018; $^{£}$0.106). The adjusted repeatability ($r$), with associated 95% CrI, represents the within-year repeatability of aggression parameters

| | Approach distance$^{a}$ | No. calls | Time decoy | Occurrence of attack | Enter nest box |
|---|---|---|---|---|---|
| Fixed effects | $\beta$ (95% CrI) | $\beta$ (95% CrI) | $\beta$ (95% CrI) | $\beta$ (95% CrI) | $\beta$ (95% CrI) |
| Intercept | 0.31 (0.10; 0.53) | 1.11 (0.55; 1.67) | 2.13 (1.40; 2.88) | −0.75 (−1.28; −0.21) | 0.24 (−0.21; 0.69) |
| Tie size | −0.12 (−0.33; 0.09) | 0.06 (−0.51; 0.60) | 0.00 (−0.70; 0.73) | 0.13 (−0.42; 0.65) | −0.08 (−0.51; 0.37) |
| Age$^{b}$ | *−0.64 (−0.95; −0.34)* | 0.74 (−0.09; 1.52) | *−2.53 (−3.66; −1.38)* | −0.74 (−1.63; 0.10) | *−0.98 (−1.64; −0.32)* |
| DecoyTW$^{c}$ | 0.06 (−0.08; 0.20) | −0.03 (−0.26; 0.22) | 0.00 (−0.44; 0.46) | −0.31 (−0.69; 0.08) | −0.06 (−0.38; 0.26) |
| Tie size × age | *0.39 (0.08; 0.72)* | 0.05 (−0.79; 0.85) | 0.54 (−0.56; 1.65) | 0.36 (−0.51; 1.22) | −0.11 (−0.80; 0.55) |
| Tie size × decoyTW | 0.00 (−0.14; 0.14) | 0.00 (−0.27; 0.26) | 0.23 (−0.25; 0.72) | 0.08 (−0.29; 0.48) | 0.16 (−0.16; 0.49) |
| Random effects | $\sigma^2$ (95% CrI) | $\sigma^2$ (95% CrI) | $\sigma^2$ (95% CrI) | $\sigma^2$ (95% CrI) | $\sigma^2$ (95% CrI) |
| ID | 0.33 (0.25; 0.43)$^{\#}$ | 4.08 (3.13; 5.17)$^{*}$ | 3.22 (2.44; 4.19)$^{\$}$ | 1.10 (0.83; 1.42)$^{\S}$ | 0.29 (0.22; 0.38)$^{£}$ |
| Residual | 0.55 (0.44; 0.69) | 1.11 (0.95; 1.30) | 5.50 (4.50; 6.66) | 1.00 (1.00; 1.00) | 1.00 (1.00; 1.00) |
| | $r$ (95% CrI) | $r$ (95% CrI) | $r$ (95% CrI) | $r$ (95% CrI) | $r$ (95% CrI) |
| Repeatability | 0.38 (0.29; 0.47) | 0.78 (0.74; 0.82) | 0.37 (0.31; 0.43) | 0.20 (0.16; 0.25) | 0.06 (0.04; 0.08) |

[a] Approach distance was multiplied by − 1 prior to analysis

[b] First-year breeding females as reference category

[c] Tie width of the decoy female used during simulated territorial intrusion

and related to the investment in current reproduction. We found that older females with larger tie size consistently approached same-sex intruders more closely compared to older females with smaller tie size. No such relationship was observed in first-year breeding females. Hence, we demonstrate that female tie size covaries with certain aspects of aggressiveness, but not others, and moreover in an age-dependent way. The latter suggests age-related changes in the information content of female tie size, potentially resulting from differences in the strength of selection across age classes. Additionally, although first-year females, on average, produced fledglings with lower body mass compared to older females, tie size related positively to fledgling mass, but not fledgling number. Hence, female tie size appears to give information about offspring viability, but not fecundity, and males could potentially gain fitness benefits in choosing females with larger tie size.

## Variation in female tie size

Female tie size was moderately repeatable across years ($r = 0.40$), with an estimate of similar magnitude as previously reported for males only ($r = 0.41$; Kölliker et al. 1999) and both sexes combined ($r = 0.31$; Nicolaus et al. 2016). In addition, tie size increased with age within females and tended to decrease with age among females. A within-individual increase in tie size with age has been previously reported (Hegyi et al. 2007; Nicolaus et al. 2016) and potentially reflects age-related changes in an individual's social status (Järvi and Bakken 1984; Poysa 1988). The observation that tie size tended to decrease with age among females suggests the underrepresentation of females with larger ties in older age classes. Interestingly, a recent study in another Western European great tit population found strong support for a decrease in tie size with age among individuals (in both sexes; Nicolaus et al.

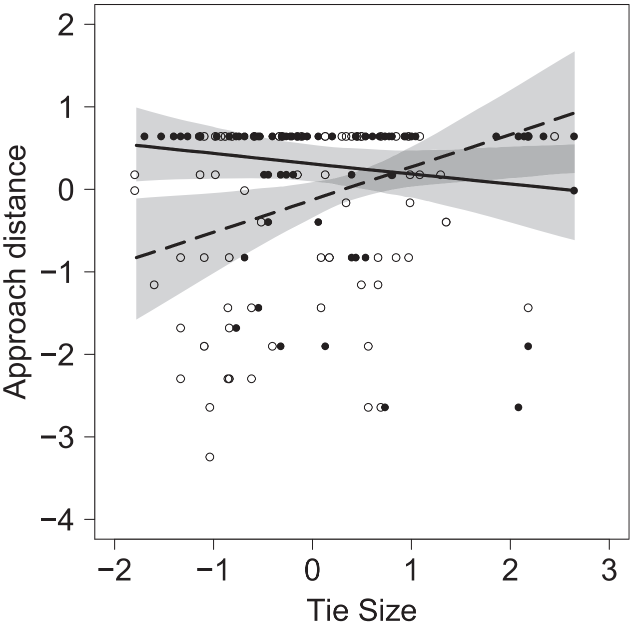

**Fig. 1** Approach distance with respect to tie size differed between age classes (first-year, $N = 56$, full circles; older, $N = 46$, open circles) in female great tits. Average regression lines for first-year breeding females (solid line) and older females (dashed line), as predicted by the model in Table 2, are given with 95% credible intervals (shaded area). Approach distance and tie size are centered and standardized to unit variance

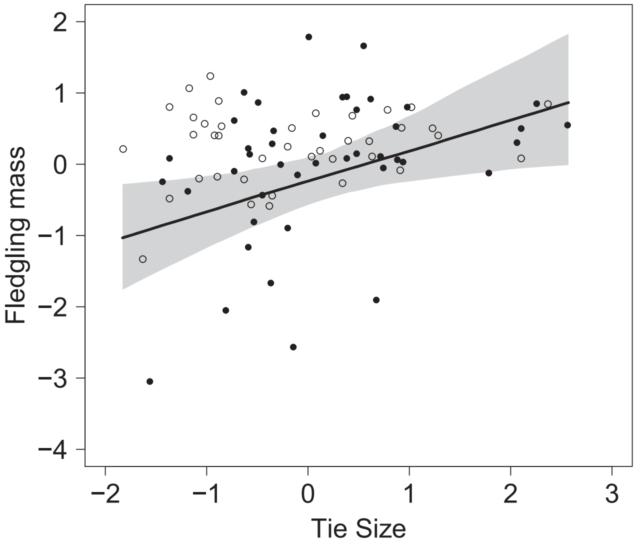

**Fig. 2** Fledgling mass with respect to female tie size in great tits ($N = 83$). The average regression line (solid), as predicted by the model presented in Table 3, is given with 95% credible intervals (shaded area). First-year breeding females ($N = 44$) are represented by full circles, older females ($N = 39$) by open circles. Note: fledgling mass is centered and standardized to unit variance within years, female tie size is centered and standardized to unit variance across years

**Table 3** Results of linear models predicting fledgling number and fledgling body mass (i.e. average nestling body mass at day 15) for female great tits ($N = 83$). Mean estimates for fixed effects are given with their associated 95% credible intervals (CrI). Fixed effects with strong support are denoted in italics. Note: fledgling number, fledgling mass and lay date were centered and standardized to unit variance within years, tie size was centered and standardized to unit variance across years prior to analysis

| | Fledgling number | Fledgling mass |
|---|---|---|
| Intercept | 0.30 (0.10; 0.51) | − 0.23 (− 0.57; 0.11) |
| lay date | − 0.01 (− 0.16; 0.15) | − 0.05 (− 0.31; 0.20) |
| Tie size | 0.12 (− 0.10; 0.32) | *0.43 (0.08; 0.78)* |
| Age[a] | 0.08 (− 0.22; 0.39) | *0.49 (0.01; 0.99)* |
| Tie size × age | − 0.12 (− 0.43; 0.19) | − 0.33 (− 0.79; 0.16) |

[a] First-year breeding females as reference category

2016). Moreover, this study found that tie size related to longevity, with individuals with large tie size living relatively shorter than individuals with small tie size. Together, this suggests that older birds with larger ties may selectively disappear from the population (Nicolaus et al. 2016), potentially because larger melanin-based ornaments are more costly to produce and maintain (Roulin 2016). Nonetheless, in our population we fail to find strong support for a decrease of tie size with age among females, with an effect size ($\beta = -0.09$) in the same direction but only half the magnitude of the effect size observed in Nicolaus et al. (2016; $\beta = -0.18$). The absence of a strong among-individual age effect in our population may result from differences in survival selection on tie size between populations (Senar et al. 2014). Moreover, survival selection on tie size presumably also differs between sexes (but see Nicolaus et al. 2016) and years within populations, which remains to be tested.

## Female aggressiveness and tie size

Our findings that females consistently differed in their aggressive response towards same-sex intruders and that first-year females were on average more aggressive than older females extend our previous work in the same population (Thys et al. 2017). Somewhat contrary to predictions, female tie size related only to approach distance and not to the other repeatable aspects of aggressiveness (i.e. the number of calls, time on the decoy and occurrence of attack). These findings appear to suggest that female tie size only plays a limited role in the context of same-sex aggressiveness. However, previous work on male great tits has demonstrated that approach distance during same-sex territorial intrusion represents a reliable predictor of the overall intensity of aggressiveness (Araya-Ajoy and Dingemanse 2014, 2016). This might also be the case in female great tits, given that approach distance positively covaries with the time spent on the decoy and the occurrence of attacks (Table S1; see also Thys et al. 2017). Interestingly, approach distance of male great tits towards a potential predator has been directly linked with tie size, while other aggressiveness parameters (latency to respond and number of alarm calls) were not (Quesada and Senar 2007). Hence, approach distance in particular might reflect aggressive intensity in both female and male great tits and, if so, tie size might generally be involved in signalling in the context of aggressiveness (see also Järvi and Bakken 1984; Poysa 1988).

Surprisingly, we only found support for a relationship between approach distance and tie size in older females, and not in first-year breeding females. One potential explanation for this finding, when combined with the observed population-level age-effect on aggressiveness, is that the strength of selection on female aggressiveness and tie size varies across age classes. In first-year breeding females, there might be strong selection for high aggressiveness as to ensure successful territory and nest site maintenance. That is, territory or nest site value might be higher for first-year breeding females compared to older females, for example because the former have more difficulties maintaining a territory, regaining an obtained territory when lost and/or are less familiar with other territories in the area due to their lack of breeding experience (see, e.g. Garamszegi et al. 2006; Hegyi et al. 2008). Hence, in first-year breeding females, the value of winning a contest for maintaining a territory or nest site, relative to the cost of getting injured due to overt aggression, might be too great for status signalling to be involved (Maynard Smith and Harper 1988; Johnstone and Norris 1993). Older females, on the other hand, commonly reoccupy their territory from the previous year (Kluijver 1951; Harvey et al. 1979), which might be relatively easier to maintain (see, e.g. Krebs 1982; Jakobsson 1988). If so, then older females might rely on status signalling to settle same-sex contests over breeding territories or nest sites (Maynard Smith and Harper 1988; Johnstone and Norris 1993). In this case, tie size might only become an important and honest signal of aggressiveness in female great tits after their first breeding season, possibly due to differences in the cost-benefit ratio of competition for a territory or nest site between age classes. On the other hand, we cannot exclude that the observed relationship between female aggressiveness and tie size is a genetically correlated (non-functional and non-adaptive) by-product of selection on males (Lande 1980). In other words, strong correlational selection on the association between tie size and aggressiveness in males may result in the same, though non-functional, association in females. If so, tie size does not signal aggressiveness in females. Hence, experimental studies are now necessary to assess whether variation in female tie size results in differential success during aggressive interactions over reproductive resources (i.e. female tie size is used as an armament), and hence whether there is direct (social) selection acting on female tie size in the context of female-female competition.

Asymmetry in ornament size between opponents is commonly expected to influence the cost-benefit ratio of aggressive interactions (Maynard Smith and Parker 1976). Here, we found no support for any effects of the ornament size of the decoy female on aggressiveness. These findings should be interpreted with caution, as we measured tie characteristics differently between responding and decoy females, making direct comparison difficult. In addition, we did not manipulate female tie size, so any effect of tie size on aggressiveness could be the result of correlated ornamental traits we did not measure. This is rather unlikely since other plumage traits with a potential signalling function in the great tit (e.g. yellow breast, black crown, white cheeks) have been found to be largely unrelated to tie size (Hegyi et al. 2007; Remeš and Matysioková 2013). Nonetheless, future studies should consider measuring tie size the same way in responding and decoy birds, while simultaneously manipulating tie size of decoy females.

Unfortunately, our limited sample size of females repeatedly assessed across years for both aggressiveness and tie size prevented us from partitioning the phenotypic correlation between these traits into its among- and within-individual correlations (Dingemanse and Dochtermann 2013). This will be a fruitful future endeavour as it will clarify the mechanisms underlying the observed phenotypic correlation between female aggressiveness and tie size (see, e.g. Nicolaus et al. 2016; Santostefano et al. 2019). Specifically, aggressiveness and tie size may change in concert within females across years (i.e. within-individual correlation), as a result of correlated changes in within-individual plasticity (and/or correlated measurement error). On the other hand, or in addition, aggressiveness and tie size may form an integrated suite of traits among females (i.e. among-individual correlation), proximately underpinned by the effects of maternal, permanent environmental and genetic correlations. In the latter case, aggressiveness and tie size might not be able to evolve independently in response to selection (Blows 2007; see also Nicolaus et al. 2016).

## Tie size and reproductive investment

Females with larger tie size produced fledglings with higher body mass compared to females with smaller tie size, which is in line with previous findings in another great tit population (Remeš and Matysioková 2013). In addition, although first-year breeding females, on average, produced fledglings with lower body mass than older females, we found no support for differences in the relationship between fledgling mass and tie size across age classes. Given the observational nature of our data, we cannot exclude the possibility that the relationship between female tie size and offspring mass is the result of unmeasured variables that covary with tie size. It is important to note that the local environment (e.g. habitat and territory quality) typically can have an influence on offspring mass (e.g. Norris 1990; Riddington and Gosler 1995). Hence, if females with different tie size are non-randomly distributed across territories, for example due to non-random mating, the observed relationship might be driven by territory and/or male quality, rather than female quality. Here, we found no support for non-random mating according to tie size (see Hegyi et al. 2007 and Remeš and Matysioková 2013 for similar results), nor any evidence that male tie size, rather than female tie size, was predicting fledgling mass. This suggests that the relationship between female tie size and offspring mass was not driven by male tie size, although our limited sample size for this analysis prevents making strong conclusions. In addition, since a male's tie size does not necessarily reflect the quality of his territory (Norris 1990), territory quality per se may still have played a role. On the other hand, a recent cross-fostering experiment has revealed that tie size of the genetic mother can explain variation in offspring mass, indicating a causal relationship between female tie size and offspring mass (Remeš and Matysioková 2013). Hence, we argue that female tie size in combination with female age at least partially explains variation in offspring mass, but not offspring number, in our population.

Poorer condition of offspring produced by first-year breeding females compared to older females might be the result of age-related changes in reproductive performance. That is, first-year breeders commonly produce fewer or poorer-quality offspring than older birds, at least up to a certain age, after which reproductive performance declines again (e.g. Perrins and McCleery 1985; Dhondt 1989; but see Bouwhuis et al. 2009). Nonetheless, within each age class, female tie size seems to convey information about offspring body mass. Since offspring mass shortly before fledging is a good indicator of post-fledging survival, recruitment and adult mass in great tits (e.g. Both et al. 1999; Naef-Daenzer et al. 2001; Perrins and McCleery 2001), males might gain benefits in mating with older females and/or females with a larger tie (i.e. female tie size is used as an ornament). If so, females and males are expected to mate non-random according to age and/or tie size, which awaits more solid validation. As a consequence, direct evidence for the (relative) importance of female age and tie size in male mate choice is currently lacking. Age itself may be a good indicator of viability, since old age necessarily indicates the capability of surviving up to that age and, as we demonstrate here, can influence reproductive performance (see also Bouwhuis et al. 2009). However, preference for old age can also arise as a by-product of preference for larger ornaments whenever there are age-related changes in ornament expression (Kokko 1997), as is the case for tie size (this study, see also Nicolaus et al. 2016).

It should be noted here that the observed population-level age-effect on fledgling mass does not necessarily reflect within-individual changes in reproductive performance. This effect might also, or in addition, be the result of selective disappearance of poor-quality breeders from the population, resulting in on average higher quality breeders in older age classes (see Bouwhuis et al. 2009). Disentangling the contribution of both processes (i.e. within-individual changes and/or selective disappearance) in explaining population-level age-effects on reproductive performance is informative in itself, but will be of particular importance in study systems where both reproductive performance and exaggerated trait expression show age-related changes. Addressing the latter requires data on a large number of individuals repeatedly assessed for reproductive performance and exaggerated trait expression across reproductive attempts, which we are currently lacking. In addition, the same data will enable to assess whether female tie size is associated with differences in life history strategies. Both correlational and experimental evidence is suggesting that females with larger tie size invest more in current reproduction (in terms of offspring mass; Remeš and Matysioková 2013), but also have lower survival probability (Nicolaus et al. 2016), compared to females with smaller tie size. These findings raise the interesting possibility that the melanocortin system is involved in the trade-off between current and future reproduction in female great tits, which remains to be investigated (Ducrest et al. 2008; see also Immonen et al. 2018).

## Conclusions

We demonstrate that a well-known melanin-based plumage trait (tie size) covaries with certain aspects of intrasexual aggressiveness during the breeding season in females of a socially monogamous passerine. Surprisingly, this relationship was only evident in older females, but not in first-year breeding females, suggesting age-related changes in the information conveyed by female tie size. In addition, female tie size appears to provide information about the average body mass, but not the number, of offspring produced. This suggests that males may gain certain fitness benefits in choosing females with larger tie size, but whether they do so remains to be tested. Together, the here observed relationships are in line with predictions within the armament-ornament hypothesis, although experimental studies are now necessary to exclude potential alternative (non-functional) hypotheses. In addition, future studies should aim at obtaining a large sample size of females repeatedly assessed for aggressiveness, tie size and reproductive performance across years. Such studies will be able to partition phenotypic correlations between aggressiveness and tie size, and between offspring mass and tie size, into its among- and within-individual components, thereby clarifying underlying mechanisms. Moreover, these data will enable to assess age-related changes in individual traits and trait correlations, as well as selective disappearance of individuals with certain traits or combinations of traits. In general, our results indicate that greater attention should be paid to the potential dual function of female trait exaggeration in species with traditional sex roles (including socially monogamous species), while simultaneously taking into account potential age-related changes in the information conveyed in different contexts.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Experiments were approved by the ethical committee of the University of Antwerp (ID 2014-88 and ID 2017-23) and performed in accordance with Belgian and Flemish laws. The Royal Belgian Institute of Natural Sciences provided ringing licences for all authors and technicians.

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