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Title: Pathways linking female personality with reproductive success are trait- and year-specific

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RUNNING TITLE: Year-specific personality-fitness links

TITLE AND ABSTRACT

Pathways linking female personality with reproductive success are trait- and year-specific

Personality (i.e. among-individual variation in average behavior) often covaries with fitness, but how such personality-fitness relationships come about is poorly understood. Here, we explore potential mechanisms by which two female personality traits (female-female aggression and female nest defense as manifested by hissing behavior) were linked with annual reproductive success in a population of great tits (*Parus major*), a socially monogamous species with biparental care. We hypothesized that personality-related differences in reproductive success result from variation in reproductive decision (lay date, brood size) and/or parental provisioning rates. Relative support for these mechanisms was evaluated using path-analysis on data collected in two successive years. We reveal that larger broods were provisioned at a higher rate by both parents and that female, but not male, provisioning rate was involved in the trade-off between offspring number (brood size) and fledgling mass. Among-individual variation in female aggression, via its association with female provisioning rate, was negatively linked to fledgling mass (i.e. indirect effect), yet only in one of the study years. Male provisioning rate did not influence these relationships. In contrast, among-individual variation in hissing behavior was directly and negatively linked with fledgling mass in both years, via an underlying mechanism that remains to be identified (i.e. direct effect). Together, our findings emphasize that personality-fitness relationships may come about via different mechanisms across personality traits and/or years, thereby illustrating additional complexity in how selection might act on and maintain among-individual variation in behavioral phenotypes in the wild.

INTRODUCTION

Over the past two decades it has become apparent that individuals from the same population can show repeatable variation in behavioral traits (i.e. personality) and that multiple behavioral traits often covary among individuals into suites of correlated traits (i.e. behavioral syndromes; Sih et al. 2004; Réale et al. 2010). Meta-analyses have revealed that behavioral traits such as aggression, boldness and exploratory behavior can covary with proxies for fitness such as survival and reproductive success (Smith and Blumstein 2008; Moiron et al. 2020), indicating that behavioral phenotypes may be generally subject to natural selection. For example, different behavioral types may be favored under different environmental conditions (Sih et al. 2004; Dingemanse and Réale 2013) and/or individual differences in behavior may mediate trade-offs between life history traits (Wolf et al. 2007; Nicolaus et al. 2016) and affect overall fitness (Sih et al. 2004). Yet, the potential mechanistic pathways that underlie the covariation between personality traits and reproductive success are often implied rather than quantified explicitly, so our insights into how personality variation translates into reproductive success (e.g. offspring number and quality) are still limited (Dingemanse and Réale 2013).

In species with parental care, food provisioning to offspring might be one of the key factors mediating the relationship between personality variation and reproductive success (Mutzel et al. 2013). On the one hand, parental provisioning is an important aspect of reproductive investment that typically directly relates to reproductive success (Clutton-Brock 1991; Royle et al. 2012). On the other hand, evidence is growing that variation in provisioning behavior can be linked with among-individual differences in various other behaviors, such as exploration (Mutzel et al. 2013; Serrano-Davies et al. 2017; but see also Patrick and Browning 2011), aggression (Rosvall 2011a; Cain and Ketterson 2013; Mutzel et al. 2013) and nest defense (Rytkönen et al. 1995; Wetzel and Westneat 2014). Hence, the potential interplay between personality traits, provisioning behavior and reproductive success emphasizes the need for integrative studies that explicitly quantify pathways by which among-individual (co)variation in behavior may translate into reproductive success. Doing so requires statistical tools that allow to simultaneously quantify direct and indirect effects between multiple variables, such as path-analysis, thereby revealing underlying mechanisms and assessing the relative support for each of them (Shipley 2000).

By using a path-analytic approach on behavioral and reproductive data collected over two successive breeding seasons in the great tit (*Parus major*), a socially monogamous passerine with biparental care, we aim to reveal whether and how personality differences translate into proxies for annual reproductive success. For the purpose of this study we focused on two specific behavioral traits previously shown to be short-term (within-year) and long-term (cross-year) repeatable in our study population, i.e. female-female aggression and female anti-predatory nest defense (so-called hissing behavior; Sibley 1955; Thys et al. 2017; Thys et al. 2019; B Thys, in preparation). First, female great tits are known to consistently differ in their aggressive response when challenged with a same-sex conspecifics inside their breeding territory (Thys et al. 2017). High levels of aggression might prevent the intruder from taking over the territory, nest site or mate, i.e. key resources for reproductive success (Slagsvold 1993), but simultaneously incur costs in terms of risk of injury (hence survival) or time and energy available for maternal care (Stiver and Alonzo 2009; Rosvall 2011b). However, few studies have directly assessed potential trade-offs between aggressive behaviors and maternal care and it remains largely unclear whether and how variation in female-female aggression relates to parental investment and reproductive success (but see Rosvall 2011b; Tobias et al. 2012). Second, we focused on hissing behavior, which is a form of anti-predatory nest defense displayed by some incubating and brooding females when confronted with a predator inside the nest cavity (Sibley 1955). Hissing behavior consists of the production of hissing calls - often accompanied with intense flapping of the wings and lunging at the predator - which can have deterring effects on predators (Zub et al. 2017; Dutour et al. 2020). Recent work indicates that the production of hissing calls can positively correlate with adult survival (Krams et al. 2014) but negatively affect offspring production and breeding success (Koosa and Tilgar 2016; Thys et al. 2019; Tilgar and Koosa 2019), suggesting that different hissing behavioral types may prioritize different components of fitness. Yet, how these relationships come about and whether this is mediated by differential investment into parental activities such as provisioning behavior remains to be studied.

Here, we simultaneously considered the following literature-based and hypothesis-driven pathways relating female aggression, female hissing behavior, provisioning behavior and reproductive success (Figure 1). Aggression and hissing behavior were expected to positively covary among females (path 1) and hence to form a behavioral syndrome (Sih et al. 2004). This presumed female aggression-hissing behavioral syndrome might subsequently influence reproductive success in a number of different ways. First, we assessed how female aggression and hissing behavior related to provisioning rates. These relationships have rarely been studied in females but theory predicts trade-offs between offspring provisioning and aggressive territory/nest defense (Trivers 1972) and between current and future reproduction

(Wolf et al. 2007; Stiver and Alonzo 2009). These trade-offs can be complex but are generally thought to arise due to time, energy or resource constraints and/or because physiological mechanisms that mediate aggressive behaviors (e.g. testosterone) reduce the capacity of females to invest in parenting behaviors (Stiver and Alonzo 2009; Rosvall 2013). Hence, we predict that aggression and hissing behavior negatively affect female provisioning rate (paths 2 and 8). Additionally, in biparental systems, males could play an important role in the resolution of the potential trade-off between female aggressive behaviors and maternal care. One means by which males might mitigate the potential cost of female aggression is by increasing paternal care (Rosvall 2010; Cain 2014). If so, female aggression/hissing behavior should positively relate to male provisioning rate (paths 3 and 9; Krieg and Getty 2020). Moreover, male provisioning rate might also be directly influenced by female provisioning rate (or *vice versa*; path 14), either negatively (partial compensation hypothesis; Harrison et al. 2009) or positively (matching hypothesis; Hinde 2006; Iserbyt et al. 2019). Provisioning rate is also expected to increase with brood size (paths 20 and 21; Wright and Cuthill 1990) and should positively and directly influence reproductive success (paths 15, 16, 18 and 19; Clutton-Brock 1991). Together, these relationships represent a pathway by which a presumed aggression-hissing behavioral syndrome may be linked to reproductive success via female and/or male provisioning rates (Mutzel et al. 2013).

Second, female-female aggression has been shown to play an important role in competition for reproductive resources in many species, where more aggressive females are generally better at obtaining and securing high quality mates, nest sites and/or breeding territories (e.g. Kempenaers 1995; Rosvall 2008; Krieg and Getty 2020). In great tits, there is competition among females for males that own a territory (Gosler 1993). Hence, if more aggressive females outcompete less aggressive females for males with higher quality territories, in which clutches are typically initiated earlier (Lambrechts et al. 2004), we expect a negative effect of female aggression on lay date (path 7). Similarly, hissing behavior is expected to negatively covary with lay date, since earlier initiated clutches are generally defended more intensely (Montgomerie and Weatherhead 1988; Thys et al. 2019; path 13). Moreover, aggression and hissing behavior may have a direct and negative effect on brood size (paths 6 and 12), since females may pay a reproductive cost in terms of egg number and hence offspring number they produce (Thys et al. 2019). Lay date also typically has a negative effect on brood size (path 17; Lambrechts et al. 2004). Brood size, in turn, is expected to positively influence fledgling number (path 22) but to negatively affect fledgling weight (path 23), since provisioning rate per nestling typically decreases with increasing brood size (Perrins 1965; Nur 1984). Hence, as a second overall pathway, among-individual (co)variation in aggression and hissing behavior might translate in reproductive success via its links with lay date and/or brood size (i.e. reproductive decisions).

Third and finally, among-individual (co)variation in aggression and hissing behavior might also directly affect reproductive success via, as of yet, unknown mechanisms (cf. Mutzel et al. 2013). Hence, we considered direct pathways linking female aggression and hissing behavior with proxies for reproductive success (paths 4, 5, 10 and 11).

Overall, by simultaneously considering multiple pathways by which female personality might translate into reproductive success, we aimed to identify selective mechanisms that may act on female behavioral phenotypes. As outlined above, reproductive consequences of different behavioral phenotypes are predicted to depend on the mechanism, or combination of mechanisms, underlying the hypothesized personality-reproductive success relationships. Moreover, previous studies aiming to identify mechanisms linking personality traits with fitness typically used data of a single year (e.g. Mutzel et al. 2013; Serrano-Davies et al. 2017; Thys et al. 2019), or combined data of different years (Zhao et al. 2016), thereby overlooking potential annual differences in mechanisms (Dingemanse and Réale 2013). Therefore, we analyzed data of two breeding seasons combined, as well as separately, thereby aiming to identify whether and which patterns were either general or year-specific.

MATERIAL AND METHODS

Study population and general field procedures

Data were collected during two successive breeding seasons (2018-2019) in a population of free-living great tits in the surroundings of Wilrijk, Belgium (51°09’44”N – 4°24’15”E). Birds in the population are provided with a metal leg ring and fitted with a unique combination of three plastic color rings, one of which containing a Passive Integrated Transponder tag (Eccel Technology Ltd, Aylesbury, UK). Age of birds was determined either using hatching records (resident birds) or plumage characteristics upon first capture (first-year or older). Reproductive activities of breeding pairs were monitored throughout the nesting cycle to determine lay date, hatch date and fledgling number. Brood size was determined upon installation of RFID antenna systems (*see below*), i.e. when nestlings were 11 days old (hatch day = 1). When 15 days old, nestlings were ringed and weighed to the nearest 0.1g, which was used as a proxy for fledgling mass (Both et al. 1999). Average fledgling number and mass were similar across breeding seasons. Moreover, nest success and breeding density were high and similar in both years, suggesting a close match between the caterpillar abundance and nestling feeding peak (Nager and van Noordwijk 1995), as well as overall favorable breeding conditions (see the electronic supplementary material, table S1 for comparisons between years). We considered first clutches since none of the birds included in this study produced second clutches in the given breeding seasons.

Female-female aggression

Aggression in females was assessed using simulated territorial intrusion, following methods described in Thys et al. (2017). Briefly, a taxidermic mount of a female great tit (decoy) was placed on top of the focal female’s nest box, at day two and five of the egg-laying period. After the focal female entered within a radius of 15 meters around the nest box, or when she was already present at the start of the test, her behavior was observed for 5 minutes. From a distance of approximately 15 meters, the observer (one out of six) scored the following aggression parameters: the number of alarm calls produced, the minimum distance to the decoy (approach distance; in meters), the time spent on the decoy (in seconds), and the number of attacks towards the decoy. A total of 287 aggression tests were successfully performed at 165 nests (82 nests in 2018 and 83 in 2019; with a total of 28 females found breeding in both years).

Female hissing behavior

As a form of anti-predatory nest defense from inside the nest cavity, we quantified female hissing behavior. Hissing tests were performed on day two and five of the incubation period, following procedures described in Thys et al. (2019). Briefly, the observer (one out of six) inserted the head of a taxidermic mount of the great spotted woodpecker (*Dendrocopos major*) into the entrance hole of a focal female’s nest box. The woodpecker was held in this position for one minute, during which the number of hissing calls produced (easily heard from outside the nest box) were counted (cf. Krams et al. 2014; Grunst et al. 2018; Thys et al. 2019). A total of 329 hissing tests were successfully performed at the above mentioned 165 nests.

Parental provisioning behavior

Parental provisioning behavior was collected using circular radio-frequency-identification (RFID) antennas installed around the nest box opening (Iserbyt et al. 2018). Antenna systems were installed at the above mentioned 165 nests when nestlings were 11 days old and collected in the afternoon of day 12 (N = 32) or day 13 (N = 133). Processing RFID data relies on the isolation of independent visits from superfluous, non-independent detections, which requires validation of RFID data with visual observations (see Iserbyt et al. 2018 for full discussion). Hence, at 20 randomly selected nest boxes, RFID antennas were combined with infrared cameras (Pakatak PAK-MIR5, Essex, UK) underneath the nest box roof lid. These video recordings were analyzed for parental visits and parents were found to bring food for the nestlings at 100% of the observed visits (N = 626). By determining exact entrance and exit times of observed visits of both parents, we were able to determine optimal cut-off values to process RFID data (females: 29 seconds ; males: 23.5 seconds; see the electronic supplementary material, text S1 and figure S1 for details on RFID data validation and determination of cut-off values). Specifically, these cut-off values were used to isolate exact arrival times from successive redundant RFID registrations (within this cut-off value), and remaining registrations were considered as independent individual visits (cf. Iserbyt et al. 2018). Correlations between visit rates based on video data and visit rates based on processed RFID data were high (females r = 0.78; males r = 0.90) and comparable to reported correlations in studies using the same or similar setups (see Iserbyt et al. 2018 and references therein). Hence, all RFID data were processed using the above mentioned cut-off values, thereby calculating the number of visits per hour per individual (henceforth visit rate). Since visit rate was highly repeatable across day 12 (R [95% CrI] = 0.90 [0.88 ; 0.91]; N_{ID} = 322) and across subsequent days (i.e. day 12 and 13; R = 0.87 [0.85 ; 0.89]; N_{ID} = 260), we used the average visit rate during five hours in the morning of day 12 (8:00 – 13:00; available for all 165 nests) as a proxy for nest visit rate in further analyses.

Statistical analyses

First**,** a principal components analysis (PCA) was performed on the aggression parameters scored during simulated territorial intrusion. This analysis resulted in a single principal component (PC1) with eigenvalue larger than one (EV = 1.40) explaining 49% of the total variance. High scores on PC1 reflected closer approach distance, more time on the decoy and more attacks, but producing less alarm calls (see the electronic supplementary material, table S2). This PC was used in further analyses as a measure of aggression (henceforth female aggression).

Second, although both female aggression and hissing behavior have been shown to be short- and long-term repeatable in our study population (Thys et al. 2017; Thys et al. 2019; B Thys, in preparation), we calculated the within-year (i.e. short-term) repeatability of both behavioral traits for the datasets at hand. Specifically, we ran two univariate mixed models per year (one for each behavioral trait) with random intercepts for female identity. Random intercepts for observer identity explained little to no variation in behaviors and were removed from the models (see the electronic supplementary material, table S3). Repeatability was calculated as the among-individual variance divided by the sum of the among-individual and residual (within-individual) variance (Nakagawa and Schielzeth 2010). Best linear unbiased predictors (BLUPs), representing individual-specific values of female aggression and hissing behavior, were extracted from these models to be used in further analyses (Henderson 1975).

Third, variance-covariance matrices were obtained by fitting three multivariate models, one for the data of both years combined and one for the data of each year separately. Each model included behavioral traits (BLUPs of female aggression and hissing behavior), parental investment (female and male visit rate), reproductive decisions (lay date, brood size) and proxies for reproductive success (fledgling number and average fledgling mass) as response variables (see electronic supplementary material, tables S4, S5 and S6). Variance-covariance matrices were adjusted for potential effects of female age (two-level factor; first-year versus older) by including the latter as a fixed effect. The models were implemented in a Bayesian framework (*MCMCglmm* package; Hadfield 2010) to ensure that uncertainty around posterior mean estimates was appropriately taken forward across analyses (see the electronic supplementary material, text S2 for details on prior specification). Next, path-analysis (*sem* package; Fox 2006) was applied to the estimated variance-covariance matrices from these models. Path analysis allows to estimate partial correlation (i.e. path) coefficients between two variables while controlling for effects of all other variables in the model (Shipley 2000). To obtain posterior mean estimates and credible intervals (CrI) for path coefficients, we ran a path-analysis on each of the estimated matrices (Mutzel et al. 2013; Thys et al. 2019). Since we wanted to assess the relative support of paths between variables that were hypothesized *a priori*, we present results of the full path model (cf. Mutzel et al. 2013; Zhao et al. 2016; Serrano-Davies et al. 2017).

All analyses were performed in R 3.6.1 (R core team, 2019). Prior to analyses, continuous variables were standardized to unit variance within years. Uni- and multivariate models were fitted assuming Gaussian error distribution. Autocorrelation among samples and model convergence was carefully assessed. Results presented are posterior mean estimates with associated 95% CrI (based on 2000 simulations) and estimates were considered to find strong support if 95% CrI did not overlap with zero. When CrI only slightly overlapped with zero we calculated the proportion of estimates that were positive (or negative), which gives a value comparable with a *p*-value (cf. Mutzel et al. 2013; Zhao et al. 2016).

RESULTS

Among-individual (co)variation in behavior

In both breeding seasons we found strong support for short-term repeatability of female aggression (2018: R = 0.48 [0.38 ; 0.59]; 2019: R = 0.50 [0.40 ; 0.59]) and female hissing behavior (2018: R = 0.86 [0.81 ; 0.89]; 2019: R = 0.78 [0.72 ; 0.83]), with estimates of similar magnitude as reported previously in our population (Thys et al. 2017; Thys et al. 2019). Despite that both behavioral traits were repeatable, we found no strong support that they were correlated among females in either breeding season (i.e. no behavioral syndrome; table 1; path 1).

Additionally, we found strong support for age-effects on female aggression in both breeding seasons, with first-year females being on average more aggressive than older females (see the electronic supplementary material, table S7). Also, in 2019, first-year females fed offspring on average at a higher rate compared to older females. Other effects of female age on behavioral traits, parental investment, reproductive decisions or reproductive success found no support.

Brood size, provisioning rates and reproductive success

Path models for breeding seasons combined, and breeding seasons separately, revealed that brood size positively covaried with visit rates (paths 20 and 21), as well as the number of fledglings produced (figure 2a,b,c; table 1; path 22). In addition, female visit rate was negatively associated with average fledgling mass in both years (table 1; path 16). Interestingly, even though brood size was not directly linked with the mass of fledglings (path 23), it was indirectly and negatively linked with fledgling mass via female visit rate (table 1; compound path A). Together, these findings suggest that female visit rate is involved in the trade-off between offspring number (brood size) and offspring mass. No support was found for a link between lay date and brood size in either year (table 1; path 17).

Female personality, provisioning rates and reproductive success

The path model for both breeding seasons combined revealed that hissing behavior negatively covaried with average fledgling mass (table 1; path 11; figure 2a). Similar effects were found when breeding seasons were analyzed separately (table 1; path 11), yet they found no strong support, most likely due to a lack of power associated with the smaller sample sizes in the latter analyses. No support was found for any other links between hissing behavioral type on the one hand and provisioning behavior, reproductive decisions or fledgling number on the other hand (figure 2a,b,c; table 1).

In addition, path models revealed year-specific pathways linking female aggression with proxies for reproductive success (figure 2b,c; table 1). That is, in 2018, female aggression was neither linked with parental investment nor with proxies for reproductive success (table 1). More aggressive females did initiate clutches earlier (figure 2b; table 1; path 7) but lay date did not affect brood size (table 1; path 17). In contrast, in 2019, more aggressive female behavioral types had higher visit rates (table 1; path 2) and female visit rate, in turn, covaried negatively with fledgling mass (table 1; path 16). Moreover, even though female aggression did not directly covary with fledgling mass (table1; path 5), it was indirectly and negatively associated with fledgling mass via female visit rate (figure 2c; table 1; compound path B). At the same time, female aggression was negatively linked with male visit rate (figure 2c; table 1; path 3). In addition, female and male visit rates were found to positively covary in 2019 (figure 2c; table 1; path 14), indicating that partners matched their visit rates. Together, these findings indicate that, in 2019, female aggression did not covary with fledgling number, but it was indirectly linked with average fledgling mass via female visit rate.

DISCUSSION

We revealed pathways that were strongly supported in two successive breeding seasons, with larger broods being provisioned at a higher rate by both parents. Surprisingly, female, but not male, provisioning rate was negatively linked to fledgling mass. Moreover, variation in female hissing behavior tended to directly and negatively covary with fledgling mass in both breeding seasons. At the same time, we revealed that estimated pathways linking female-female aggression with reproductive success varied across years, with female-female aggression not being associated with reproductive success in one year, but indirectly (i.e. via female provisioning rate) and negatively covarying with fledgling mass in the other year. Provisioning rate of male partners did not influence these relationships. Our findings illustrate that mechanisms linking personality with reproductive success can vary across personality traits and years, and thereby the importance of considering the dynamic nature of personality-fitness relationships.

Brood size, provisioning rates and reproductive success

We revealed patterns between brood size, provisioning rate and reproductive success that were present in both years. That is, larger broods were provisioned at a higher rate by both parents, corroborating with both experimental (reviewed in Gow and Wiebe 2014) and observational evidence (Patrick and Browning 2011; Mutzel et al. 2013). In addition, brood size had a very strong positive effect on the number of fledglings, indicating that nestling mortality was very low after day 11 post-hatching. Variation in the investment in parental provisioning did not appear to play an important role in nestling survival after day 11 post-hatching, given the unsupported direct effects of provisioning rates on fledgling number. Under favorable environmental conditions, as observed in the given breeding seasons, nestling mortality is most likely higher earlier in the nestling period compared to later in this period (see van Balen 1973). Indeed, nestling mortality appeared to be higher from hatching to day 11 post-hatching (2018: 8% ; 2019: 13%) compared to from day 11 up to fledging (2018: 1% ; 2019: 3%). Hence, variation in parental investment in the first half of the nestling period (e.g. female brooding and female and male provisioning) might have been of relatively more importance for nestling survival in the given years. Nonetheless, our findings indicate that, once nestlings reached a certain age, parents could provide sufficient food for nestlings to survive up to fledging.

In both years, we also found strong support for a negative link between female provisioning rate and average fledgling mass, which is likely the outcome of interactions between parental investment and both offspring demand and offspring number (Clutton-Brock 1991; Royle et al. 2012). That is, nestlings in larger broods and/or broods in poorer condition may have begged more, to which parents responded with higher provisioning rate (Neuenschwander et al. 2003; Smiseth et al. 2008). Yet, higher provisioning rate may still result in lower fledgling mass if parents cannot fully meet the higher demands of larger broods and/or broods in poorer condition. Indeed, we showed that although brood size did not directly covary with fledgling mass, it was indirectly and negatively linked with fledgling mass via female provisioning rate. In other words, although larger broods were provisioned at a higher rate by females, this higher maternal effort could seemingly not compensate for the higher demands associated with larger broods, resulting in relatively lower mass of fledglings. In line with this, female (but not male) provisioning rate per nestling significantly decreased with increasing brood size ($r = -0.19$; $P = 0.01$), suggesting that the quantity of food brought by females at least partially explained lower nestling mass in larger broods (see also Perrins 1965; Nur 1984; Gow and Wiebe 2014). Alternatively, or in addition, we cannot rule out the possibility of lower nestling mass partially resulting from higher energetic costs of sibling competition within larger broods (e.g. Neuenschwander et al. 2003). However, provisioning rate as such does not necessarily reflects total maternal investment into provisioning behavior. That is, faster visiting parents are often found to bring lower quality (i.e. less nutritious) or smaller amounts of food per feeding trip (van Balen 1973; Wright et al 1998) and differences in prey type and/or load size, potentially linked with territory quality (Riddington and Gosler 1995; Wilkin et al. 2009), may have contributed to the negative relationship between female provisioning rate and fledgling mass. Future studies may hence benefit from including aspects of food and/or territory quality in explaining the here observed negative relationship between female provisioning rate and fledgling mass.

Female personality, provisioning rates and reproductive success

Despite their moderate to high repeatability, female aggression and hissing behavior were not found to be correlated among females (i.e. no behavioral syndrome). Additionally, female age affected aggression, but not hissing behavior, with first-year females being on average more aggressive compared to older females, in line with previous findings in our population (Thys et al. 2017; Thys et al. 2019). In 2019, first-year females also fed offspring more frequently compared to older females. Therefore, all reported path coefficients were controlled for these effects of female age.

For hissing behavior, we show that more fiercely hissing females tended to produce fledglings of lower mass, an effect that only found support when the data of the two breeding seasons were analyzed together. Interestingly, this was not caused by hissing behavioral phenotypes making different reproductive decisions or because they differentially invested into provisioning behavior. First, this indicates the absence of a parental care behavioral syndrome between hissing behavior (as a form of aggressive nest defense) and provisioning rate (Sih et al. 2004; but see Wetzel and Westneat 2014). Second, this suggests that the direct link between variation in hissing behavior and fledgling mass may be the result of other, not mutually exclusive, underlying mechanisms. For example, territory quality is known to influence offspring mass (e.g. Riddington and Gosler 1995; Wilkin et al. 2009) and more fiercely hissing behavioral phenotypes may settle in territories of lower quality. However, if so, we would have expected that more fiercely hissing behavioral phenotypes initiated clutches later (Lambrechts et al. 2004), for which we did not find support. In addition, variation in the investment in incubation and brooding behavior can influence offspring mass, with lower temperatures during incubation/brooding typically negatively influencing the mass of offspring produced (e.g. O'Neal et al. 2008; Ardia et al. 2010; Rosvall 2013). Although it is reasonable to assume that more fiercely hissing females invest less in incubation and brooding behavior, for example due to life history trade-offs (*see introduction*) or proximate constraints (Rosvall 2013; de Jong et al. 2016), this remains to be investigated. Also, earlier findings in the same population, but in a different year, revealed that more fiercely defending females laid smaller clutches, suggesting they paid a reproductive cost in terms of egg number (Thys et al. 2019). In both years of the current study, however, we found no strong support for a link between hissing behavior and brood size (the latter being highly correlated with clutch size; r = 0.82; N = 165) and more fiercely defending females did not appear to pay such a reproductive cost. Previous work in other great tit populations has also shown that costs and benefits associated with differences in hissing behavior might be manifested in terms of female survival (Krams et al. 2014) and/or reproductive parameters other than clutch size *per se* (i.e. the proportion of eggs and hatchlings relative to fledglings; Tilgar and Koosa 2019). Together, this suggests that the reproductive (and potentially survival) costs and benefits associated with different hissing behavioral types might vary across years and populations, which requires long-term, cross-population studies.

In contrast to hissing behavior, estimated pathways linking among-individual variation in female aggression with reproductive success varied between years. In one study year (2018), variation in aggression was not linked, neither directly nor indirectly, to fledgling number and fledgling mass. In the other year (2019), more aggressive females were found to produce fledglings of lower body mass, via the positive link with female provisioning rate, but effects of female aggression on fledgling number were absent. Specifically, more aggressive females fed a given number of offspring (i.e. brood size) at a higher rate but this resulted in relatively lower fledgling mass (see earlier). This indicates that female provisioning rate was more determinant for fledgling mass (given the direct effect), yet, since aggression positively covaried with provisioning rate, more aggressive females ended up with fledglings of lower mass. Importantly, these patterns did not result from differences in the male's contribution to offspring provisioning. That is, although males of more aggressive females provisioned offspring at a lower rate in this year, we found no support that this affected fledgling mass. That male partners did not differentially influence reproductive success of different aggressive behavioral phenotypes, at least via their provisioning rate, contrast earlier suggestions that males can mitigate the potential costs associated with female aggression (see e.g. Rosvall 2010; Cain 2014; Krieg and Getty 2020). This raises the, as of yet untested, possibility that males influence reproductive success of different female aggressive behavioral types by other means than provisioning behavior (e.g. indirectly via their genetic quality) and/or that males influence female allocation strategies depending on the relative (dis)similarity of behavioral phenotypes within a pair (see e.g. Sheldon 2000; Both et al. 2005; Rosvall 2010; Royle et al. 2010; Schuett et al. 2011).

Contrary to our initial prediction (cf. Trivers 1972), we found that female aggression was either not related to female provisioning rate (in 2018) or more aggressive females fed offspring at a relatively higher rate (in 2019). Hence, females apparently did not face a direct trade-off between aggression and provisioning rate. Positive relationships between female aggression and female provisioning rate have also been observed in at least three other songbird species (tree swallows (*Tachycineta bicolor*), Rosvall 2011a; dark-eyed juncos (*Junco hyemalis*), Cain and Ketterson 2013; and house wrens (*Troglodytes aedon*), Krieg and Getty 2020). Interestingly, fitness consequences associated with female aggression in terms of offspring mass differed across these species (i.e. being positive; Krieg and Getty 2020; negative; Rosvall 2011a; or absent; Cain and Ketterson 2013), illustrating that costs and benefits associated with female-female aggression can be species-specific, complex and therefore potentially not easily identified (see Stiver and Alonzo 2009; Rosvall 2011b; Tobias et al. 2012; Cain and Rosvall 2014). Here, we have revealed that more aggressive female great tits, at least in one year, ended up with offspring of lower mass. Importantly, this effect would have remained undetected if we had not applied a multivariate and integrative approach, given it was not the result of a simple (bivariate) trade-off between aggression and provisioning rate. The complexity of relationships between female aggression, reproductive investment and reproductive performance is increasingly being recognized (e.g. Stiver and Alonzo 2009; Rosvall 2011b; Cain and Rosvall 2014) and here we illustrate that integrative approaches may help in capturing and revealing this complexity.

Overall, our study demonstrates that pathways linking personality with reproductive success can differ between years and assessed personality traits. Year-to-year variation in fitness consequences associated with differences in personality have often been found to relate to spatial or temporal variation in environmental conditions (e.g. resource abundance, population density; see Dingemanse and Réale 2013; Nicolaus et al. 2016). Yet, similar nest success and breeding density in both of our study years suggest overall similar breeding conditions. As a consequence, we cannot currently ascertain whether, and which form(s) of, environmental heterogeneity may have caused pathways to differ between years. In addition, certain fitness benefits of variation in female aggression and hissing behavior may accrue over longer time periods (e.g. adult survival and/or offspring recruitment), which would require a life time perspective (e.g. Cain and Rosvall 2014; Krams et al. 2014). Along this line, our sample size of females assessed across years (N = 28) was too low to assess whether the observed pathways represent long-term among-individual relationships and/or short-term within-individual relationships caused by correlated plasticity in behavioral responses (Dingemanse and Dochtermann 2013). It should also be noted that small and subtle effects of behavior on reproductive success might not have found strong support due to a lack of statistical power (type II error) associated with our moderate sample sizes when analyzing data of years separately. Indeed, the negative effect of hissing behavior on fledgling mass only found support when data of years were combined. Larger sample sizes within years might therefore reveal subtle effects (i.e. paths with point estimates relatively close to zero) for which we were unable to find support. Hence, future studies would largely benefit from data collected on a large number of individuals across their life time, allowing to partition pathways into among- and within-individual components with sufficient power, as well as to assess life time fitness consequences of variation in behavioral phenotypes.

CONCLUSIONS

By using an integrative and multivariate approach on behavioral and reproductive data collected across two successive breeding seasons we were able to reveal general patterns supported in both years, as well as year-specific patterns linking female aggressive personality with reproductive success. Importantly, these patterns would have been obscured when considering simple bivariate relationships, illustrating the added value of applying multivariate and path-analytical approaches to study how selection might act on behavioral phenotypes. Moreover, our findings emphasize that observed pathways between specific personality traits and reproductive success within a given year should not necessarily be generalized, not even across years with seemingly similar breeding conditions. This has important implications for our understanding of how personality variation translates into fitness and illustrates the necessity of including yearly variation into meta-analyses that consider personality-fitness relationships. Future studies should also aim at identifying (population wide and fine-scale) environmental heterogeneity that may cause among-year variation in pathways between certain personality traits and reproductive success.

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DATA ACCESSIBILITY

Analyses reported in this article can be reproduced using the data provided by Thys et al. (2020).

COMPETING INTEREST

The authors declare no conflict of interest.

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ETHICS STATEMENT

Experiments were approved by the ethical committee of the University of Antwerp (ID 2017-61) and performed in accordance with Belgian and Flemish laws. The Royal Belgian Institute of Natural Sciences (KBIN) provided ringing licences for all authors and technicians.

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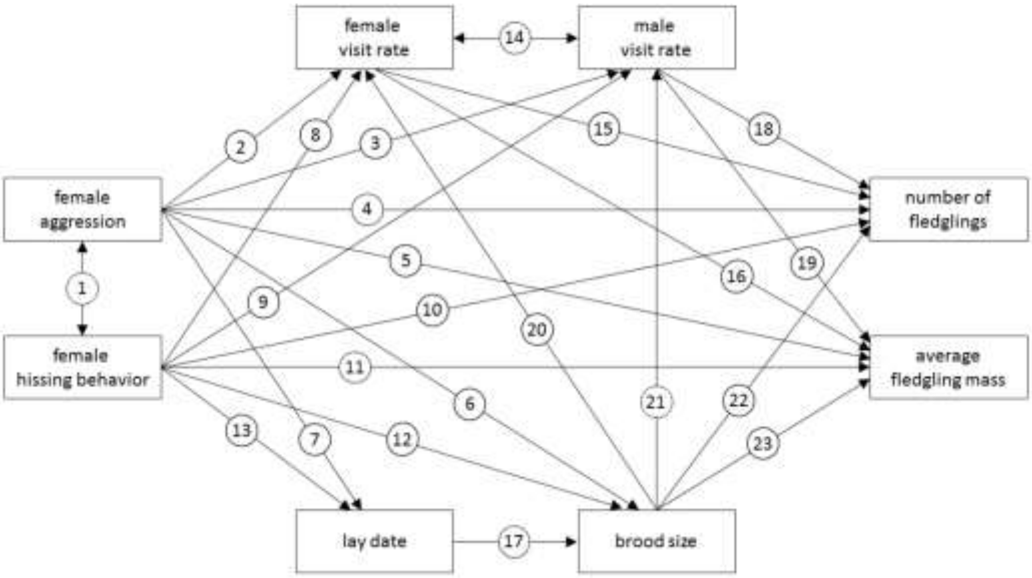

FIGURES

Figure 1. Hypothesized path model for female great tits. One-headed arrows depict the direction of hypothesized causal relationships, double-headed arrows depict simple hypothesized correlations without a causal relationship. Path numbers are given in circles.

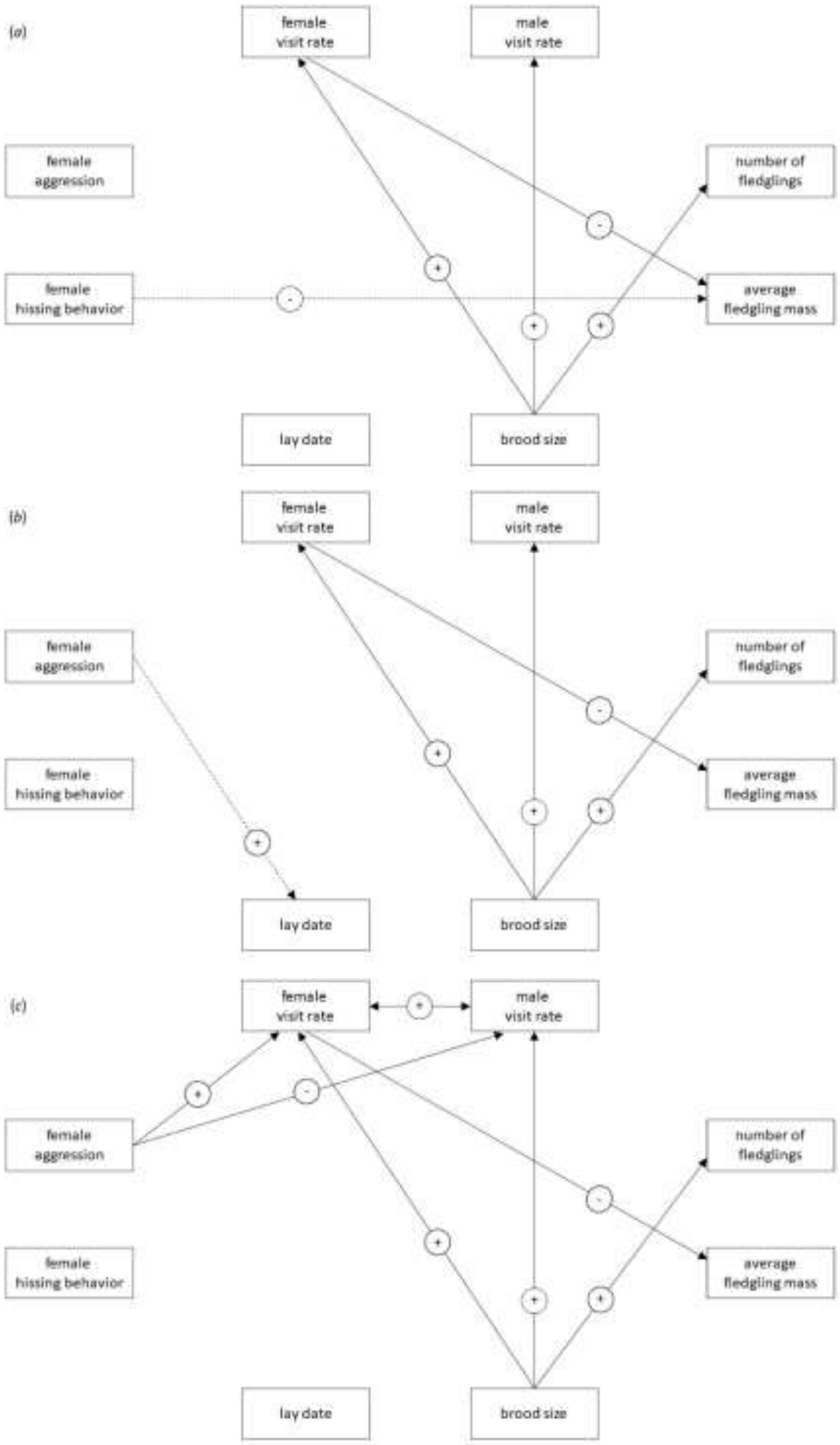

Figure 2. Supported paths in the model for female great tits in (a) both years combined, (b) 2018 and (c) 2019. Solid black lines indicate strong support (credible intervals do not overlap with zero). Dashed black lines indicate some support (credible intervals overlap with zero but $p < 0.05$). The sign of the estimated path coefficients are given in circles.

Table 1: Estimated partial regression coefficients from the hypothesized path model for great tits.

Path no.	hypothesized link	Full data	2018	2019
		path coefficient (95% CrI)	**path coefficient (95% CrI)**	**path coefficient (95% CrI)**
1	aggression ←→ hissing behavior	0.05 (-0.12 ; 0.19)	-0.02 (-0.19 ; 0.23)	0.09 (-0.12 ; 0.29)
2	aggression → female visit rate	0.11 (-0.08 ; 0.25)	-0.09 (-0.27 ; 0.17)	**0.23 (0.03 ; 0.40)**
3	aggression → male visit rate	-0.13 (-0.26 ; 0.05)	0.09 (-0.06 ; 0.32)	**-0.22 (-0.39 ; -0.01)**
4	aggression → no. fledglings	-0.02 (-0.06 ; 0.01)	0.02 (-0.00 ; 0.04)	-0.04 (-0.09 ; 0.01)
5	aggression → fledgling mass	0.02 (-0.15 ; 0.18)	-0.07 (-0.24 ; 0.17)	0.04 (-0.17 ; 0.29)
6	aggression → brood size	0.04 (-0.12 ; 0.21)	-0.08 (-0.30 ; 0.17)	0.06 (-0.18 ; 0.29)
7	aggression → lay date	0.03 (-0.18 ; 0.17)	*0.20 (-0.02 ; 0.41)*	-0.20 (-0.40 ; 0.03)
8	hissing behavior → female visit rate	0.06 (-0.09 ; 0.21)	0.10 (-0.14 ; 0.26)	0.05 (-0.11 ; 0.27)
9	hissing behavior → male visit rate	0.08 (-0.08 ; 0.21)	0.10 (-0.12 ; 0.25)	0.11 (-0.07 ; 0.31)
10	hissing behavior → no. fledglings	-0.02 (-0.05 ; 0.01)	-0.01 (-0.03 ; 0.01)	-0.02 (-0.06 ; 0.03)
11	hissing behavior → fledgling mass	*-0.16 (-0.31 ; 0.01)*	-0.11 (-0.31 ; 0.07)	-0.13 (-0.32 ; 0.08)
12	hissing behavior → brood size	-0.03 (-0.22 ; 0.11)	-0.01 (-0.19 ; 0.24)	-0.12 (-0.36 ; 0.07)
13	hissing behavior → lay date	0.04 (-0.14 ; 0.18)	0.02 (-0.16 ; 0.27)	-0.10 (-0.33 ; 0.09)
14	female visit rate ←→ male visit rate	0.04 (-0.09 ; 0.16)	-0.01 (-0.17 ; 0.18)	**0.17 (0.04 ; 0.35)**
15	female visit rate → no. fledglings	-0.02 (-0.06 ; 0.01)	-0.01 (-0.03 ; 0.01)	-0.03 (-0.08 ; 0.03)

16	female visit rate → fledgling mass	**-0.36 (-0.50 ; -0.17)**	**-0.38 (-0.54 ; -0.16)**	**-0.27 (-0.52 ; -0.04)**
17	lay date → brood size	-0.06 (-0.23 ; 0.10)	-0.09 (-0.24 ; 0.19)	-0.12 (-0.30 ; 0.13)
18	male visit rate → no. fledglings	0.04 (-0.01 ; 0.08)	0.00 (-0.02 ; 0.02)	0.04 (-0.02 ; 0.10)
19	male visit rate → fledgling mass	0.02 (-0.18 ; 0.18)	-0.18 (-0.39 ; 0.05)	0.12 (-0.17 ; 0.31)
20	brood size → female visit rate	**0.30 (0.15 ; 0.47)**	**0.25 (0.08 ; 0.50)**	**0.36 (0.20 ; 0.56)**
21	brood size → male visit rate	**0.40 (0.26 ; 0.57)**	**0.39 (0.22 ; 0.60)**	**0.47 (0.29 ; 0.67)**
22	brood size → no. fledglings	**0.97 (0.94 ; 1.01)**	**0.99 (0.97 ; 1.02)**	**0.97 (0.92 ; 1.01)**
23	brood size → fledgling mass	-0.02 (-0.21 ; 0.17)	0.07 (-0.16 ; 0.29)	-0.08 (-0.30 ; 0.17)
Compound path	Individual path numbers			
A	20 x 16	**-0.10 (-0.18 ; -0.03)**	**-0.11 (-0.19 ; -0.01)**	**-0.11 (-0.21 ; -0.01)**
B	2 x 16	-	-	**-0.07 (-0.14 ; -0.01)**

The path coefficient of a compound path is the product of the coefficients along this path. Path coefficients that found strong support (credible intervals do not overlap with zero) are indicated in bold. Path coefficient that found some support (credible intervals slightly overlap with zero but $p < 0.05$) are given in italics. Sample sizes: Full data (N = 165); 2018 (N = 82), 2019 (N = 83).