



Original Article

Functional relations between body mass and risk-taking behavior in wild great tits

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Natural selection often favors particular combinations of functionally-related traits, resulting in adaptive phenotypic integration. Phenotypic integration has been proposed as a potential mechanism explaining the existence of repeatable among-individual differences in behavior (i.e., animal personality). In this study, we investigated patterns of covariation between morphology and behavior in a population of free-living great tits (*Parus major*) monitored for 7 years. In particular, we aimed to disentangle the effect of structural size versus body condition on risk-taking behavior. To do so, we repeatedly quantified multiple morphological (body mass, wing, tarsus, and bill length) and behavioral traits (aggressiveness and exploration) in 742 individual males. Structural equation modeling (SEM) allowed us to test causal a priori hypothesized relationships between the different morphological and behavioral traits. Our best-fitting SEM model supported the existence of a behavioral character, “risk-taking behavior” that covaried simultaneously with the latent variable “body size,” and “body condition.” Our findings thus demonstrate that an individual’s morphological and behavioral traits represent expressions of an integrated phenotype, suggesting a role for phenotypic integration in generating animal personality in a wild bird population.

Key words: behavioral syndrome, body condition, body size, morphology, *Parus major*, structural equation modeling.

INTRODUCTION

Behavioral ecologists have devoted much research effort towards understanding the existence and maintenance of among-individual differences in behavior (i.e., “animal personality”), and of among-individual correlations between behaviors (i.e., “behavioral syndromes”) (Sih et al. 2004; Réale et al. 2007; Biro and Stamps 2008; Dingemanse and Wolf 2010). Concurrently, behavioral ecologists have devoted much research effort towards understanding the link between morphological and physiological traits (e.g., body size, body condition) and behavior (see meta-analysis by Niemelä and Dingemanse 2018). Phenotypic integration across different functionally-related traits as an explanation for animal personality variation has, however, received little attention to date. Given that behavior represents a component

of a more complex multivariate phenotype, it is necessary to simultaneously explore the link between behavioral and morphological traits to be able to draw general conclusions regarding patterns of trait integration in nature. Indeed, the few empirical studies that focused on morphological and behavioral traits in the context of individual differences and phenotypic integration investigated the question by quantifying single variables of each morphological and behavioral trait (but see Brodie 1993; Kim and Velando 2015; Royauté et al. 2015).

In this study, we addressed this research gap by investigating patterns of morphological and behavioral covariation among individuals in a natural population of great tits (*Parus major*). Testing patterns of phenotypic integration between functionally-related traits is challenging because the morphological and behavioral traits of interest often cannot be captured adequately by simply quantifying single traits. This is because in many cases, the morphological and behavioral traits are latent variables (Araya-Ajoy and Dingemanse 2014). For example, approach distance to

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a dummy, probability of attack, and number of calls and songs are observable expressions of “territorial aggressiveness” in male great tits (*Parus major*). Aggressiveness can thus be quantified as a latent variable representing the shared physiological and neurobiological pathways determining the expression of the different agonistic behaviors. This latent variable has likely evolved because correlational selection favored phenotypic integration of agonistic behaviors (Araya-Ajoy and Dingemanse 2014). Here, we measured 6 morphological and behavioral traits (body mass, tarsus length, bill length, wing length, aggressiveness, and exploration behavior) in breeding male individuals for each of 7 consecutive years (2010–2016). First, we investigated the existence of a latent variable “body size,” representing the investment in growth of an individual (Figure 1). Second, we investigated the existence of a behavioral syndrome, i.e., existence of covariance among individuals between exploration behavior and aggressiveness, representing “risk-taking behavior” (Figure 1). The “risk-taking behavior” hypothesis was based on the extended evidence showing positive covariance between aggressiveness, antipredator boldness, and exploration behavior as part of a general “aggressiveness-boldness syndrome” (reviewed by Garamszegi et al. 2012). Thus, individuals that usually take more risks when confronted with a conspecific also do so when confronted with a new, unfamiliar environment. In great tits, aggressiveness and exploration behavior have also been found to correlate among individuals in both the laboratory (Verbeek et al. 1994) and the field (Hollander et al. 2008). In addition, it is known that more exploratory individual great tits invest more in current (as opposed to future) reproduction (Nicolaus et al. 2015), obtain higher social dominance (Dingemanse and de Goede 2004), and secure more resources under competition (Quinn et al. 2012).

As a third step, we investigated the overall pattern of phenotypic integration between morphology and behavior. Specifically, here, we investigated how size-independent and dependent variation in body mass was related to the behavioral traits. Measuring variation in body size and size-independent body mass in live vertebrates such as birds is, however, a difficult task. Body size is usually defined as the structural size of an organism independent of its

energetic reserves (Piersma and Davidson 1991). Energetic reserves are the amounts of nutrients (especially fat and protein) that individuals store in order to survive periods of negative energy balance (Lindstrom and Piersma 1993). Body mass certainly contains information about both body size and energetic reserves, however, the failure to properly quantify and differentiate between the 2 variables can result in misleading interpretations. The quantification of both body size and body condition in birds has consequently attracted large empirical attention (e.g., Rising and Somers 1989; Green 2001; Piersma and Davidson 1991). There have been suggested multiple approaches and indices to quantify body size and body condition. To quantify body size in birds, different indices or composite variables such as the Body Size Indicator (i.e., the ratio between mass and a linear measure of body size) or the first principal component of a principal component analysis (PCA) on different skeletal measures (reviewed by Rising and Somers 1989; Piersma and Davidson 1991) have been proposed. To quantify body condition in birds, numerous nondestructive methods have been used and are based on relating body mass to linear measures of body size (reviewed by Green 2001). This extensive variety of metrics of body size and body condition highlights the fact that body size and body condition cannot be measured directly as they represent latent variables. Here, we explicitly focused on disentangling the relationships between behavior, structural size and body condition by means of structural equation modeling (SEM). More specifically, we tested whether “risk-taking behavior” (detailed above) covaries with body mass above and beyond the general allometric covariation caused by the latent variable “body size.” One hypothesis is that body mass would simply be an expression of the latent variable “body size” and the behavioral variables would thus be linked directly to “body size”, and only indirectly linked to body mass (Figure 1, Table 1, models 2–9). Alternatively, the behavioral variables could be associated with the specific trait body mass (i.e., where size-independent variation in body mass represents a proxy for body condition). The existence of an unmeasured “body condition” variable can occur independently if the behavioral variables are directly related to the latent variable “body size” (Figure 1, Table 1, Models 10–12) or not (Figure 1, Table 1, Models 13–18).

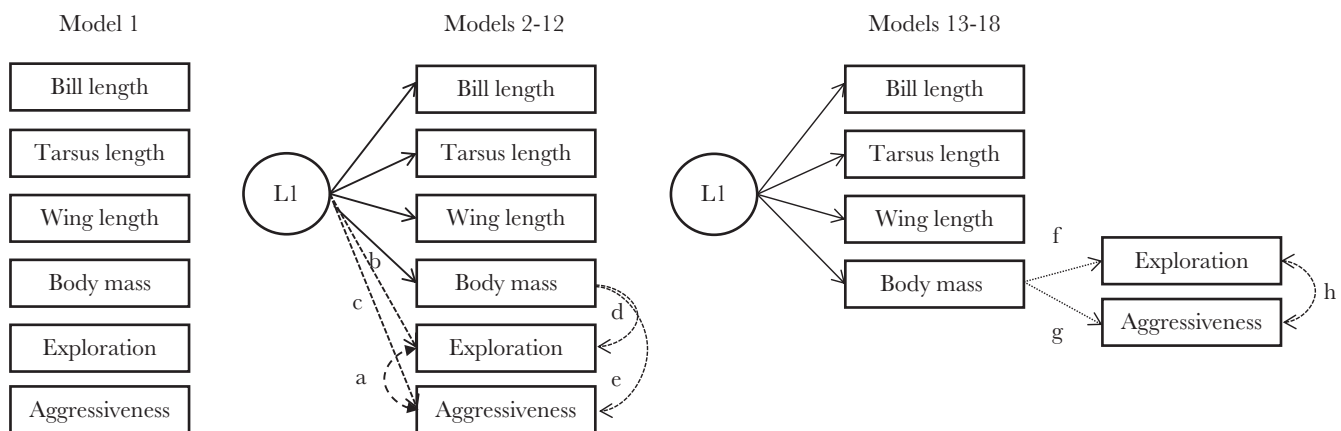


Figure 1

Models (1–18) of hypothesized relationships between morphological and behavioral traits. Models are described in Table 1. Unidirectional arrows represent causal relationships between traits; bidirectional arrows represent undefined correlations. Solid lines represent relationships present across the whole set; dashed lines represent relationships expressed in specific cluster structures. “L1” represents a latent variable. Path “a” is active in model 3; “a-c” in model 4; “b-c” in model 5; “b” is active in model 6; “a-b” are active in model 7; “c” is active in model 8; “a” and “c” are active in model 9. Paths “a-e” are active in model 10; “a-d” is active in model 11; “a-c” and “e” are active in model 12; Path “f” and “g” are active in model 13; “f” is active in model 14; “g” is active in model 15; paths “f” and “h” are active in model 16; “g” and “h” are active in model 17; and “f-h” are active in model 18.

Table 1
A priori hypotheses of morphological and behavioral integration in male great tits

Model	Hypothesis
Model 1	Null model of trait independence
Model 2	All morphological traits are linked by a latent variable, and behavioral traits are uncorrelated (with each other and with the morphological traits)
Model 3	All morphological traits are linked by a latent variable, and behavioral traits are correlated with each other, but not with the morphological traits
Model 4	All traits are linked by a latent variable, and there is additional covariance between behaviors independent of the latent variable
Model 5	All traits are linked by a latent variable
Model 6, 8	All morphological traits are linked by a latent variable and either exploration (6) or aggressiveness (8) is linked by the latent variable
Model 7, 9	All morphological traits are linked by a latent variable and either exploration (7) or aggressiveness (9) is linked by the latent variable. There is additional covariance between behaviors independent of the latent variable
Model 10–12	All traits are linked by a latent variable; and there is a causal influence of body mass on both behaviors at the same time (10), either exploration (11) or aggressiveness (12)
Model 13–15	All morphological traits are linked by a latent variable; and there is a causal influence of body mass on both behaviors at the same time (13), either exploration (14) or aggressiveness (15)
Model 16–17	All morphological traits are linked by a latent variable; behaviors are correlated and there is a causal influence of body mass on either exploration (16) or aggressiveness (17)
Model 18	All morphological traits are linked by a latent variable; there is a causal influence of body mass on both behaviors and there is additional covariance between behaviors independent of the latent variable

In both cases (Figure 1, Models 10–18), “body condition” would represent an unmeasured variable that is covarying with the latent variable “body size.” We also modeled the existence of an additional covariance between the 2 behavioral traits, representing a behavioral syndrome that is present above and beyond variation in body size and body condition (Figure 1, Table 1, Models 3, 4, 7, 9–12, 16–18). Although we could also predict that risk-taking and body size may be directly linked, our data structure does not allow testing for such a relationship. As we only measured 2 behavioral traits, risk-taking behavior as a latent variable itself would not be identifiable (Shipley 2004). Importantly, by comparing these different SEM models, we were able to test alternative causal relations between the different traits. For instance, by comparing Model 10 versus Model 18 one could reveal the direct effect of body size on risk-taking behavior; and by comparing Model 10 versus Model 4, the indirect effect of body size on risk-taking behavior via body mass.

In sum, here we tested for the existence of one latent variable labeled as “body size” linking all the morphological traits; the existence of size-independent covariance between “body condition” and “risk-taking behavior,” and the existence of an additional covariance between exploration behavior and aggressiveness, representing the behavioral syndrome “risk-taking behavior” (Figure 1). We then examined whether these 6 different traits were part of a single integrated phenotype in great tits, and explicitly investigated the role of body mass in the integration of phenotypic traits. We tested these alternative hypotheses of phenotypic integration at the among-individual level. To do so, we used mixed-effect models combined with SEM to test the relative fit of distinct biological hypotheses of among-individual integration between morphological and behavioral traits.

METHODS

Population and study site

Our study was carried out in a nest-box population of great tits consisting of 12 plots, established in autumn 2009 in Bavaria, southern Germany (Starnberg; 47° 58' N, 11° 14' E). Each plot consisted of a forest patch with 50 nest-boxes positioned in a

regular grid with 50 m between each box. The population was monitored from 2010 onwards following the same fieldwork protocol to collect morphological, behavioral, and life-history data for every breeder. All birds in the current study were adult males ($n = 742$), given that we only measured aggressiveness in males. Our field protocol consisted of checking nest-boxes twice a week from April through July to determine lay date and clutch size (see Nicolaus et al. 2015 for more details). Once an egg was found, we assessed aggressiveness of each focal male 4 times; twice during the egg-laying stage and twice during the egg-incubation stage (see below). When chicks were 7 days old, parents were caught with a spring trap inside the nest-box and marked with a unique combination of rings if not previously marked and assessed for their exploration behavior (see below). After the test, birds were measured and a small blood sample was taken. Sex and age (first-year vs. older breeder) were determined based on plumage characteristics, body mass was measured using a Pesola spring balance to the nearest 0.1 g, tarsus length and bill length were measured with slide callipers to the nearest 0.1 mm, and wing length (third primary) was measured with a wing ruler to the nearest 0.5 mm. We collected morphological and behavioral data for a 7-year period (2010–2016) for all first broods produced by great tit pairs in our study plots. First broods were defined as those broods initiated within 30 days of the first clutch of the year (Van Noordwijk et al. 1995).

Experimental protocol

Aggressiveness

We quantified male aggressiveness by simulating territorial intrusions at each focal nest. We performed 4 tests per nest per year, twice during the egg-laying stage and twice during the egg-incubation stage. The aggression test consisted of a taxidermic mount of a male great tit presented on a 1.2 m wooden pole with a playback song 1 m away from the subject's nest-box. Once the focal male had entered a 15-m radius around the box, we recorded the behavior of the individual for 3 min. Details of the experimental setup and assayed behaviors are provided in Araya-Ajoy and Dingemanse (2014). Following previous work, we used the minimum distance of the focal male to the mount as our measure of

the intensity of an aggressive response for both breeding stages (Araya-Ajoy and Dingemanse 2014; Araya-Ajoy et al. 2016; Araya-Ajoy and Dingemanse 2017). For ease of interpretation, approach distance was multiplied by -1 so that higher values represented more aggressive responses (Araya-Ajoy and Dingemanse 2014). Observations where males did not arrive within 15 min were scored as nonresponsive. Previous work from the same population of great tits showed that the cross-context correlation (r) between aggressiveness expressed during the laying versus incubating stages was much lower than one ($r \pm 95\%$ credible interval [CI] = 0.51 [$0.31, 0.60$]) (Araya-Ajoy and Dingemanse 2014), indicating that aggressiveness during the 2 different breeding stages did not fully represent the same character (Roff 1997). Araya-Ajoy and Dingemanse (2014) also showed that correlations between expressions of aggressiveness were tighter during the egg laying compared to the incubation stage (Araya-Ajoy and Dingemanse 2014). For the statistical analyses presented here, we pragmatically chose to focus on aggressiveness expressed during the laying stage, using the mean of the 2 repeated measures collected annually during laying for each individual, thereby best approximating their individual-specific annual values (Araya-Ajoy and Dingemanse 2017). In cases where there was only one data point available (i.e., the individual did not respond to one of the behavioral assays), we took the single score as a proxy for the mean score. Reassuringly, our decision to use the mean score of aggressiveness during laying stage (vs. incubation) did not alter our conclusions (Results not shown).

Exploration behavior

We assayed exploration behavior of males directly following capture when their nestlings were 7 days old. For 2 min, we recorded the behavior of the captured individual in a $61 \text{ L} \times 39 \text{ W} \times 40 \text{ H cm}$ cage adapted from the classic “novel environment test” (for more details, see Stuber et al. 2013). The total number of movements between different sections of the cage (see Figure 1 in Stuber et al. 2013) was used to measure an individual's activity in a novel environment, labeled “exploration behavior” (Araya-Ajoy et al. 2016).

Statistical analyses

We conducted 2 sets of statistical analyses. First, we estimated patterns of (co)variance among traits at different hierarchical levels using a multivariate mixed-effect model. As a second step, we fitted structural equation models (SEMs) to study the hypothesized relationships between the phenotypic traits at the among-individual level. Our ability to test for different alternative hypotheses of phenotypic integration at the among-individual level hinged on the availability of repeated measures per individual of multiple behavioral and morphological traits collected across years. Our dataset comprised a total of 742 individuals with between 1 and 6 observations per individual across all traits. The mean number of observation per individual was 1.47 for body mass, bill length, tarsus length and wing length; 1.49 for exploration behavior; and 1.18 for aggressiveness. Furthermore, the morphological traits and exploration behavior were measured during the chick-provisioning stage while aggressiveness was measured during the egg-laying stage. Therefore, there was approximately a 3-week interval between these measurements for any given individual. We modeled all 6 variables assuming a Gaussian error distribution and scaled each to standard deviation units (i.e., mean centered and variance standardized) to facilitate comparison of the relative magnitudes of variance components across traits. To meet the normality

requirement, aggressiveness was squared-root transformed prior to analyses (Araya-Ajoy and Dingemanse 2014).

Multivariate mixed-effects modeling

We estimated among-trait (co)variance at the among-individual, among-observer and within-individuals-among-year levels using a multivariate mixed-effects model. To do so, we fitted all 6 traits as response variables and individual and observer identity as random effects. We only included those random effects that explained substantial variation (i.e., individual and observer identity) to avoid over-parameterization (for detailed information, see Supplementary Table S1). The resulting among-observer and within-individuals among-years covariance matrices were not important to our study question and thus not discussed further (Results not shown). The multivariate mixed-effects model was fitted using a Bayesian framework implemented in R v. 3.3.3 (Team R Core 2017) with the R-package “MCMCglmm” (Hadfield 2010). We used an inverse gamma prior and ran 3,005,000 iterations per model with a burn in period of 5000 and a thinning interval of 3000 iterations. Posterior means and 95% CI were estimated for (co)variances and correlations. We also checked whether our estimates were a function of the choice of prior, which was not the case; and whether our variance estimates were similar to the ones estimated using univariate analyses, which was the case (Supplementary Table S1).

SEM

To test the relative fit of alternative biological hypotheses of phenotypic integration, we applied SEM to 18 a priori conceived scenarios assessing how the different traits were associated among individuals (Figure 1, Table 1). Of the 18 models, model 1 represents a (biologically unrealistic) statistical “null” expectation; models 2–9 represent different scenarios of phenotypic integration and quasi-independence between body size and risk-taking behavior; and models 10–18 represent hypotheses of body size as a latent variable and causal influences of body mass (as proxy for the “body condition”) on the risk-taking behavior. We used the among-individual correlation matrix estimated with the multivariate mixed-effects model to test our SEM hypotheses with the R-package “SEM” in R v. 3.3.3 (Team R Core 2017). We then compared the model fit using the Akaike information criterion (AIC) (Burnham and Anderson 2004) and evaluated the relative support based on AIC differences relative to the best-fitting model (ΔAIC).

RESULTS

All phenotypic traits (i.e., body mass, tarsus length, wing length, bill length, exploration behavior and aggressiveness) showed considerable variation among individuals (Table 2). In addition, most morphological traits were strongly correlated (Table 2). In general, heavier birds had longer tarsi, wings and bills. Furthermore, individuals that were on average relatively aggressive toward conspecifics were also relatively active in a novel environment (i.e., more “explorative”) (Table 2).

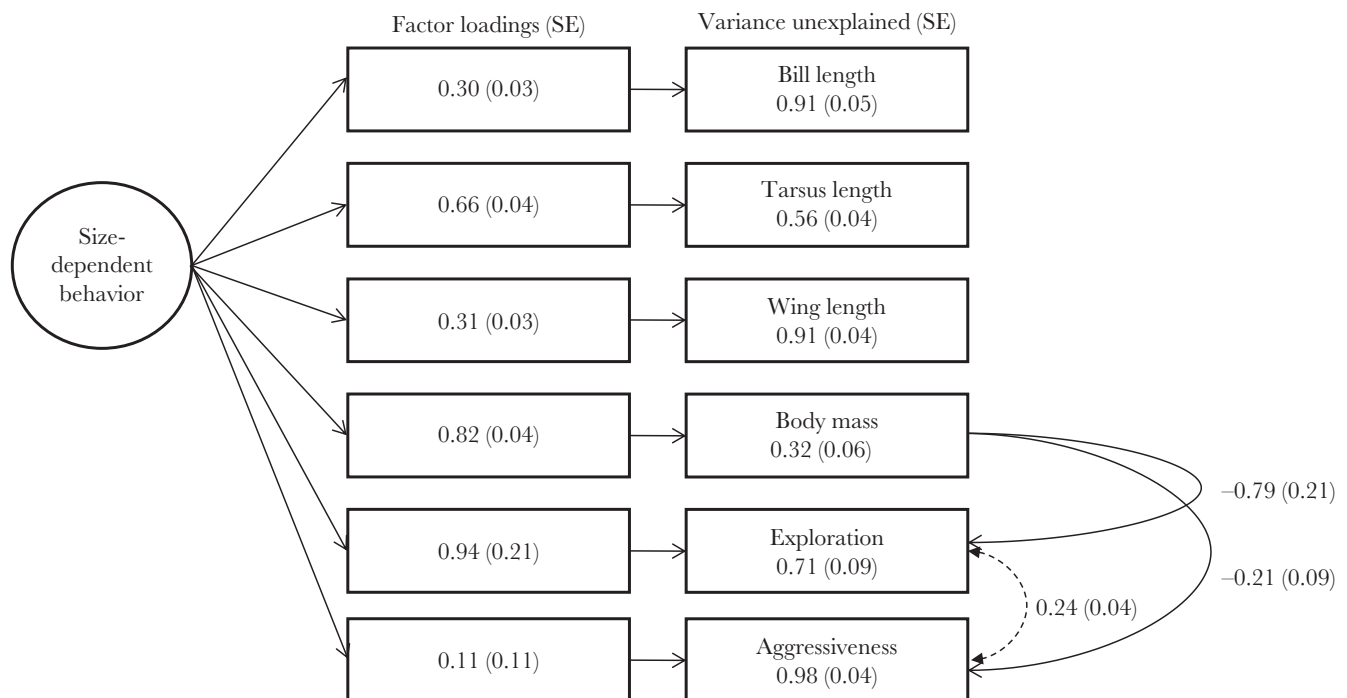
SEM comparisons identified model 10 as best explaining the among-individual correlation matrix (as it had the lowest AIC value, the AIC weight suggests that is 4.6 times more likely to be the best model, and explains 88% of the multivariate variance; Supplementary Table S2). Model 10 posited an overall phenotypic integration of the 6 morphological and behavioral traits, representing the latent variable “body size-dependent behavior.” This overarching latent variable included paths positively affecting the expression of

Table 2

Parameter estimates with associated 95% CI for trait variance (diagonal) and among-individual correlation (below diagonal) for 6 morphological and behavioral traits

	Body mass	Exploration	Aggressiveness	Tarsus length	Wing length	Bill length
Body mass	0.59 (0.50, 0.70)					
Exploration	−0.02 (−0.16, 0.12)	0.39 (0.30, 0.48)				
Aggressiveness	−0.12 (−0.32, 0.08)	0.28 (0.02, 0.49)	0.25 (0.15, 0.38)			
Tarsus length	0.54 (0.44, 0.64)	0.18 (0.04, 0.31)	−0.10 (−0.31, 0.07)	0.63 (0.54, 0.73)		
Wing length	0.31 (0.18, 0.45)	−0.01 (−0.18, 0.16)	0.06 (−0.15, 0.31)	0.20 (0.08, 0.34)	0.36 (0.28, 0.46)	
Bill length	0.19 (0.03, 0.35)	0.24 (0.07, 0.43)	0.11 (−0.16, 0.38)	0.25 (0.08, 0.38)	−0.02 (−0.20, 0.16)	0.28 (0.20, 0.37)

Variances and correlations were estimated using a multivariate approach and controlling for the effects of Observed Identity and residual variance. Values in bold face indicate important correlations, owing to 95% CI not overlapping zero.

**Figure 2**

Parameter estimates of the structural equation model that best fitted our data (Model 10) based on males great tits ($n = 742$). For each trait, we report the variance unexplained by the SEM structure and factor loadings with the corresponding standard error extracted from the SEM model (SE) in parentheses. Solid lines represent causal relationships, and dashed lines are linking the behavioral traits between them (i.e., constituting “risk-taking behavior”).

all traits with an additional covariance between the behavioral traits (Model 10; Figure 2). Furthermore, variation in body mass not attributable to the latent variable “body size-dependent behavior” was negatively linked to both behavioral traits, implying that “body condition” (i.e., body mass variation independent from body size variation) was also covarying with “risk-taking behavior.”

DISCUSSION

This study investigated patterns of among-individual covariance and causal relations between morphology and behavior in free-living male great tits as an explanation for “animal personality.” We made use of SEM to test a priori hypothesized causal relationships between the different measured traits. We found evidence for integration between behavior and morphology mediated by 2 distinct mechanisms: one integration mechanism between behavior and morphology acted through the overarching latent variable “body size-dependent behavior” while another integration mechanism was

mediated by size-independent variation in body mass (i.e., “body condition”). These integration patterns revealed that all morphological and behavioral traits were positively linked, but body condition and the 2 behavioral traits were negatively linked among individuals. Thus, by using structural equation models we were able to effectively disentangle those 2 distinct pathways by which body mass was linked to behavior. Our results suggest the existence of phenotypic integration between morphology and behavior among-individual male great tits.

Behavioral ecologists have put great emphasis on the link between “state” features (e.g., body size, body condition) and behavioral traits (Houston and McNamara 1999) (see meta-analysis by Niemelä and Dingemanse 2018). Nevertheless, there are few empirical studies that have viewed state and behavioral traits as evolutionary characters in the context of animal personality. Additionally, body features like size or body condition have been among the most frequently invoked state variables in state-dependent behavior theory. Models based on those body features predict

that the energy that an organism obtains typically depends on its size or reserves, and the organism's body features will be influenced by its behavioral responses (Houston and McNamara 1999). The central problem in testing these models is the difficulty of empirically quantifying body size and body condition, given that both are latent variables. A common approach to measure any of these 2 distinct body features is by quantifying the total mass of an individual. A major strength of this paper is that we were able to disentangle different aspects of the effect of body mass on risk-taking behavior. On the one hand, behavior and morphology were integrated by an overarching latent variable representing "body size-dependent behavior." Individuals that defended their territories more strongly against conspecifics and explored their environment more actively also had higher mass and longer tarsi, wings and bills. Risk-takers were thus relatively large individuals. This finding might be driven by a more favorable cost-benefit ratio of competitive encounters for large individuals (e.g., large individuals are more likely to win, and less likely to get hurt even if they lose). Another interpretation is that (structurally) larger animals have higher energy requirements, and therefore are more willing to expose themselves to risk in order to acquire resources. Simultaneously, behavior was additionally linked to the portion of body mass that was independent of "body size" (i.e., "body condition"). We found that the 2 behavioral traits were negatively associated to the variation in body mass independent of the latent variable "body size-dependent behavior." Individuals that defended their territories more vigorously against conspecifics and explored their environment more actively had a lower size-independent body mass. Risk-takers thereby presented lower body condition compared to risk-avoiding individuals. This finding implies that individuals that had on average low body condition were relatively explorative and aggressive (i.e., took more risks), likely as a way to secure more resources. In contrast, higher body condition allows individuals to behave more cautiously and avoid taking risks. An alternative interpretation of this finding is that birds that are relatively heavy (independent of body size) have a higher wing-loading (Bednekoff and Houston 1994), and consequently, take less risk due to their greater vulnerability to predation. These different explanations cannot be disentangled with our study design. Yet, our findings do confirm the general notion that morphological and behavioral traits from different functional contexts covary. Our study therefore implies that phenotypic integration of behavior and morphology may be a common phenomenon among organisms (Dochtermann and Jenkins 2007; Carter and Feeney 2012; Araya-Ajoy and Dingemanse 2014), and that selection is likely operating differently on different components of body mass.

The opposing effects of body mass (as a measure of both body size and body condition) on behavior highlight the benefits of using statistical approaches (such as SEM) that enable multiple relationships between traits to be estimated simultaneously. Our analyses suggest that empiricists interested in the relationships between body size, body condition, and behavior should focus on quantifying latent variables instead of considering single traits such as total body mass. Remarkably, we observed that body mass was not correlated with any of the 2 behaviors (Table 2) but complex relationships between the different components of body mass and risk-taking behavior were revealed via SEM. Our findings thus offer a solution to the long-running debate focusing on whether body mass more strongly reflects body condition or structural body size (Piersma and Davidson 1991). This is because we demonstrate here that both components can be statistically partitioned, and therefore can be studied simultaneously. Furthermore, our evidence

for phenotypic integration between behavior and morphology is particularly insightful given the considerable theoretical and conceptual literature predicting the evolution of animal personality (Dingemanse and Wolf 2010). Our results convincingly demonstrate that body size and risk-taking behavior were integrated functionally-related traits, suggesting that phenotypic integration plays a role in generating repeatable individual differences in behavior.

Overall, our work expands upon a classic body of research predicting that selection pressures generate among-individual correlations between and within morphological and behavioral characters, being a potential mechanism explaining the existence of "animal personality." We found that behavioral traits were linked to morphological traits by an overarching latent variable as part of a unique phenotypic character and to the single trait body mass, representing "body condition." This finding thus implies that an individual's morphological and behavioral traits may represent expressions of a uniquely evolved character, ultimately having consequences for evolutionary trajectories (i.e., selection can potentially act more rapidly when functionally-related traits are correlated among the line of least resistance (Schluter 1996)). Future empirical work can contribute to our understanding by demonstrating the nature of these trait correlations, i.e., whether the observed trait correlations are indeed adaptive and the result of correlational selection; whether they are the result of linkage disequilibrium or pleiotropic effects of genes, mechanisms that are not necessarily adaptive; or even whether some of the correlations are simply the result of physical (allometric) constraints. Overall, this study highlights the broad applicability of multivariate analyses (e.g., SEM) in personality research and brings new exciting possibilities to behavioral ecologists studying complex relationships between phenotypic traits among individuals, and other key levels of biological organization.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

ETHICS

All animal handling procedures complied with guidelines from the District Government of Upper Bavaria (Regierung von Oberbayern) for Animal Care.

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

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