Partitioning within-species variance in behavior to within- and between-population components for understanding evolution

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30 **Abstract**

31 Phenotypes vary at multiple hierarchical levels, of which the interspecific
32 variance is the primary focus of phylogenetic comparative studies. However, the
33 evolutionary role of particular within-species variance components (between-
34 population, between- or within-individual variances) remains neglected. Here
35 we partition the variance in an anti-predator behavior, flight initiation distance
36 (FID), and assess how its within- and between-population variance are related to
37 life history, distribution, dispersal and habitat ecology. Although the
38 composition of within-species variance in FID depended on the phylogeny, most
39 variance occurred within populations. When accounting for allometry, density-
40 dependence, uncertainty in the phylogenetic hypothesis, and heterogeneity in
41 data quality, within-population variance was significantly associated with
42 habitat diversity and population size. Between-population variance was a
43 significant predictor of natal dispersal, senescence and habitat diversity.
44 Accordingly, not only species-specific mean values of a behavioral trait, but also
45 its variance within and among populations can shape the evolutionary ecology
46 of species.

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Introduction

Observations can be summarized as moment statistics such as the first moment, variance, skewness and kurtosis (Wright 1968). Since the days of Fisher (1930), a primary interest in biology focuses on different variance components. Variances can be decomposed into variance within individuals, which relates to phenotypic plasticity (West-Eberhard 2003; Dingemanse *et al.* 2010). Variance among individuals is typically what most evolutionary studies target when investigating phenotypic variation in relation to fitness (Williams 1966), but it also has consequences for estimating repeatability, heritability and other quantitative genetic parameters (Falconer & Mackay 1996). Variance among populations reflects differentiation among populations leading to insipient speciation (Coyne & Orr 2004). Finally, variance among species and higher taxa reflects evolutionary processes on a phylogenetic scale giving rise to adaptive radiation (Schluter 2000).

Given the different biological relevance of particular variance components, inferences are typically made at a certain hierarchical level, while variances at lower level(s) remain under-appreciated. For example, studies aiming at identifying the proximate or ultimate determinants of phenotypic variation among individuals typically target individual-specific mean trait values and inherently consider within-individual variance to be negligible (Dingemanse *et al.* 2012). Furthermore, phylogenetic studies often focus on interspecific trait variance requiring species-specific mean trait values with imperceptible within-species variance (Ives *et al.* 2007). However, as phenotypic variation is likely caused by processes operating at multiple hierarchical levels, the focus on a single variance component stands on weak biological foundations. Therefore, understanding why a given phenotype is expressed in a given observation, in a given individual from a given population of a given species necessitates hierarchically structured data, from which the importance of within-individual, between-individual, between-population and between-species components can

be evaluated in parallel. Although the partitioning of within- and between-individual variances based on the use of repeated observations of the same individuals in a mixed-model framework is becoming a common practice (Westneat *et al.* 2014), such appraisals at higher organization levels are scarce at best due to data limitation (Albert *et al.* 2011; Siefert *et al.* 2015).

Theory and simulation suggest that within-species variance can be a confounding factor when investigating patterns of variance at the among-species level in a phylogenetic context (e.g. Ives *et al.* 2007; Hansen & Bartoszek 2012). These concerns arise primarily from the statistical perspective emphasizing that within-species variance can cause bias in the estimation of the evolutionary parameter of interest. Accordingly, within-species variance is an unwanted factor that needs to be accounted for in a phylogenetic comparative study, but it is not of biological interest. From the statistical point of view, it is also irrelevant whether within-species variance emerges because the populations within species are different, because there is remarkable between-individual variance, or because individuals display their phenotypes with high plasticity (Garamszegi 2014). However, species may be different not only in their mean phenotype, but also in how they divide the phenotypic expression of a trait among different hierarchical levels. Therefore, biologically, different within-species variance components may play different evolutionary roles.

In a phylogenetic comparative study, we here show that assessing the evolutionary importance of different within-species variance components concordantly can be straightforward for understanding how different selective factors shape highly plastic traits like behaviour on a phylogenetic time scale. For our exemplary analysis, we used extensive data on flight initiation distance (FID), which is a well-studied phenomenon in both the within- and between-species contexts in many animal taxa (Stankowich & Blumstein 2005). FID is an estimate of risk taking behaviour, and it can be measured as the distance at which an individual animal flees when approached by a potential predator. FID

has been studied mostly in birds and displays substantial variance at different hierarchical levels, with each having biological relevance. At the between-individual level, FID has clear fitness links because individual birds that fall prey to a predator have shorter FID than survivors (Møller 2014). Differences among individuals in FID can partially be explained by the genetic determination of the trait as reflected by studies reporting associations with different genetic markers (Garamszegi *et al.* 2014, 2015b). Interspecifically, FID correlates with many ecological and evolutionary factors, such as predation pressure (Møller 2008; Møller *et al.* 2010), morphology (Fernandez-Juricic *et al.* 2006), life history (Blumstein 2006), urbanization (Møller 2010; Carrete & Tella 2011) and plumage vividness (Hensley *et al.* 2015). Previously, we have analysed means and variances in FID in European birds in an attempt to identify the most important predictors of these moment statistics (Møller & Garamszegi 2012). Both of these were correlated with a number of variables describing habitat selection, breeding range and population size, dispersal, and life history. Although these findings lend support to the evolutionary importance of the within-species variance in FID, it remains elusive which component of within-species variance is responsible for the detected patterns.

The objectives of this study, therefore, were to partition variance components and investigate the effects of such partitioning for the evolution of life history characters. We used information on FID for 254 species collected in seven geographically distant localities. From data on almost 10,000 individuals, we calculated site-specific means and variances of FID for each species under the assumption that different sites represent different populations. The species-specific between-population variance was estimated based on the site-specific estimates. This tabulation of data permitted us to investigate the relationship between different variance components and also to estimate their repeatability. Finally, we evaluated how these variance components were related to geographic distribution and life history of different species as reflected by

habitat preference, number of habitats, breeding range, population size, natal dispersal, age at first breeding, survival, longevity and the duration of the breeding season.

Material and methods

Observations

APM recorded FID in the field in Denmark, Finland, France, Iceland, Norway, Spain and Ukraine (one site in each country, see Figure 1) during the non-breeding seasons 2006-2016. These data amounted to 9901 observations in total. When an individual bird had been located with a pair of binoculars or with eyesight, APM moved at a normal walking speed towards the individual, while recording the number of steps (which approximately equals the number of meters). The distance at which the individual took flight was recorded as the FID, while the starting distance was likewise recorded (i.e. the experimenter-subject distance when approach began, Blumstein 2003). There was only a weak correlation between FID and starting distance, probably because the observer made efforts to approximate all individuals around 30 meters (GLMM with species as a random effect and locality as a fixed effect and starting distance as a covariate: $F = 34.18$, $df = 1, 933.7$, $P < 0.0001$; effect size $r = 0.006$). Thus we did not consider starting distance in the subsequent analyses. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest meter. APM only recorded FID on days with fine weather conditions and little or no wind or precipitation. FID was estimated as the Euclidian distance, which equals the square-root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein 2006). APM avoided effects of pseudo-replication by only recording a single individual of a given sex, age and species at a given site. Note by measuring individuals only once we actually cannot separate between-individual and within-individual variances, as the detected phenotypic variance within a population is a combination of both

(Westneat *et al.* 2014). With this shortcoming (see Discussion), resampling by mistake does not lead to additional limitations for the purpose of this study. All FID data analysed here were collected in the same way by the same person implying that there was no scope for among-observer variation.

We assume that different sites from different countries represent independent populations. This assumption arises because the data were collected within a radius of 10 km in each country, and considering that the study organisms are flying birds, this distance likely covers socially interacting individuals. Furthermore, the smallest distance between these sampling sites is ~300 km (Figure 1), and thus within-site distance is negligible as compared to the between-site distance. However, we cannot exclude that some variance within sites emerges due to habitat heterogeneity, whereby different populations may segregate within sites. To avoid overestimation of the within-population variance, we repeated our analyses based on a stricter definition for populations, in which we considered larger habitat similarity by focusing on observations that correspond to rural environments only. In a similar vein, within-site variance may be biased due to the fact that different sites were sampled in different years. Therefore, we also repeated our analyses after excluding sites, for which data were available for less than three years. The results obtained under these considerations and relying on different subsamples are presented as Supporting Information.

The repeatability of variance components and their relationship

To assess the repeatability of within- and between-population variances and investigate their association, we tabulated the data as follows. First, we obtained estimates for the mean and the standard deviation (SD) of the phenotypic observations of FID within each population of each species. The SD of phenotypes was assumed to reflect within-population variance (SD_{wn}) that, given the available data structure, combines between-individual and within-individual

variance). Population-specific mean estimates were used to derive between-population variance in the form of the SD of the means across populations in each species (SD_{bw}), and these were weighted by the underlying sample size (for species, which were sampled in a single country only, such information could not be obtained thus could not be included in the respective analyses). We also calculated the weighted mean of the within-species SDs to obtain species-specific estimates for the within-species variance (SD_{spec}). The joint log-transformation of the mean and the variance can only be achieved by approximations (Ives *et al.* 2007). Therefore, for the analyses relying on the log-scale, we first performed a $\log_{10}$ -transformation on the raw individual-specific FID values, then calculated means and SDs over the transformed variables (Garamszegi 2014).

The repeatability of the within-population variance was based on the population-specific estimates. We built a linear mixed model, in which the SD_{wn} on the log-scale was used as a response variable and species identity was a random factor. The model also contained a fixed factor for the country of origin, and the population-specific mean of $\log_{10}$ -transformed FID as a predictor (to control for the statistical phenomenon that a larger mean is typically associated with a larger variance, Wright 1968). To account for differences in sample size, we weighted each population-specific observation based on the underlying sample size. We used $\log_{10}$ -transformed number of observations to avoid overemphasis on species with very large sample sizes (Garamszegi & Møller 2010). The repeatability of SD_{wn} of FID could be estimated from this model by subtracting the appropriate between-species variance component of the trait and relating it to the total variance (Nakagawa & Schielzeth 2010). The 95% confidence interval (95% CI) was obtained by parametric bootstrap.

To calculate the repeatability of between-population variance, we selected species for which FID estimates were available for at least four localities (20 species). In each of these species, we randomly selected two populations and

calculated the weighted SD_{bw} of their respective mean FID (both moments on the log-scale). We also derived such a metric for the remaining populations, and thus we could obtain two parallel estimates for the species-wise between-population variance. To estimate the repeatability of between-population variance, we estimated the correlation between these two sets of estimates by first controlling for their respective means. We extracted residuals from a regression model that characterises the relationship between the $\log_{10}$ -transformed mean and the SD_{bw} of FID. Given that the random selection of populations within species could result in several combinations, we repeated the above process 10,000 times. The mean and the 95% quantile range of the correlation estimates (that were weighted by sample size) were used to make implication about the 95% CI of the repeatability of SD_{bw} .

Comparative analyses

Data on species-species ecology, life history and distribution originated from different sources mainly from Cramp and Perrins (1977-2002). The description of variables and details of data extraction are given in Møller and Garamszegi (2012). Briefly, body mass reflected the mean body mass of adults during breeding. Habitat scores of 1, 2 and 3 reflected grassland, shrub and trees, respectively. The number of habitat types on which the given species occurs during reproduction was used as a measure of habitat exploitation. Distribution was the area in km^2 of the breeding range. Population size was the number of breeding pairs in the Western Palearctic listed by Burfield and van Bommel (2004). Age at first reproduction was the mean age at first reproduction in years. Natal dispersal was the geometric mean distance between natal site and subsequent breeding site according to Paradis et al. (1998). Fecundity was clutch size multiplied by the maximum number of clutches per year. Survival was the adult survival rate. Longevity was the maximum longevity in years according to EURING (<http://www.euring.org>). Duration of the breeding season was the

number of 10 day periods with reproduction. Study effort was the number of publications for each species as listed by Web of Science. The variables were $\log_{10}$ -transformed except survival rate that was square-root arcsine transformed. The comparative dataset is provided as an electronic supplementary material.

To control for effect due to common descent in our statistical models we used information on the phylogenetic relationships of species from Jetz *et al.* (2012). We downloaded 100 trees representing a set of equally likely hypotheses for the underlying phylogeny (see one example in Figure 2). Variance across these trees reflects the uncertainty in the phylogenetic hypothesis, for which we accounted by multimodel inference (Garamszegi & Mundry 2014). Accordingly, we fitted a Phylogenetic Generalized Least Squares (PGLS) model on each tree, in which we forced the correlation structure of residuals to follow the phylogenetic relatedness of species as described for the underlying phylogenetic tree (Paradis 2011). In these models, we allowed the phylogenetic scaling factor, λ to take its maximum-likelihood value (Freckleton *et al.* 2002). This parameter can vary from 0 reflecting no phylogenetic signal in the residuals to +1 indicating strong phylogenetic constraints. We applied a model averaging technique over the 100 models corresponding to different trees to derive the parameter of interest (i.e. regression slope or λ).

Sample sizes varied among species, which can raise issues about heterogenous data quality (Garamszegi & Møller 2010). Accordingly, we weighted each observation in the phylogenetic models based on the underlying within-species number of observations of FID following procedures from Garamszegi (2014). We used $\log_{10}$ -transformed weights, which were strongly positively correlated with the number of populations from which the data originated ($r = 0.701$, $N = 254$, $P < 0.001$) and also with the number of years when the species were sampled ($r = 0.844$, $N = 254$, $P < 0.001$).

We constructed PGLS models to test for the mean/variance relationship on both non-transformed and log-scale. The latter models relied on the mean of

log₁₀-transformed FID as predictor, and one of the variance estimates (either SD_{wn} or SD_{bw} of log₁₀-transformed FID) as response. Log₁₀-transformed SD estimates were entered into a PGLS model investigating whether they vary independently from each other. To assess the relationship between variance components and the considered species-specific traits, we built multivariate PGLSs, in which we accounted for different potentially confounding factors under the following particular considerations.

We expected that species would be using more habitats if their breeding range was larger because a larger range would imply a greater opportunity to encounter different habitats. For the analysis of population size we included range size because a larger range would imply more individuals. For natal dispersal we included population size and range size because a larger population size for a given area would increase density-dependent natal dispersal. For age at first reproduction we included population size and range size because higher density favours early start of reproduction. For survival and fecundity, we included population size and breeding range to account for density-dependence. For longevity we included survival rate because higher survival increases longevity. In this model, we also included population size and breeding range to account for density-dependence, as well as research effort in terms of total number of recoveries of banded birds (as well-sampled species are more likely to be found to have older individuals). Each model included body mass to account for any allometry effects.

Results

Partitioning variance components of FID

The repeatability of SD_{wn} was 0.603 (when we weighted each population-specific observation based on the underlying sample size, we obtained a similar estimate: R = 0.581). The associated 95% CI yielded a range that was above zero (0.482 to 0.707), and it could thus be considered statistically significant.

The mean estimate of the repeatability of SD_{bw} was smaller ($R = 0.261$) and corresponded to a 95% CI (-0.063 to 0.616) that could not be statistically distinguished from zero, probably due to the small sample size.

There were 84 species for which we had estimates for both the within- and between-population variance components. A pairwise comparison revealed that SD_{wn} was consistently larger than SD_{bw} ($t = 5.978$, $df = 83$, $P < 0.001$). In terms of variances, on average, the within-population variance in FID was 74.13% (s.e. = 3.10%) of the total within-species variance, and the remaining 25.87% (s.e. = 2.95%) could be attributed to the between-population variance. However, this partitioning was not homogeneously expressed across the phylogenetic tree, as the proportional distribution of the two components varied among species depending on their phylogenetic positions (the weighted PGLS estimate of the phylogenetic signal of $\log_{10}$ -transformed SD_{wn} minus $\log_{10}$ -transformed SD_{spec} , reflecting within-population variance relative to the total variance was $\lambda = 0.560$, which was associated with a 95% CI = 0.515 to 0.617 across trees; Figure 2).

There was a strong positive relationship between mean FID and estimates of variance on the non-transformed scale (SD_{wn} : beta = 0.258, 95% CI = 0.211 to 0.306; SD_{bw} : beta = 0.161, 95% CI = 0.062 to 0.261). However, these relationships were not present on the log-scale (SD_{wn} : beta = -0.024, 95% CI = -0.063 to 0.014; SD_{bw} : beta = -0.006, 95% CI = -0.081 to 0.069, Figure 3A and B), and thus we did not consider the mean/variance relationships further in analyses on the log-scale. We detected no significant association between SD_{wn} and SD_{bw} (beta = 0.188, 95% CI = -0.124 to 0.499, Figure 3C) indicating that the two estimates were statistically independent.

Variance components of FID and distribution, dispersal and life history

The results of the multi-predictor models accounting for different potentially confounding factors are shown in Table 1. We repeated the same sets of

analyses by using different subsets of the data, which were compiled under stricter criteria for habitat homogeneity within sites and balanced sampling effort, respectively. These supplementary analyses yielded somewhat different patterns (Tables S1 and S2) than the outcomes relying on the full data. Hence we point to those effects only that are robust and consistently appear across the different control approaches. There was concordance in that SD_{bw} was a positive predictor of natal dispersal, and explained more than 10% in interspecific variance of the trait (Figure 4A). With a similar effect size, SD_{bw} was negatively associated with longevity (Figure 4B). Both SD_{wn} and SD_{bw} , independently accounted for ~5% of variance in the number of habitats (Figures 4C and 4D). Noteworthy, SD_{bw} was strongly and positively associated with population size when using the full data (Table 2), but this relationship was considerably weakened when we restricted our analysis to observations originating from similar habitats (Table S1). We also detected that at least ~10% of the variance in population size and the duration of breeding season can be attributed to mean FID (Table 1).

Discussion

The main findings of this study were the following. First, variation in anti-predator behavior as reflected by SD_{wn} and SD_{bw} of FID differed significantly, as the within-population component was consistently larger than the between-population component, and this was coupled with larger repeatability. Second, the composition of within-species variance depended on the phylogenetic relationships of species. Finally, SD_{wn} and SD_{bw} of FID differed in their ability to predict species-specific characteristics of life history, distribution, dispersal and habitat ecology. These findings are important because they show that different components of variance capture different biological mechanisms.

Most comparative studies focusing on interspecific variance neglect the importance of within-species variance in the studied trait (Garamszegi & Møller

2010). In our analyses focusing on the within-species variance of a plastic behavioral trait, we demonstrated that this component can respond to selective mechanisms (Møller & Garamszegi 2012 ; this study). Our previous analyses revealed that habitat use, range size, population size and several life history traits are associated with SD_{spec} of FID. The interpretation of these results was that species that sustain a greater diversity of anti-predator behavior can cope more efficiently with unpredictable environmental conditions allowing them to exploit more habitats, disperse over larger distribution areas, establish higher population densities and adopt fast reproductive strategies. Our current appraisal is mostly in line with this suggestion, even if minor differences in the results appear to be due to dissimilarity in methodology and sample size. The current study adds the important amendment that different evolutionary roles apply to different components of the within-species variance.

Although evolutionary processes can concordantly mediate both components of within-species variance, they can also have different consequences at different levels. For example, diversifying selection would shift population-specific means in opposite directions thereby increasing between-population variances, while leaving within-population variances unaffected or even decreased (Freeman & Herron 2007; Møller 2008). On the other hand, diversifying or disruptive selection can also occur within populations, which would in turn increase within-population variance while eroding among-population variance. If these selection mechanisms at different hierarchical levels are mediated by different ecological factors, between-population and within-population variances will be decoupled. Our results showing that SD_{wn} and SD_{bw} of FID are independent, characterized by different repeatability and have different predictive value support that the two components are responsive to different selective forces.

Dispersal is a demographic process, which has profound effects on population differentiation and ecological plasticity via gene flow (Johnson &

Gaines 1990). Long-distance dispersal is an important mediator of processes whereby organisms find and successfully colonize novel environments (Shaw 1995; Owens *et al.* 1999). Accordingly, dispersal ability can be hypothesized to either have a homogenizing effect on populations or generate population divergence through improved invasion success (Belliere *et al.* 2000). Our findings support the second hypothesis, as they show that longer natal dispersal is coupled with higher variance among populations. Furthermore, it is also plausible that longer natal dispersal favors colonizer individuals to settle in more diverse habitats, which would in turn increase variance in behaviors (Riechert & Hall 2000). The relationship between the number of habitats and the variance components of FID is in line with this scenario.

Pace of Life Syndromes (POLS) arise as a consequence of underlying effects of physiology and life history being responsible for behavior (Réale *et al.* 2010). Such POLS are mediated by life history trade-offs, by which individuals or species prioritize future over current reproduction (Roff 2001), and this can have consequences for risk-taking behavior (Wolf *et al.* 2007). At the inter-specific level, fast-lived species reproduce at an earlier age, have longer breeding seasons, higher annual fecundity and they senesce faster than slow-lived species (Reynolds 2003). Suites of behavior as those linked to predation (or parasitism) can be considered important elements of such POLS axes, because organisms should be sensitive to predation (or parasitism) risk depending on their residual reproductive value (Wolf *et al.* 2007). Here we have made extensive analyses of one measure of anti-predator behavior, and shown that species adopting fast reproductive strategies (i.e. have shorter lifespan) also maintain higher between-population variance in the trait. Therefore, in addition to mean behavior their variance components should also be considered for the evolution of POLS and determine ecological plasticity. Accordingly, ecologically plastic species exploit more habitats and can disperse over distant areas partly because maintaining larger variation in behavior allows them to

cope effectively with unpredictable environments.

Intraspecific phenotypic variation could emerge due to phenotypic plasticity or true between-individual differences in behavior (Dingemanse *et al.* 2010; Westneat *et al.* 2014). Unfortunately, with the available data we were unable to decompose variance below the population level. Studies on different species show great diversity in how FID can vary within individuals, as the trait can depict very high (Carrete & Tella 2010), moderate (Keyel *et al.* 2012; Møller 2014) or low (Garamszegi *et al.* 2015a) repeatability. Therefore, we cannot exclude that some amount of the within-population variance originates from within-individual plasticity, at least in some species. Furthermore, results in association with between-population variance should be interpreted with care. Accordingly, differences in the population-specific mean estimates of FID can arise because individuals from different populations express their phenotypes from different parts of the same reaction norms, or because the between-individual distribution of trait expression is shifted between populations due to sorting or selection (Schlichting & Pigliucci 1998; Laurila *et al.* 2002; Edge *et al.* 2013). Therefore, future studies are needed from which the evolutionary role of within-individual variance could be assessed.

In conclusion, we have shown that different components of variance in behavior display patterns at the interspecific level that can be the signature of adaptive mechanisms and affect variance components independent of the species-specific mean trait expression. These findings suggest that different variance components of behavior constitute evolved mechanisms that link the variance in behavior within individuals, among individuals and among populations. Therefore, the comparative analyses of within-population and between-population variances of phenotypic traits offer promising avenues for understanding the evolution of such traits.

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Table 1.

Means and different variance components for FID in relation to variables describing species-specific ecology, distribution and life history. Estimates of regression slopes were given by phylogenetic models that were averaged across available phylogenetic trees and that were weighted by underlying sample sizes (number of individuals). Each model included the mean and the two estimates of SD as predictors together with a specific set of confounders (see footnotes for details). For each model we provide the underlying sample size in terms of the number of species, and the 95% CI of the phylogenetic scaling factor λ as estimated across trees. For illustrative purposes, slopes and 95% CI that differed significantly from zero are underlined (for interpretations see text).

Response variable	Mean FID		Within-population SD in FID		Between-population SD in FID	
	<i>slope</i>	<i>95%CI</i>	<i>slope</i>	<i>95%CI</i>	<i>slope</i>	<i>95%CI</i>
	<i>(upper/lower)</i>		<i>(upper/lower)</i>		<i>(upper/lower)</i>	
Habitat ^A N = 77 $\lambda_{95} = 1/1$	0.310	-0.362/0.982	3.119	-0.015/6.253	-1.161	-3.146/0.824
Number of habitats ^{A, B} N = 82 $\lambda_{95} = 0/0$	<u>0.278</u>	<u>0.014/0.542</u>	0.947	-0.004/1.897	<u>0.892</u>	<u>0.049/1.736</u>
Distribution area ^A N = 83 $\lambda_{95} = 0/0$	-0.270	-0.582/0.041	0.527	-0.623/1.677	0.164	-0.865/1.194
Population size ^{A, B} N = 83 $\lambda_{95} =$	<u>-1.135</u>	<u>-1.733/-0.537</u>	<u>3.349</u>	<u>1.123/5.576</u>	-1.377	-3.155/0.401

0.366/0.431

Natal dispersal^{A, B, C} 0.767 -0.017/1.550 0.847 -1.577/3.270 3.032 0.731/5.333

N = 48

 $\lambda_{95} = 0/0.262$

Age at first reproduction^{A, B, C} 0.055 -0.040/0.150 -0.228 -0.592/0.135 -0.097 -0.408/0.214

N = 83

 $\lambda_{95} = 0.930/1$

Fecundity^{A, B, C} -0.127 -0.271/0.018 0.406 -0.137/0.949 -0.197 -0.655/0.261

N = 83

 $\lambda_{95} = 0.949/1$

Survival^{A, B, C} 0.049 -0.081/0.179 -0.095 -0.567/0.376 -0.006 -0.355/0.343

N = 74

 $\lambda_{95} =$

0.380/0.491

Longevity^{A, B, C, D, E} -0.040 -0.174/0.095 -0.482 -1.000/0.036 -0.551 -0.907/-0.195

N = 73

 $\lambda_{95} =$

0.636/0.688

Duration of the breeding season^A -0.295 -0.442/-0.148 0.444 -0.016/0.904 0.239 -0.186/0.664

N = 83

 $\lambda_{95} = 0.682/1$

670 Variables controlled for in the models: ^A: body mass, ^B: distribution area, ^C: population size,
 671 ^D: survival; ^E: research effort

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Legends to figures

Figure 1. A map of sampling sites in Europe, where information on FID were obtained to estimate within- and between-population variance of the trait. Data were collected within a radius of 10 km in each site.

Figure 2. A phylogenetic hypothesis of bird species (taken from Jetz et al. 2012) with information on within- and between-population variance in FID. Pie charts at the tip of labels show estimated composition of within-species variances (black: between-population, white: within-population variance).

Figure 3. (A-D) The relationship between species-specific estimates of mean FID (flight initiation distance) and its SD reflecting two different components of the within-species variance when using untransformed data (**A, B**) and on a logarithmic scale (**C, D**). **(E)** The relationship between SD_{wn} and SD_{bw} of FID. Regression slopes (black lines) were estimated from phylogenetic models that were averaged across the available phylogenetic trees (grey lines are for particular trees) and that were weighted by the underlying sample size (number of individuals). Model averaged slopes shown with thin dashed lines represent non-significant relationships.

Figure 4. Different variance components (as estimated by SD_{wn} and SD_{bw}) in FID in relation to **(A)** natal dispersal, **(B)** longevity and **(C-D)** number of habitats. Regression slopes (black lines) were obtained from phylogenetic models that were averaged across available phylogenetic trees (grey lines are for particular trees) and that were weighted by the underlying sample size (number of individuals). Slopes and data (in the form of residuals) were extracted from the respective multi-predictor PGLS model that included potentially confounding factors (Table 1). The size of the points is proportional to the

703 underlining sample size (number of individuals that was used as a weight factor
704 in the statistical models).