



27 **Abstract**

28 Body size plays a key role in the ecology and evolution of all organisms. Therefore, quantifying the  
29 sources of morphological (co)variation, dependent and independent of body size, is of key  
30 importance when trying to understand and predict responses to selection. We combine structural  
31 equation modeling with quantitative genetics analyses to study morphological (co)variation in a  
32 meta-population of house sparrows (*Passer domesticus*). As expected, we found evidence of a latent  
33 variable ‘body size’, causing genetic and environmental covariation between morphological traits.  
34 Estimates of conditional evolvability show that allometric relationships constrain the independent  
35 evolution of house sparrow morphology. We also found spatial differences in general body size and  
36 its allometric relationships. On islands where birds are more dispersive and mobile, individuals  
37 were smaller and had proportionally longer wings for their body size. While in islands where  
38 sparrows are more sedentary and nest in dense colonies, individuals were larger and had  
39 proportionally longer tarsi for their body size. We corroborated these results using simulations and  
40 show that our analyses produce unbiased allometric slope estimates. This study highlights that in  
41 the short term allometric relationships may constrain phenotypic evolution, but that in the long term  
42 selection pressures can also shape allometric relationships.

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44 **Keywords** : Evolutionary Constraints, Factor Analysis, **G** matrix, Latent Variables, Phenotypic  
45 Integration, Pleiotropy

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54 **Introduction**

55 The size of an organism is one of its most important features (Calder 1984; Peters 1986) and has  
56 been extensively studied in both micro- and macro-evolutionary contexts (Maurer et al. 1992;  
57 Kingsolver and Pfennig 2004). Across species, body size predicts characteristics such as  
58 metabolism, fecundity, lifespan, population size and extinction risk (Stearns 1983; Sibly and Brown  
59 2007). Within species body size has also been shown to affect key fitness components, such as  
60 fecundity, survival and mating success (Kingsolver and Pfennig 2004). Body size variation within-  
61 and among-species can therefore determine population and community level processes (Marquet et  
62 al. 1995). Despite its importance in ecological and evolutionary processes, body size is generally  
63 loosely defined. In many studies, body size is used interchangeably with body mass or other  
64 morphological measurement, ignoring the fact that body size is being measured indirectly through a  
65 proxy morphometric measurement (e.g. body mass, tarsus length, snout-vent length). Here, we  
66 argue that studying body size variation as a latent variable affecting the growth of all other  
67 morphological traits will improve our understanding of its evolutionary role in shaping  
68 morphological diversity.

69 From a developmental perspective, body size reflects the common growth regulatory  
70 mechanisms affecting all morphological structures of an organism (Gokhale and Shingleton 2015),  
71 whereas from an evolutionary perspective it reflects investment in somatic growth (Perrin and Sibly  
72 1993). Thus, variation in body size can be viewed as variation in investment in somatic growth  
73 affecting all morphological traits through shared growth regulating pathways, resulting in the  
74 allometric patterns of morphological covariation observed in most organisms. This notion emerged  
75 early in evolutionary thinking with Darwin's consideration of the "correlations of growth", in which  
76 he noted that slight evolutionary variation in one part of an organism would result in other parts also  
77 being modified accordingly (Darwin 1859). The study of morphological covariation and its  
78 evolutionary implications has continued ever since within the fields of allometry, phenotypic  
79 integration, modularity and evolutionary quantitative genetics (Klingenberg 2008). Common to all

80 these fields is the idea that genetic and environmental variation influencing investment in growth  
81 during development shape the observed patterns of morphological covariation among individuals,  
82 populations, and species.

83         Phenotypes develop in a hierarchical manner and the covariation between morphological  
84 traits partly reflects this hierarchical pattern (Klingenberg 2014). All traits descend from the same  
85 ancestral cell, and developmental switch-points create phenotypic modules composed of traits that  
86 share the same developmental precursor (West-Eberhard 2003). For instance, in birds genetic  
87 variation in the processes regulating early developmental events concerning the muscles and  
88 skeleton will cause positive covariation between all morphological traits. Therefore, bigger birds are  
89 heavier, have larger beaks, wings and legs (Björklund 1994). Later on, processes leading to beak  
90 development start at around day 6 of embryo development, (e.g. Darwin's finches, Abzhanov et al.  
91 2004). The different parts of the beak thus share a common developmental history with all other  
92 morphological traits, but they also share a more recent developmental precursor with any other  
93 traits specifically associated with the beak. This should lead to an even stronger pattern of  
94 correlation between beak features, caused by the processes regulating beak development. This  
95 developmental view of morphological covariation hinges upon the assumption that variation is  
96 generated from a single origin and passed on to multiple traits (Klingenberg 2008). More generally,  
97 the modular patterns of covariation between morphological traits will also reflect their common  
98 ontogenetic and evolutionary histories (Melo et al. 2016). The independent evolution of phenotypic  
99 traits arising from the same developmental module is constrained, at least in the short term, by  
100 developmental ancestry (Wagner and Stadler 2003). However, the structure of these developmental  
101 modules will also have come into being via evolution through natural selection over a longer time  
102 frame. Therefore, developmental modules will have been selected to couple or decouple variation in  
103 different morphological traits, depending upon the prevailing adaptive landscape.

104         Selection for a larger body size will result in selection for an increase in the size of all  
105 morphological traits. Similarly, selection for increased size in one trait can lead to an increase in the

106 overall size of an organism. For instance, selection for bigger beaks could lead to bigger birds in  
107 general, because bigger birds have bigger beaks (Grant and Grant 2002). Selective pressures can  
108 also affect size-independent variation in morphological traits, altering allometric relationships with  
109 body size. For example, there could be selection for smaller beaks relative to overall body size, if  
110 there is antagonistic selection where smaller beaks increase foraging success, but smaller birds  
111 suffer a competitive disadvantage during agonistic interactions. Statistically partitioning the  
112 (co)variance in morphological traits caused by body size from those independent of body size  
113 would allow us to connect the multivariate study of morphological evolution with the  
114 developmental processes that generate morphological variation (Klingenberg 2014). Furthermore,  
115 disentangling the genetic and environmental sources of size-dependent and size-independent  
116 (co)variation between morphological traits will provide further insights concerning how evolution  
117 shapes the genetic and phenotypic patterns of morphological covariation.

118 Allometric relationships between body size and any morphological trait can be described as  
119 a power function (Huxley 1932; Peters 1986) and have been commonly estimated as the linear  
120 relationship between log-transformed measurements of a trait and a surrogate measure of body size.  
121 The accuracy of the allometric slopes estimated using such surrogate measurements will depend  
122 upon the correlation between the proxy measure and body size. If we define body size as investment  
123 in somatic growth through common growth-regulating mechanisms affecting all morphological  
124 traits, each of the surrogate measures of body size will also contain some variation caused by  
125 factors that are not shared with all the other morphological measurements (i.e. size-independent  
126 variation). Jolicoeur (1963) offered a solution to this problem: run a principal component analysis  
127 (PCA) on the covariance matrix of log-transformed measurements and use the resulting first  
128 principal component as the estimate of the common allometric axis (body size). In this framework,  
129 the allometric slopes can be characterized in relationship to the axis of best-fit in the multivariate  
130 space of log-transformed measurements. A similar approach has been suggested using factor  
131 analyses, where body size is explicitly estimated as a latent variable affecting the (co)variation of

132 morphological traits. Structural equation modeling (SEM) provides a general set of models that  
133 include factor analyses (Grace et al. 2010). SEM can be used to both determine the variation in  
134 morphological traits caused by the effects of body size, and to estimate specific additional  
135 (co)variation in morphological traits unrelated to body size (e.g. beak measures co-varying  
136 independently of body size). An SEM approach to quantifying size-dependent and size-independent  
137 genetic and environmental (co)variation in morphological traits makes it possible to study the  
138 multivariate nature of morphological traits in a framework that is consistent with allometric,  
139 developmental and evolutionary theory.

140         In this study, we combine quantitative genetic analyzes with SEM to study morphological  
141 (co)variation in a house sparrow (*Passer domesticus*) metapopulation. We explore (co)variation in  
142 beak depth, beak length, body mass, tarsus length and wing length in over 5000 house sparrows  
143 using data collected from 1994 to 2014 in 11 island populations. We first quantify genetic and  
144 environmental sources of (co)variation in house sparrow morphological measurements. We then use  
145 SEMs to study the covariance between morphological measurements caused by body size and  
146 estimate the allometric slopes generating the observed pattern of covariation. Our expectation was  
147 that common growth regulatory mechanisms shared by all the morphological traits will result in a  
148 pattern of genetic and environmental covariation, which could be characterized statistically as a  
149 latent variable, defined as ‘body size’. We then quantify the amount of size-independent variance in  
150 the different morphological traits, which determines their potential for independent evolution. We  
151 also estimate size-independent covariance between beak features, with the expectation that a more  
152 recent shared developmental history will result in additional genetic and environmental covariation  
153 above and beyond the general allometric covariation caused by body size variation.

154         We complement our analyses with simulations to assess the suitability of SEM to estimate  
155 allometric slopes from a biological model where body size causes covariation between all the  
156 measured morphological traits, and we compare it with commonly used alternative approaches  
157 (bivariate regression and PCA). We also describe how to derive key evolutionary parameters using

158 this approach, such as scaled allometric slopes and conditional evolvabilities. Furthermore, house  
159 sparrows are sexually dimorphic and sex-specific patterns of morphological covariation have been  
160 documented in this meta-population (Jensen et al. 2003). Ecological conditions also vary  
161 consistently between the islands in our metapopulation. Previous studies on this metapopulation  
162 have documented differences in several demographic traits related to island characteristics: adult  
163 and juvenile survival (Ringsby et al. 1999; Holand et al. 2016), survival and growth rate (Sæther et  
164 al. 1999), onset of breeding and subsequent recruitment (Ringsby et al. 2002), population growth  
165 rate, demographic variance (Engen et al. 2007), and dispersal (Pärn et al. 2012). We therefore also  
166 assess the sex differences and the effect of differing ecological conditions on the morphology of  
167 these house sparrows to explore the extent to which selection may have shaped the allometric  
168 relationships in different parts of this metapopulation of house sparrows.

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## 170 **Methods**

### 171 *Study system*

172 This study was carried out on a metapopulation of 11 insular house sparrow populations at  
173 Helgeland in northern Norway (66°N 13°E; see map (Baalsrud et al. 2014)). Each time an adult bird  
174 was caught, we used slide calipers to measure tarsus length, bill depth and bill length to the nearest  
175 0.01 mm, and a wing ruler to measure wing length to the nearest mm. Body mass was measured  
176 using a Pesola spring balance to the nearest 0.1 g. All linear morphological measurements (except  
177 body mass) that were taken by different fieldworkers were adjusted to T.H.R. measurements by  
178 adding mean differences when found significant ( $P < 0.05$ ) using paired t-tests on a set of ca. 30  
179 individual birds measured independently by the fieldworker and T.H.R. (Kvalnes et al. 2018). All  
180 birds in the current study were adult males (n=2866) or females (n=2716) measured between 1994  
181 and 2014. 32% of the individuals were only measured once as adults, 20% were measured twice,  
182 and 48% three or more times in the same or different years (see Harald et al. 2002; Jensen et al.  
183 2008; Parn et al. 2012; Baalsrud et al. 2014 for further details on the fieldwork). We used all the

184 repeated measures to separate out measurement error and within-individual variation from the  
185 among-individual variation (see below). Population-specific genetic pedigrees were constructed  
186 based upon 14 neutral microsatellite markers (for further details, see Jensen et al. 2004; Billing et  
187 al. 2012). Individuals were genotyped for only 8 (Aldra, Gjerøy, Hestmanøy, Indre Kvarøy, Myken,  
188 Nesøy, Selvær, and Træna) out of the 11 populations, thus the quantitative genetic analyses were  
189 limited to 3940 individuals.

190 The 11 islands in this metapopulation study can be divided into two distinct groups with  
191 different environmental conditions. One set of inner islands (n = 6; Aldra, Gjerøy, Hestmanøy,  
192 Indre Kvarøy, Lurøy, and Nesøy), are situated closer to the mainland and the sparrow populations  
193 live closely associated with active dairy farms with access to cattle-food and shelter all year round  
194 (17345 measurements from 3530 individuals). The second set of outer islands (n = 5; Lovund,  
195 Myken, Selvær, Sleneset, and Træna), are situated further from the mainland, lack agricultural  
196 farms and sparrows move around feeding in various gardens (7512 measurements from 2065  
197 individuals). On these outer islands the sparrows are exposed to more unpredictable and fluctuating  
198 environmental conditions. Thus, adults on populations on the inner farm islands experience a  
199 seemingly more benign and predictable environment than in populations on the outer non-farm  
200 islands. Throughout the manuscript we refer to these two groups as inner farm islands and outer  
201 non-farm islands.

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### 203 *Univariate analyses*

204 We first studied the sources of variation in the different morphological measurements (tarsus length,  
205 wing length, beak length, beak depth and body mass). Morphological trait  $z$  of individual  $j$  at  
206 instance  $k$  was modeled as:

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$$208 \quad z_{jk} = c + s \text{sex}_j + t \text{type}_j + d \text{age}_{jk} + I_j + f_l + m_t + y_m + e_{jk} . \quad (\text{eq. 1})$$

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210 Coefficients  $s$  and  $d$  relate the morphological measurement to the sex and the age of the individual,  
211 and  $t$  to the island type (inner-farm islands versus outer-non-farm islands). Individuals differ in  
212 their morphological measurements ( $I_j$ ) due to genetic differences and permanent environmental  
213 effects, as well as environmental effects associated with population differences ( $f_l$ ). Individuals  
214 were measured repeatedly within and across years, therefore within-individual variation could be  
215 associated with reversible plasticity in response to within year seasonal variation (i.e. across  
216 months;  $m_t$ ), yearly variation in environmental conditions ( $y_m$ ) and within year within individual  
217 variation in environmental conditions and or measurement error,  $e_{jk}$ . Parameters  $I_j, f_l, m_t, y_m$  and  $e_{jk}$   
218 were all assumed to come from normal distributions with means of zero and variances to be  
219 estimated ( $V_I, V_f, V_m, V_y$  and  $V_e$ ). These parameters were estimated using separate mixed-effects  
220 models for each of the morphological measurements, with age and age-squared as fixed covariates  
221 (min age = 1, max age = 10) to model the linear and non-linear effects of age, with sex as a fixed  
222 factor (2 levels) and random intercepts for year of measurement (21 years), month of measurement  
223 (12 months), population (11 populations) and individual identity (5582 individuals). We extended  
224 this model to an animal model by including the genetic pedigree information (Kruuk 2004). This  
225 allowed us to partition the individual level effects,  $I_j$ , into the additive genetic effects (breeding  
226 value)  $a_j$  and permanent environmental effects  $pe_j$  for each morphological trait. Both  $a_j$  and  $pe_j$   
227 were assumed to come from normal distributions with variances  $V_a$  and  $V_{pe}$ . Note that this model  
228 was applied to only a subset of the data where the pedigree information was available (3924  
229 individuals from eight islands).

230

### 231 *Multivariate analyses*

232 When studying the covariation between all the morphological traits, we log-transformed the  
233 morphological measurements so that their expected exponential relationship with body size  
234 becomes linear. We first studied the phenotypic covariance and modeled each log-transformed  
235 morphological trait  $z_i$  of individual  $j$  at measurement  $k$  as:

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$$z_{ijk} = c_i + s \text{sex}_j + I_{ij} + e_{ijk}, \quad (\text{eq. 2})$$

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where  $c_i$  is the metapopulation mean for the morphological trait  $i$ ,  $I_{ij}$  is the deviation of morphological trait  $i$  of individual  $j$  from the metapopulation mean  $c_i$ , and  $e_{ijk}$  is the deviation of measurement  $k$  from an individual's mean value  $I_{ij}$ . Parameters  $I_{ij}$  and  $e_{ijk}$  were assumed to be a realization of multinormal distribution with a mean of zero and covariance matrix  $\mathbf{P}$  and  $\mathbf{R}$ . These parameters were estimated using a multivariate mixed-effects model with random intercepts for individual identity (n=5582 individuals). We chose not to fit the same random and fixed effect structure for the multivariate and univariate models in order to avoid over-parametrization, because the main goal of this analysis was to estimate the among-individual covariation matrix ( $\mathbf{P}$  matrix).

We extended this multivariate mixed-effects model into an animal model by including the genetic pedigree information (Kruuk 2004). This model allowed us to partition the individual level covariance matrix ( $\mathbf{P}$  matrix) into its additive genetic ( $\mathbf{G}$  matrix) and the permanent environmental ( $\mathbf{PE}$  matrix) components. The  $\mathbf{P}$  matrix describes the (co)variation between the mean values of each individual for the different morphological traits. The  $\mathbf{G}$  matrix describes the (co)variation between morphological traits caused by pleiotropic effect of genes and linkage disequilibrium. The  $\mathbf{PE}$  matrix describes the (co)variation between the morphological measurements caused by the effects early in life of correlated environmental variables and environmental variables with pleiotropic effects on the different traits. Thus, the  $\mathbf{PE}$  matrix can be understood as the integrated developmental plasticity of the different morphological traits in response to the environment. These estimated covariance matrices were then analyzed using structural equation models (SEMs). Note that we also estimated the residual covariance matrix ( $\mathbf{R}$  matrix), which is caused by correlated reversible plasticity and/or correlated measurement error, but this covariance matrix was not further analyzed.

262 *Structural equation modeling and body size*

263 Allometric theory states that the effects of body size ( $m$ ) on a phenotypic trait  $z$  can be described by  
264 an exponential relationship (Huxley 1932; Peters 1986):

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$$266 \quad z = am^b. \quad (\text{eq. 3})$$

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268 The relationship between body size and a phenotypic trait is linear on the logarithmic scale and can  
269 thus be described by equation 4:

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$$271 \quad \log(z_{ij}) = \log(a_i) + b_i \log(m_j) + \log(e_{ij}), \quad (\text{eq. 4})$$

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273 where  $a$  and  $b$  are constants that relate a body size  $m$  to a phenotypic measurement  $z$ . This equation  
274 captures the proportional change in phenotypic measures as a function of proportional changes in  
275 body size.  $b$  is commonly referred to as the allometric slope (Peters 1986). The term  $\log(e_{ij})$   
276 reflects the residual effects of factors not related to body size that are unique to the different  
277 morphological measurements. Thus, this model assumes multiplicative errors. Based upon this  
278 equation, we proceeded to examine the  $\mathbf{P}$  matrix as well as the  $\mathbf{G}$  and  $\mathbf{PE}$  matrices using SEM to  
279 test our hypothesized model of morphological covariation. We expected that a latent variable  $m$ ,  
280 that we defined as body size, would explain the covariance between all measured morphological  
281 traits (equation 5). This approach estimates the vector of coefficients  $\gamma_i$ , that maximize the  
282 likelihood of a covariance matrix, in this case  $\mathbf{P}$ ,  $\mathbf{G}$  and  $\mathbf{PE}$  matrices. For instance, the structural  
283 equation model for  $\mathbf{P}$  can be described as:

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$$285 \quad \mathbf{P} = \gamma_i \eta + \varepsilon_i \quad (\text{eq. 5})$$

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$$\eta \sim N(0, 1)$$

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$$\varepsilon_i \sim mvn(0, \theta) .$$

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289           Thus, our hypothesized model consisted of a latent variable  $\eta$  that determines the growth of  
290 morphological trait  $z_i$  proportional to coefficient  $\gamma_i$ . We assumed that the latent variable  $\eta$  had a  
291 mean of zero and a variance of 1. Deviations of each morphological trait from values predicted by  
292 the latent variable are represented by  $\varepsilon_i$ , which was assumed to be a realization of a multi-normal  
293 distribution with a mean of zero and covariance matrix  $\theta$ . The  $\theta$  matrix thus represents body size-  
294 independent variation and covariation between morphological traits. Our hypothesized model was  
295 constructed to allow all the variances in the  $\theta$  matrix and one covariance to be estimated.  
296 Specifically, because of their more recent shared developmental history and functional relationship,  
297 we hypothesized a covariance between beak length and beak depth over and above the covariance  
298 caused by their allometric relationships with body size. We further proceeded to study the  
299 differences in the allometric relationships and evolvabilities between the sexes and between  
300 individuals living on different islands with different environmental conditions (i.e. inner farm  
301 versus outer non-farm islands) by fitting multivariate models and SEM models separately for each  
302 sex and island type.

303

#### 304 *Estimating evolvability*

305           Evolvabilities measure the potential proportional change of a trait in response to a unit of selection.  
306 This is generally calculated as a mean standardized additive genetic variance, however additive  
307 genetic variance of log-transformed measurements accurately approximates their evolvabilities.  
308 This metric is thus related to both the additive genetic variance of a trait and its mean value, in  
309 comparison to heritabilities that are a direct function not only of the additive genetic variance but  
310 also of other (environmental) sources of phenotypic variation (Hansen et al. 2011). We estimated  
311 evolvabilities from univariate animal models applied to log-transformed morphological  
312 measurements. Conditional evolvabilities were calculated using the variance not explained by body  
313 size for each trait. Structural equation models (SEM) were applied to the  $\mathbf{G}$  matrix of the log-

314 transformed measurements, and therefore variance not explained by body size could be interpreted  
315 as conditional evolvabilities. We also estimated autonomy, which in this case is the fraction of  
316 additive genetic variance that is unrelated to body size. We further estimated the conditional  
317 evolvabilities for the whole  $\mathbf{G}$  matrix in order to compare them with estimates from the SEM  
318 approach (i.e. conditional on body size). Conditional evolvabilities on all the other traits were  
319 calculated following Hansen and Houle (2008), using the inverse of the  $\mathbf{G}$  matrix as it is equal to  
320 the inverse of the diagonal elements of  $\mathbf{G}^{-1}$ .

321

### 322 *Simulations and the estimation of allometric slopes*

323 We performed a simulation study to assess the robustness of the SEM approach in recovering a  
324 biological developmental model of morphological covariances caused by body size variation (Fig  
325 1A). We compared the performance of the SEM approach against (1) bivariate regressions between  
326 the different log-transformed morphometric measurements and log-transformed body mass, and (2)  
327 principal component analyses (PCA) applied to log-scaled morphological measurements. One  
328 disadvantage of PCA and other latent variable approaches to estimating body size is that these latent  
329 constructs are unitless, and so the coefficients  $\gamma_i$  (eq. 5) cannot be directly interpreted as allometric  
330 slopes ( $b_i$ , eq. 3 and 4). We therefore suggest scaling latent variables of body size to body mass  
331 using the allometric relationships estimated in the SEM and PCA. Under the assumption that body  
332 size is a volume measure and scales isometrically with body mass ( $b_{body\_mass} = 1$ ), we can derive  
333 allometric slopes that capture the proportional changes in a morphological trait associated with a  
334 proportional change in body size measured in units of mass (Corrunci 1983). Mass-scaled  
335 allometric slopes ( $b$ ) can be estimated by dividing coefficient  $\gamma_i$  by the estimated  $\gamma$  for body mass  
336 ( $b_i = \gamma_i / \gamma_{body\ mass}$ ). In the main text, we present how the estimation of the allometric slopes is  
337 affected by the magnitude of size-independent variation in body mass. In the Appendix S1, we  
338 present code for the simulations and a complete description of the results from the simulation study.

339

340 *General statistical procedures*

341 We fitted the multivariate mixed-effects models detailed above using a Bayesian framework  
342 implemented in R v3.3 (R Core Team 2018) with the package MCMCglmm (Hadfield 2010). We  
343 ran 305,000 iterations per model, from which we discarded the initial 5000 (burn in period). Each  
344 chain was sampled at an interval of 300 iterations, which resulted in low autocorrelation among  
345 thinned samples. Posterior means, 85% and 95% credible intervals were estimated across the  
346 thinned samples for the fixed effects, (co)variances and variance ratios (i.e. repeatabilities and  
347 heritabilities). When the general goal was to compare between the limits of the posterior  
348 distributions of two estimates, we present the 85% credible interval because a lack of overlap is  
349 analogous to a  $p$ -value lower than 0.05 in the frequentist sense (Payton *et al* 2003). Fixed effect  
350 priors were normally distributed and diffuse with a mean of zero and a large variance (100). We  
351 explored the sensitivity of the variance-covariance matrix to prior choice; the results presented here  
352 correspond to an inverse gamma prior with a scale parameter of 1 and shape of 0.001. Mean values  
353 of the posterior distributions were robust to different relatively uninformative priors. The resulting  
354 1000 samples of the posterior-distribution for the covariance matrices **P**, **G** or **PE** were then  
355 analyzed using SEMs in order to obtain estimates of the credible intervals in each case. However  
356 the reported point estimates for each parameter (i.e mean) were obtained from analyzing the mean  
357 covariance matrix (**P**, **G** or **PE**). We fitted the SEMs in the R package sem (Fox 2006). Statistical  
358 significance for SEM parameters was assessed by inspecting whether the credible intervals  
359 overlapped zero.

360

361 **Results**

362 *Sources of morphological variation*

363 We found that male sparrows have deeper and shorter beaks, as well as longer tarsi and wings, as  
364 compared to females; while females were heavier than males (Table 1A). There were also  
365 morphological differences between islands with different ecological characteristics. In the inner

366 islands where birds live more closely associated to farms, sparrows had deeper and longer beaks,  
367 were heavier and had longer wings (Table 1A). Similarly, we found that older birds had deeper and  
368 longer beaks, were heavier and had longer wings and tarsi (Table 1A).

369         There were also differences between the traits in the relative contribution of the different  
370 variance components (Table 1B). The proportion of phenotypic variance caused by additive genetic  
371 variation ranged from 23% for body mass to 43% for wing length. The proportion of variation  
372 associated with permanent environmental effects ranged from 9% for wing length to 60% for tarsus  
373 length. Among measurement variation was highest for body mass 49% and smallest for tarsus  
374 length 4% (Table 1B). There was relatively little among-population variation in all the  
375 morphological measurements (less than 3%). There was also very little variation among years for  
376 all traits (less than 2%).

377

#### 378 *Body size and size-independent covariation and evolvabilities*

379 As expected, we found evidence that covariation among the five morphological traits was caused by  
380 a latent variable that we define as ‘body size’ (Fig. 1; Table 2). The existence of this body size  
381 latent variable was confirmed at the phenotypic, genetic and permanent environmental levels (Fig.  
382 1). As hypothesized, we also found that beak length and depth were still positively correlated even  
383 after accounting for the effects of body size, although the estimates at the permanent environmental  
384 level overlapped zero (Fig 1).

385         At the phenotypic and genetic levels, body mass was the measured trait that contained the  
386 smallest proportion of size-independent variation (Fig 1A and C). Thus, body mass has the lowest  
387 autonomy in relation to body size (Table 3). At the permanent environmental level, tarsus length  
388 contained the smallest proportion of size-independent variation (Fig 1B). Beak length and wing  
389 length were the traits that had the largest proportion of size-independent variation at the phenotypic  
390 level, and beak length was the trait that had the largest size-independent genetic and permanent  
391 environmental variation (Fig. 1). Therefore, beak length was the trait with highest autonomy in

392 relation to body size. The trait with the highest unconditional evolvability was body mass (Table 3),  
393 but the decrease in evolvability when conditional on body size was also strongest in this trait (Table  
394 3). Wing length and beak length had the lowest evolvability, but when conditional on body size  
395 these traits did not seem to substantially decrease their potential for evolution (Table 3). There was  
396 not much difference between estimates of evolvability conditional on all the other traits versus the  
397 estimates of evolvability conditional on body size, except for body mass.

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#### 399 *Sex and habitat differences in body size relationships.*

400 Despite mean morphological differences between the sexes in this meta-population of house  
401 sparrows, we found that the allometric relationships were surprisingly similar between males and  
402 females (Table 2A). However, we found that that the proportion of size-independent variation in  
403 body mass was greater for females than for males (Table 2B).

404         When examining morphological differences among populations in the two habitat types, we  
405 found some interesting differences (Table 2). Sparrows on the inner farm islands had proportionally  
406 longer tarsi for their body size compared to the birds breeding on the outer islands without farms.  
407 We also found that sparrows on the outer non-farm islands had proportionally longer wings for their  
408 body size (Fig. 2; Table 2A). When studying the size-independent variance in the different types of  
409 islands, we found that size-independent variance in wing length was higher for birds on the farm  
410 islands compared with the non-farm islands (Table 2C).

411

#### 412 *Evaluation of methodology using simulations*

413 The estimated allometric slopes using the SEM approach were generally unbiased (Fig. 3). In  
414 contrast, the allometric slopes estimated using bivariate regressions were underestimated with a bias  
415 proportional to the amount of size-independent variation in body mass (Fig. 3). PCA estimates of  
416 the allometric slopes also provided biased estimates (Fig. 3), the scale of which depended on the  
417 differences between traits in the degree of size-independent (co)variation. When the size-



418 independent (co)variance is the same for all the morphological traits, the allometric slopes estimates  
419 from the PCA were unbiased (Supplementary material S1). Therefore, SEMs provided the most  
420 accurate and unbiased estimates from the simulated data. However, it is important to note that when  
421 sample sizes are small, for instance less than 20 individuals, SEM may also provide biased  
422 allometric slope estimates (Fig. S3). Furthermore, to perform the analysis at the genetic level, the  
423 required sample sizes are considerably higher in order to properly estimate the additive genetic  
424 covariance matrix.

425

## 426 **Discussion**

427 We studied the patterns of (co)variation in five morphological traits of adult house sparrows in a  
428 metapopulation in northern Norway from 1994 to 2014 using a quantitative genetic analysis  
429 combined with structural equation models. We parametrize a latent variable model to describe the  
430 genetic and environmental relationships between body size and the measured morphological traits.  
431 We compare the allometric relationships between islands with different environmental and  
432 demographic characteristics and also between the sexes. Other studies have used SEM in ecological  
433 studies of morphology, for instance Crespi and Bookstein (1989) used path analysis to study the  
434 relationship between morphology and survival in house sparrows, and Morrissey (2014) described  
435 how to use these types of models within a quantitative genetics framework. The approach used in  
436 this study further shows the potential of using SEM in evolutionary studies of allometry and  
437 morphology in three main ways: 1) morphological covariation (e.g. the **G**-matrix) can be studied in  
438 a hypothesis testing framework based upon allometry theory; 2) it provides accurate estimates of  
439 allometric relationships under the hypothesis that variation in body size causes covariation between  
440 morphological traits; and 3) size-independent variation and covariation can be directly estimated.  
441 Furthermore, these estimates can be interpreted as conditional evolvabilities, describing the  
442 potential for independent responses to selection of each measured trait.

443

444 *Body size and allometric slopes*

445 Using SEMs within a quantitative genetics framework, we found support for a latent variable that  
446 we defined as ‘body size’ underpinning genetic and environmental morphological covariation. This  
447 latent variable captures the shared developmental history that underpins the expression of all the  
448 studied morphological traits. Importantly, the allometric vector captured by body size when  
449 analyzing genetic covariation is aligned with the direction with highest evolvability (Schluter 1996;  
450 Hansen and Houle 2008). Selection on body size will thus result in an integrated response of the  
451 different morphological traits. Furthermore, the allometric vector captured by analyzing the  
452 permanent environmental covariance matrix shows that morphological traits respond plastically to  
453 the developmental environment in an integrated fashion. This coordinated response ensures  
454 functional coherence (Pigliucci 2001a) when adjusting to environmental conditions. The analysis of  
455 the genetic variance-covariance matrix (the **G** matrix) thus reflects the allometric constraints on  
456 independent trait evolution, but also the correlated adaptive response to previous selective  
457 landscapes. Meanwhile, the analysis concerning the permanent environmental (**PE**) matrix reflects  
458 how shared developmental mechanisms mediate environmental variation during development.

459 We studied covariation of the log-transformed morphological measures using a latent  
460 variable model to estimate the allometric relationships with body size (Fig 1). One caveat of using  
461 latent variables to estimate allometric relations is that they are unitless. To overcome this problem,  
462 we scaled the estimated allometric relations with body size to the estimated relation with body mass  
463 (Corruccini 1983). We did this by dividing the estimated relationship between the morphological  
464 measurements and the latent variable by the estimated relation with body mass. This makes the  
465 allometric relationship between the latent variable and body mass equal to one, and thus reflects the  
466 assumption that body mass scales isometrically with body size. Scaling the coefficients in this way  
467 improves the interpretability of the allometric coefficients, because the allometric slopes describe  
468 the proportional increase in a morphological trait associated with an increase in body size measured  
469 in grams. This also facilitates comparisons with allometric slopes estimated via the commonly-used

470 bivariate regression method, depending upon the proxy measure for body size in each instance.

471 Using statistical simulations, we show that the SEM approach provides more accurate estimates of  
472 the allometric slopes than bivariate regressions and PCA.

473

#### 474 *Simulations and estimation of allometric slopes*

475 Our analyses revealed that in this house sparrow meta-population, body mass is the variable that  
476 contains the least additional size-independent variation of any morphological measurement (Fig 1).  
477 Therefore, body mass provides a good surrogate measure of body size, as we define it. Despite body  
478 mass being the trait that correlated the most with the latent variable body size in our data set, the  
479 simulations and the empirical analyzes show that the allometric slopes estimated with bivariate  
480 regressions using absolute measured body mass as a surrogate of body size tend to be  
481 underestimated (Figs 2 & 3). The bivariate regression approach uses the covariance between body  
482 mass and morphological trait  $z$  to calculate the allometric slope  $b_z$ . The allometric slope is  
483 estimated as:

$$484 \quad b_z = \frac{Cov_{z,bm}}{V_{bm}},$$

485 where  $Cov_{z,bm}$  is the covariance between body mass and morphological trait  $z$ , and  $V_{bm}$  is the  
486 variance in body mass. Importantly, the variance in body mass ( $V_{bm}$ ) can be attributed to the  
487 variance associated body size ( $V_{size}$ ) plus size-independent variance caused by other sources ( $V_{rbm}$ ),  
488 such as differences in fat storage. Thus, the variance in body mass can be estimated as  $V_{bm} =$   
489  $V_{size} + V_{rbm}$ . The bias in the allometric slope  $b_z$  will thus increase as a function of  $V_{rbm}/V_{bm}$ . It is  
490 possible to correct for the bias using the reliability index  $K$  (Fuller 1987). The reliability index  $K$   
491 equals  $1 - V_{rbm}/V_{bm}$  and the corrected allometric slope can be calculated using the formula  $b_z/K$ .  
492 When we correct the allometric slopes estimated using the bivariate regression on the simulated  
493 data it indeed produces unbiased estimates (Table S6). However, to use the  $K$  index to correct the  
494 allometric slopes it is necessary to first determine the size-independent variation in body mass.

495 *Size-independent variation and evolvabilities*

496 The approach we implement here explicitly models the causal (i.e. developmental) effects of  
497 somatic investment in growth on the measured morphological traits (see eq. 4). Hence, any  
498 morphological variation not explained by the latent variable body size can be interpreted as size-  
499 independent variation (Fig 1, Table 3). This is of key importance, because size-independent additive  
500 genetic variation determines how selection may shape a single morphological trait without affecting  
501 the overall size of the organism. We studied the covariation of log-transformed morphometric  
502 measurements in our quantitative genetics and SEM analysis, and therefore the estimated size-  
503 independent additive genetic variation for each morphological trait can be directly interpreted as a  
504 conditional evolvability (Hansen and Houle 2008). The differences between the raw evolvability  
505 and conditional evolvability are a direct measure of the degree to which allometric relationships  
506 may constraint the independent evolution of each morphological trait. The reduction in conditional  
507 evolvability was largest for body mass, implying that selection on body mass will result in a  
508 substantially correlated response in the other measured traits, thus altering the overall size of the  
509 organism. In contrast, the reduction in the potential for an evolutionary response in beak length and  
510 wing length when controlling for body size was negligible, suggesting that selection acting solely  
511 on these traits could have an effect without dramatically affecting the overall body size.

512

513 *Size-independent covariation between beak features.*

514 Within the SEM framework, it is also possible to model the size-independent correlations explicitly.  
515 For instance, we expected covariation between beak length and depth after correcting for body size,  
516 because of the functional and developmental modularity of beak features. We explicitly modelled  
517 this parameter and assessed its statistical significance by inspecting the credible intervals. Beak  
518 length and depth were correlated both at the genetic and permanent environmental levels after  
519 controlling for the covariance caused by the latent variable body size. Although the credible interval  
520 of the permanent environmental correlation overlapped zero slightly (Fig 1), this finding

521 corroborates the notion that these two beak measurements reflect a functional module that regulates  
522 beak development over and above the more fundamental functional module of body size (Abzhanov  
523 et al. 2004, 2006; Lamichhaney et al. 2015; Lundregan et al. 2018).

524         The SEM approach used in this study explicitly disentangles the common (co)variance  
525 between all traits created by variation in body size and thus distinguishes it from the unique  
526 (co)variance associated with specific factors affecting each of morphological trait separately. It  
527 makes it possible in this case to estimate the amount of size-independent (co)variation between beak  
528 features. Size-independent (co)variation is generally estimated by inspecting additional principal  
529 components orthogonal to PC1 (William et al. 2005). From a biological perspective, it is therefore  
530 often difficult to make general statements regarding the meaning of PC2 and its interpretation as  
531 ‘shape’ specifically associated with the traits that load on PC2. Furthermore, the estimation of body  
532 size using principal components analyses maybe biased depending upon the differences in size-  
533 independent variation and covariation between traits, further obscuring the interpretation of PC2  
534 (see Appendix S2). Therefore, if the goal is to test specific patterns of correlation between traits  
535 after correcting for body size, our results suggest that these parameters should be modeled explicitly  
536 using SEM instead.

537

### 538 *Population differences in allometric relations and size-independent variation*

539 It has been shown that the inner farm islands differ from the outer non-farm islands in adult and  
540 juvenile survival (Ringsby et al. 1999; Holand et al. 2016), growth rate (Sæther et al. 1999), onset  
541 of breeding and subsequent recruitment (Ringsby et al. 2002), demographic variance (Engen et al.  
542 2007) and dispersal (Pärn et al. 2012). We also found that individuals in these two types of islands  
543 differed in their morphology. Sparrows in the inner-farm islands are generally larger than birds in  
544 the outer-non-farm islands (Table 1), probably reflecting consistently higher resource abundance,  
545 competition for limited nest sites and possibly greater safety from aerial predators in the farm  
546 islands. Interestingly, we also found that sparrows in the outer non-farm islands, where individuals

547 are generally more mobile and dispersive, have proportionally longer wings for their body size, as  
548 compared to the more sedentary individuals on the inner farm islands (Table 2). Birds on the inner-  
549 farm islands also had proportionally longer tarsi for their body size, as compared with the birds in  
550 outer-non-farm islands. These differences in allometric relationships between these two types of  
551 islands suggest that contrasting environmental conditions may have shaped the allometry of house  
552 sparrows in our system. These differences may be caused by differences in the environmental  
553 and/or genetic underpinnings of the allometric relationships. We found evidence suggesting that it  
554 was the genetic underpinning for the allometric slopes in wing length that differed between inner-  
555 farm islands and outer non-farm islands (Table S2), while it was environmental underpinnings  
556 (plasticity patterns) that caused the difference in the allometric slopes between island types in tarsus  
557 length (Table S3). However, we cannot confirm these results as the 85% confidence intervals  
558 overlapped each other considerably.

559         The stability and evolution of the additive genetic variance-covariance matrix (the **G** matrix)  
560 has received considerable attention because of its implications for the evolutionary trajectory of  
561 traits (Arnold et al. 2008; Björklund and Gustafsson 2015; Houle et al. 2017; McGlothlin et al.  
562 2018). Although **G** matrices are highly conserved among some populations, they have also been  
563 demonstrated to diverge in response to both selection and/or experimental treatments (Hine et al.  
564 2009; Björklund et al. 2012). We applied the proposed SEM approach in order to compare the **G**  
565 matrix of morphological traits across populations, but the same can also be done across species.  
566 This would provide insights into the adaptive changes to the structure of the **G** matrix resulting  
567 from selection on the allometric relationships and structure of developmental modules. Allometric  
568 constraints on morphological evolution can be understood as the strength of the correlations  
569 between different morphological measures resulting from body size variation (i.e. the allometric  
570 slopes). Therefore, body size and the evolution of morphological shape can be investigated by  
571 focusing on how selection affects the various allometric slopes (Bolstad et al. 2015). For instance,  
572 selection can influence the pleiotropic effect of genes affecting the growth and development of

573 different morphological traits. This may change the allometric relationships and/or the amount of  
574 size-independent variation in a trait, causing an adaptive change in the **G** matrix. Therefore, whilst  
575 genetic correlations caused by allometric relationships may constrain morphological evolution in  
576 the short term, they can also be modified in response to selection in the long term (Arnold et al.  
577 2008; Voje et al. 2014).

578 Evolution can also influence how environmental factors affect the expression of different  
579 morphological traits. Environmental pleiotropy has received relatively little attention, but the  
580 structure of the covariance caused by environmental effects during development can be very  
581 important because it determines how organisms respond to variation in the environment in terms of  
582 adaptive and passive plasticity (West-Eberhard 2003). Importantly, the structure and evolution of  
583 environmental pleiotropy, i.e. the **PE** matrix, can be studied in the same way as the **G** matrix (see  
584 discussion above). The shared developmental mechanisms underpinning environmental correlations  
585 (**PE** matrix) will constrain the independent changes of single morphological traits. However,  
586 organisms can also be selected to change their plastic response in one or more morphological traits  
587 by diverting more or less resources to the development of different morphological traits depending  
588 on environmental conditions (Robinson and Beckerman 2013). This will in turn alter the structure  
589 of the **PE** matrix in terms of the pattern of morphological correlations caused by environmental  
590 pleiotropy. In other words, integrated plasticity in response to environmental variation during  
591 development can evolve in response to functional pressures (Pigliucci 2001b). While the **G** matrix  
592 estimated here partly reflects how selection may have shaped the morphology of house sparrows in  
593 response to their selective landscape, the **PE** matrix may reflect how house sparrow morphology  
594 evolved to respond to more immediate developmental conditions (e.g. nestling food availability).  
595 Importantly, the relatively consistent results from the SEM, as applied to the genetic and  
596 environmental covariation in the present study, indicate that the **PE** matrix partly aligns with the **G**  
597 matrix. This suggests that plasticity may aid adaptive phenotypic integration, and that both genetic

598 and (permanent) environmental factors in this system tend to affect morphometric characters  
599 through similar physiological pathways (Pigliucci 2001a; Lind et al. 2015).

600

### 601 *Conclusions*

602 This study highlights that using SEMs in combination with allometric and quantitative genetic  
603 theory provides substantial additional insight concerning our understanding of morphological  
604 evolution. We estimated conditional evolvabilities and quantified the degree to which allometric  
605 relationships can constrain the evolution of house sparrow morphology in the short term. We found  
606 differences in the allometric relationships between inner farm versus outer non-farm island  
607 populations with different environmental regimes, suggesting that environmental differences have  
608 shaped the genetic or environmental underpinnings of allometric relationships in this system. More  
609 generally, the framework developed in this study can be used to make inferences not only of the  
610 environmental and genetic covariance matrices (**PE** and **G**), but can also be applied to phylogenetic  
611 covariance patterns, in order test ecological hypotheses about the evolution of morphological  
612 diversity.

613

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615 AMM, HP, HJ, THR, B-ES collected the data. YGA-A and PSR extracted the data from the  
616 database. YGA-A analyzed the data with input from JW. YGA-A and JW (co)wrote the manuscript  
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636

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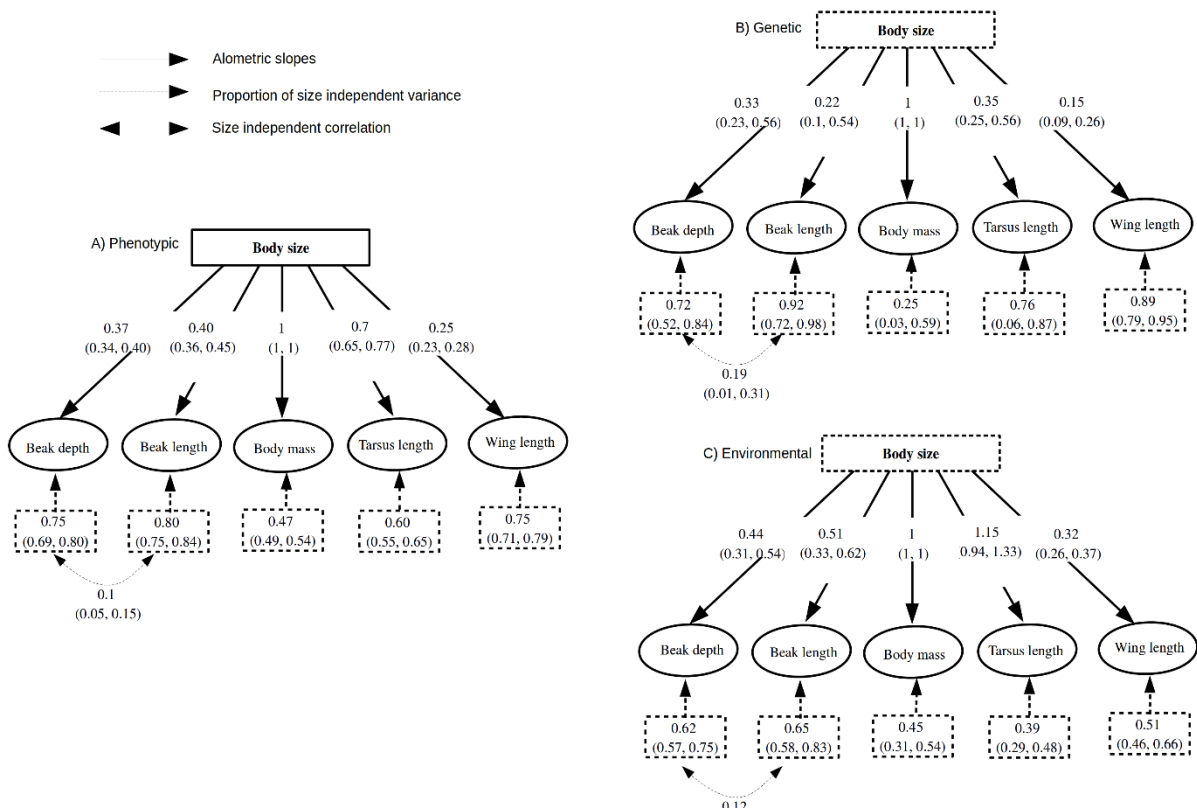
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768 **Figure 1.** Structural equation model (SEM) diagrams for the effect of the latent variable body size  
 769 on the morphological measurements and size-independent variances and covariances. SEM models  
 770 aim to tease apart the covariance between morphological measurements caused by the allometric  
 771 relationship with body size from size-independent sources of (co)variation at A) the phenotypic  
 772 level, B) the environmental level, and C) the genetic level. Solid line single-headed arrows  
 773 represent the effect of body size on the different morphological measurements (i.e. allometric  
 774 slopes) scaled to body mass. Dashed line single-headed arrows represent the proportion of size-  
 775 independent variation in the trait, and dashed line double-headed arrows represent the size-  
 776 independent correlation between pairs of traits. Estimates presented are the mean and 95% credible  
 777 intervals in parenthesis.



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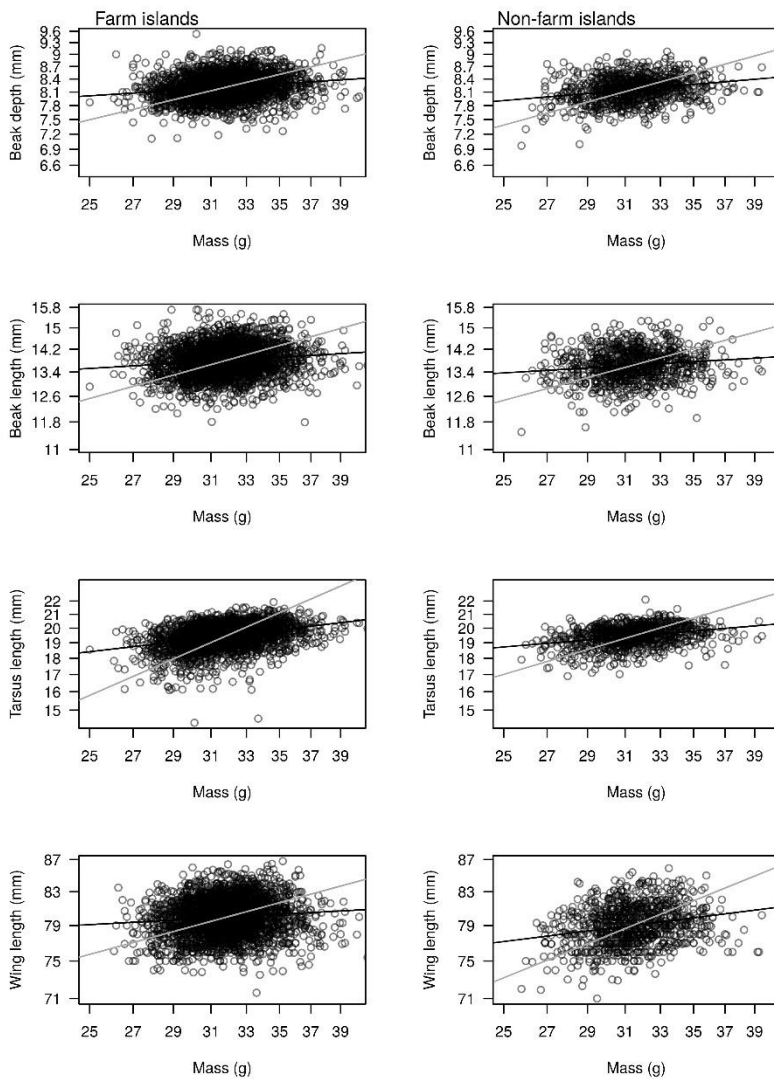
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787 **Figure 2.** Relationships between the different morphological traits with body mass estimated  
788 separately for the inner-farm islands and the outer-non-farm islands. Each point represents the mean  
789 for each individual over all the observations. Black lines represent the allometric relationships  
790 between the morphological traits and body mass. The gray lines represent the allometric  
791 relationships with body size scaled to units of mass (g), estimated from the SEM based on the  
792 phenotypic covariance matrix (see Table 2). Note that the axes are in the log scale, but for ease of  
793 interpretation the values correspond to the absolute scale.  
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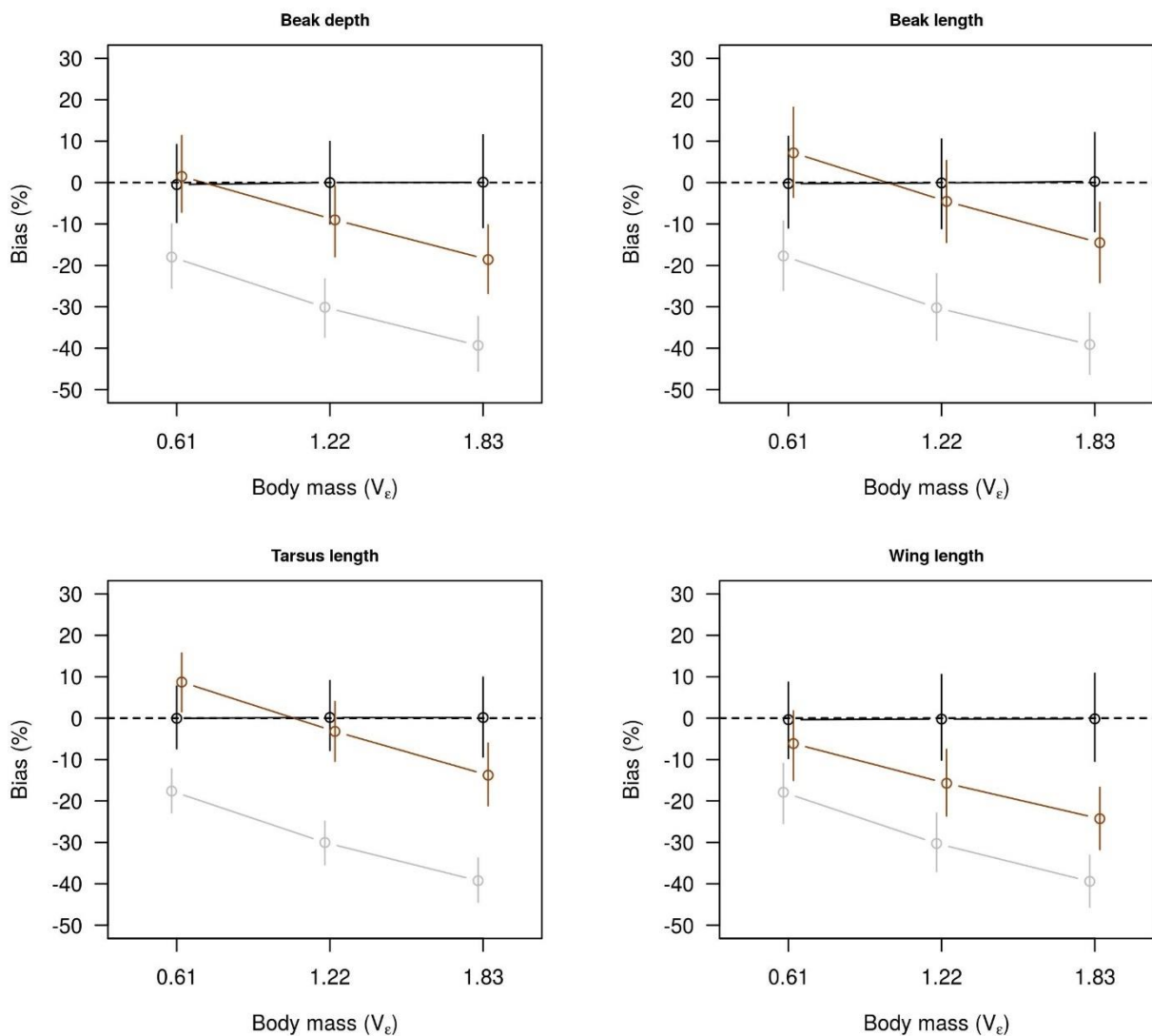
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803 **Fig 3.** Results from simulations comparing biases in the estimation of allometric slopes using SEM,  
804 PCA and bivariate regressions. Simulations were based on the covariance patterns found in the  
805 studied sparrow metapopulation. We simulated 1000 data sets for three different scenarios. In  
806 scenario 1, there was 50% size-independent variation in body mass ( $V_\epsilon$ ) than in the real data set. In  
807 scenario 2, there was the same amount of size-independent variance in body mass ( $V_\epsilon$ ) as in the real  
808 sparrow data set. In scenario 3, there was 50% more size-independent variation in body mass ( $V_\epsilon$ )  
809 than in the real data set. Percentage of bias was calculated as the mean deviation from the simulated  
810 value, divided by the simulated valued and then multiplied by 100. We present how the bias in the  
811 estimated allometric slope changes as a function of varying the size-independent variance in body  
812 mass. Black lines represent the bias in the estimates obtained using the SEM approach, light gray  
813 lines represent the bias for the estimates using bivariate regression and red lines represent the  
814 estimates obtained using PCA.



815

816 **Table 1.** Model results analyzing the sources of variation in house sparrow morphology. A) Fixed  
817 effect estimates of linear mixed-effects models determining the effects of sex, age, age-squared and  
818 island type (inner farm versus outer non-farm) in the expression of the studied morphological traits.  
819 B) Proportion of variance explained by the different random effects. Variance estimates were  
820 calculated from different univariate animal models that partition individual differences into the  
821 additive genetic variance ( $V_a$ ), unknown permanent environmental effects ( $V_{pe}$ ) and effects caused  
822 by environmental differences between populations ( $V_f$ ). The model also partitioned within-  
823 individual variation in the morphological traits due to metapopulation-wide among-year ( $V_y$ ) and  
824 among month ( $V_m$ ) variation in environmental conditions, as well as among-measurement variation  
825 ( $V_r$ ) which can be caused by measurement error or reversible plasticity in response to local  
826 environmental conditions. We present the mean and 95% credible intervals for the fixed effect  
827 estimates and proportion of variance explained by the different random effects.

Level	Beak depth (mm)	Beak length (mm)	Body mass (g)	Tarsus length (mm)	Wing length (mm)
A) Fixed effects					
Intercept	8.16 (8.07, 8.27)	13.5 (13.5, 13.8)	32.04 (30.99, 32.09)	19.4 (19.3, 19.5)	78.3 (77.9, 78.8)
Sex:males	0.1 (0.04, 0.15)	-0.09 (-0.15, -0.04)	-0.15 (-0.21, -0.1)	0.1 (0.04, 0.16)	1.16 (1.11, 1.21)
Age	0.17 (0.12, 0.22)	0.1 (0.05, 0.14)	0.07 (0.01, 0.12)	0 (-0.02, 0.01)	0.24 (0.21, 0.28)
Age-squared	-0.02 (-0.02, -0.01)	-0.01 (-0.02, -0.01)	-0.01 (-0.01, 0)	0 (0, 0)	-0.02 (-0.02, -0.01)
Islands:outer	-0.23 (-0.37, -0.07)	-0.28 (-0.47, -0.12)	-0.14 (-0.31, 0.04)	0.01 (-0.13, 0.15)	-0.33 (-0.49, -0.16)
B) Proportion of explained variance					
Additive genetic	0.29 (0.21, 0.37)	0.35 (0.27, 0.43)	0.23 (0.17, 0.29)	0.34 (0.26, 0.41)	0.43 (0.34, 0.5)
Permanent environment	0.11 (0.07, 0.16)	0.17 (0.12, 0.23)	0.18 (0.13, 0.23)	0.6 (0.52, 0.67)	0.09 (0.04, 0.13)
Among-islands	0.01 (0, 0.03)	0.02 (0, 0.07)	0.02 (0, 0.09)	0.01 (0.00, 0.03)	0.03 (0.01, 0.1)
Among- months	0.2 (0.09, 0.39)	0.11 (0.05, 0.26)	0.05 (0.02, 0.11)	0.02 (0.01, 0.04)	0.12 (0.05, 0.26)
Among-years	0.04 (0.02, 0.08)	0.02 (0.01, 0.04)	0.03 (0.01, 0.07)	0 (0, 0.01)	0.02 (0.01, 0.04)
Among- measurements	0.35 (0.26, 0.4)	0.32 (0.27, 0.36)	0.49 (0.44, 0.53)	0.04 (0.04, 0.04)	0.31 (0.26, 0.34)

829 **Table 2.** Parameter estimates for the hypothesized SEM (see Fig.1) applied to separate phenotype  
830 covariance matrices for the inner farm (n=3530) versus outer non-farm (n=2065) islands, and for  
831 males (n=2866) versus females (n=2716). We present A) the allometric relationships scaled to body  
832 mass, B) the size-independent correlation between beak depth and beak length, and C) the  
833 proportion of size-independent variance. Estimates are presented as the mean and 85% credible  
834 intervals (in parenthesis) of the SEM in order to compare the estimates between groups.

Relations	Farm	No-farm	Male	Female
A) Allometric relationships				
Beak depth	0.35 (0.31, 0.39)	0.42 (0.33, 0.52)	0.39 (0.33, 0.44)	0.35 (0.3, 0.4)
Beak length	0.39 (0.33, 0.44)	0.43 (0.32, 0.56)	0.37 (0.28, 0.46)	0.43 (0.37, 0.51)
Body mass	1 (1, 1)	1 (1, 1)	1 (1, 1)	1 (1, 1)
Tarsus length	0.81 (0.73, 0.91)	0.56 (0.45, 0.68)	0.73 (0.62, 0.85)	0.69 (0.6, 0.78)
Wing length	0.23 (0.2, 0.26)	0.32 (0.27, 0.4)	0.23 (0.18, 0.27)	0.28 (0.24, 0.32)
B) Size-independent correlation				
	0.12 (0.08, 0.16)	0.13 (0.03, 0.21)	0.08 (0.03, 0.13)	0.12 (0.07, 0.18)
C) Proportion of size-independent variance				
Beak depth	0.79 (0.75, 0.83)	0.67 (0.55, 0.76)	0.71 (0.66, 0.77)	0.78 (0.72, 0.83)
Beak length	0.82 (0.79, 0.86)	0.78 (0.7, 0.86)	0.83 (0.79, 0.87)	0.77 (0.72, 0.82)
Body mass	0.5 (0.43, 0.56)	0.54 (0.41, 0.64)	0.37 (0.29, 0.45)	0.54 (0.46, 0.61)
Tarsus length	0.55 (0.5, 0.6)	0.65 (0.57, 0.73)	0.59 (0.53, 0.64)	0.62 (0.56, 0.67)
Wing length	0.8 (0.76, 0.83)	0.6 (0.5, 0.69)	0.79 (0.75, 0.83)	0.72 (0.67, 0.77)

835

836 **Table 3.** Evolvabilities, autonomy and conditional evolvabilities dependent upon body size and the  
837 whole **G** matrix for each of the measured morphological traits. Evolvabilities were estimated from  
838 univariate animal models applied to log-transformed morphological measurements. Structural  
839 equation models (SEM) were applied to the covariance matrix of the log-transformed  
840 measurements, thus unexplained variances by body size can be interpreted as conditional  
841 evolvabilities. Conditional evolvabilities were thus calculated using the variance not explained by  
842 body size for each trait. We also present conditional evolvabilities based on the genetic variance in  
843 a log-transformed trait conditional on all the other measured traits. We present the mean and 95%  
844 credible intervals of the evolvabilities as percentages of potential trait change in response to a unit  
845 of selection.

	Evolvability	Autonomy from body size	Cond. evolvability on body size	Cond. evolvability on G
Beak depth	0.05 (0.04, 0.05)	0.64 (0.32, 0.86)	0.03 (0.02, 0.04)	0.03 (0.03, 0.04)
Beak length	0.07 (0.06, 0.08)	0.91 (0.61, 0.99)	0.07 (0.05, 0.08)	0.06 (0.05, 0.07)
Body mass	0.12 (0.1, 0.14)	0.40 (0.02, 0.61)	0.04 (0.00, 0.09)	0.10 (0.08, 0.12)
Tarsus length	0.06 (0.05, 0.07)	0.71 (0.16, 0.86)	0.05 (0.03, 0.06)	0.05 (0.04, 0.06)
Wing length	0.02 (0.02, 0.03)	0.92 (0.35, 0.98)	0.02 (0.02, 0.02)	0.02 (0.02, 0.02)

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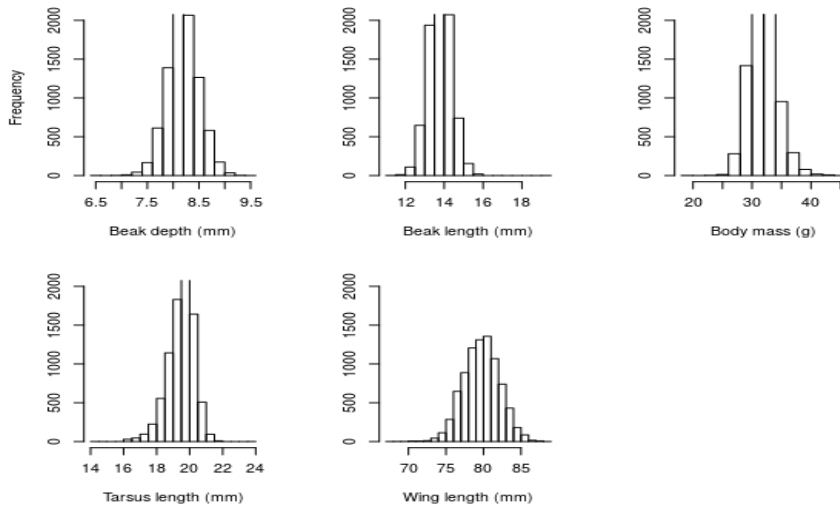
## Appendix S1. Additional analyses

**Table S1.** Pair-wise correlations between all of the morphological traits at the individual, genetic and permanent environmental levels for adult house sparrows on the studied Helgeland islands 1993-2014. We present the mean and 95% CIs.

Relationship	Individual	Genetic	Permanent environ.
Beak depth <-> beak length	0.32 (0.28, 0.37)	0.34 (0.21, 0.45)	0.4 (0.14, 0.59)
Beak depth <-> body mass	0.41 (0.37, 0.46)	0.44 (0.32, 0.56)	0.46 (0.23, 0.67)
Beak depth <-> tarsus length	0.28 (0.24, 0.32)	0.22 (0.07, 0.36)	0.43 (0.3, 0.58)
Beak depth <-> wing length	0.2 (0.15, 0.24)	0.15 (0.02, 0.26)	0.38 (0.08, 0.64)
Beak length <-> body mass	0.26 (0.21, 0.31)	0.18 (0.05, 0.32)	0.34 (0.09, 0.58)
Beak length <-> tarsus length	0.32 (0.29, 0.36)	0.22 (0.09, 0.35)	0.44 (0.32, 0.57)
Beak length <-> wing length	0.3 (0.26, 0.34)	0.25 (0.12, 0.37)	0.28 (-0.04, 0.54)
Body mass <-> tarsus length	0.46 (0.43, 0.5)	0.43 (0.31, 0.54)	0.6 (0.49, 0.72)
Body mass <-> wing length	0.35 (0.3, 0.4)	0.19 (0.08, 0.3)	0.92 (0.78, 0.99)
Tarsus length <-> wing length	0.32 (0.29, 0.36)	0.12 (-0.02, 0.24)	0.74 (0.6, 0.86)

## Appendix S2. Simulation study

1  
2 We use simulated data to study the robustness of the SEM approach in recovering a biological  
3 model of morphological covariation caused by variation in body size (Fig 1). We simulated data for  
4 5 morphological traits following a biological model, where individual variation in somatic  
5 investment generated variation and co variation between the 5 simulated morphological traits. We  
6 studied the covariation of the log-transformed morphological measurements using three different  
7 techniques. We compared the performance of the SEM approach against bivariate regressions  
8 between log-transformed body mass and the other morphometric log-transformed measurements,  
9 and principal component analyses (PCA) applied to all the morphological log-transformed  
10 measurements. The mean and variance of each trait where based on the observed measurements of  
11 the studied house sparrow meta-population in Northern Norway.



12  
13 **Figure S1.** Histograms for the observed morphological measurements of the studied house sparrow meta-populations.

14  
15 The relationship between body size ( $m$ ) and a morphological trait ( $z$ ) is described by an exponential  
16 function:

17 
$$z = am^b + e$$

18 The allometric slopes ( $b$ ) describes the effect of body size on the measured morphological trait,  
19 while  $a$  is a constant that scales each morphological measurement to body size. Trait specific  
20 factors affecting the expression of each morphological trait are represented as  $e$ . Where  $e$  is  
21 assumed to come from a multi-normal distribution with means of 0 and a variance-covariance  
22 matrix  $Ve$ . This matrix represents the patterns of size-independent (co)variation. The effect of body  
23 size on the different morphological measurements was based on the results obtained analysing the

24 morphological measurements of the studied population see (Fig 1A). Similarly, the size-  
25 independent (co)variances simulated was the same as the observed in the empirical study.

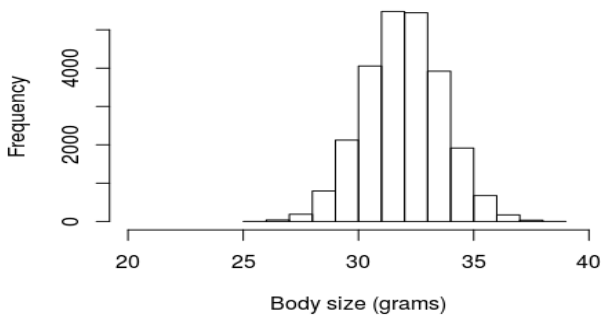
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27 **Table S5.** Simulated parameters

Trait	Mean	Variance	a	b	$V_{\epsilon}$
<b>Beak depth</b>	8.21	0.1	0.82	0.37	0.04
<b>Beak length</b>	13.8	0.35	1.24	0.4	0.17
<b>Body mass</b>	31.94	5.38	0	1	1.22
<b>Tarsus length</b>	19.49	0.66	0.51	0.71	0.39
<b>Wing length</b>	79.99	5.69	3.48	0.26	1.71

28

29 We worked under the assumption that body size is a volume measure, can be measured in units of  
30 grams, and scales isometrically with body mass. Thus, the allometric slope for body mass was one,  
31 but it is important to note that body mass also has size-independent variation not associated to body  
32 size. Body size in the simulated data had a mean equal to the mean body mass in the studied  
33 population and the variance in body size was equal to the variance in body mass explained by body  
34 size observed in the empirical study (2.85).



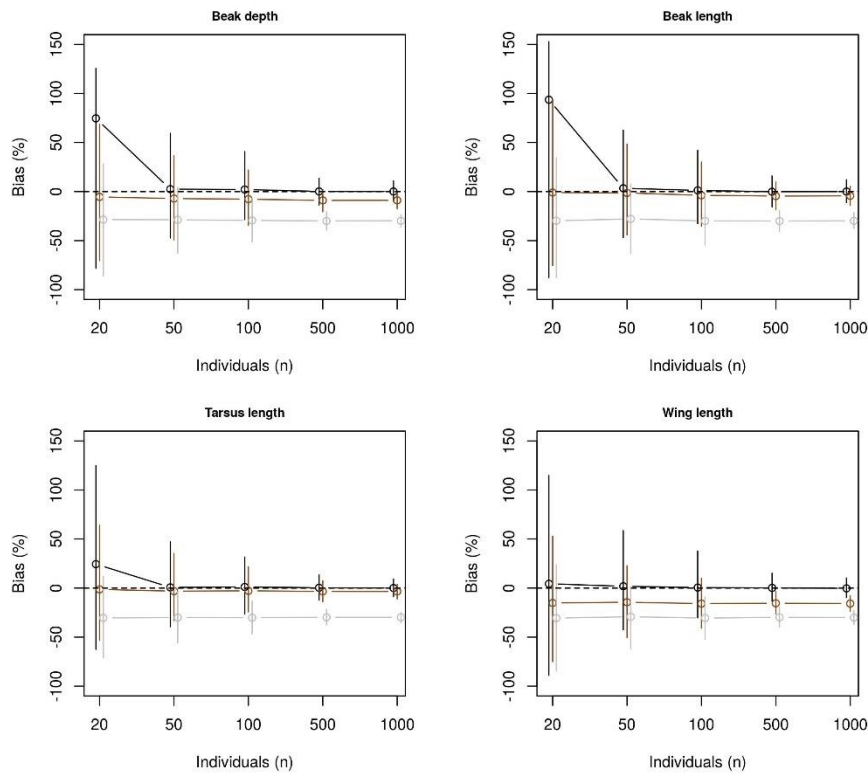
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36 **Figure S2.** Histograms for the simulated body size variation.

37

### 38 **Effects of sample size.**

39 We first explored the effect of the number of individuals sampled (100, 500, 1000, 5000) in the  
40 estimation of the allometric slopes. The results show that PCA and bivariate regression provided  
41 consistently biased estimates, while the SEM estimates where unbiased (Figure 3). This bias was  
42 independent of sample size.



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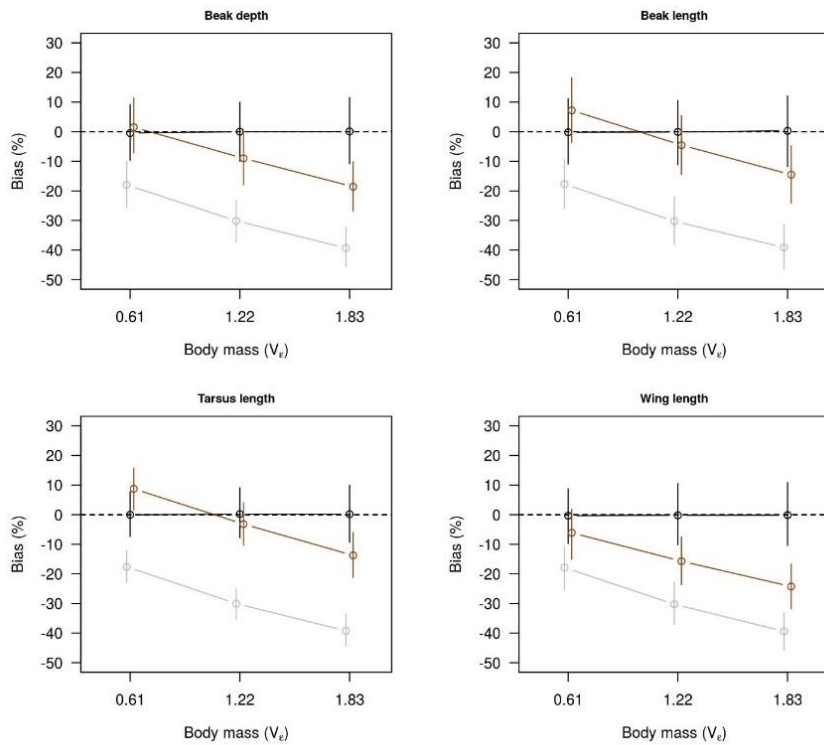
44 **Figure S3.** Bias in the allometric slopes estimated as a function of sample size. Bivariate regression is depicted by grey  
 45 lines, PCA by brown lines and SEM by black lines. Circles represent the mean estimate across simulations and lines  
 46 represent the 95% confidence intervals.

47

48 **Effects of size-independent variation in body mass.**

49 We proceeded to study how the amount of size-independent variation affected the estimation of the  
 50 allometric slopes. We varied the amount of size-independent variation in body size. We simulated 3  
 51 scenarios of varying size-independent variation in body mass. The scenarios corresponded to data  
 52 sets where the size-independent variation in body mass was: i) half of that estimated in the studied  
 53 sparrow meta-population, ii) the same size-independent variance, and iii) 1.5 times higher. Figure  
 54 S4 shows that the bias in the bivariate regression and PCA is proportional to the amount of size-  
 55 independent variation in the surrogate measure of body size (i.e. body mass).





56

57 **Figure S4.** Bias in the allometric slopes estimated as a function of the amount of size-independent variation in body  
 58 mass. Bivariate regression is depicted by grey lines, PCA by brown lines and SEM by black lines. Circles represent the  
 59 mean estimate across simulations and lines represent the 95% confidence intervals.

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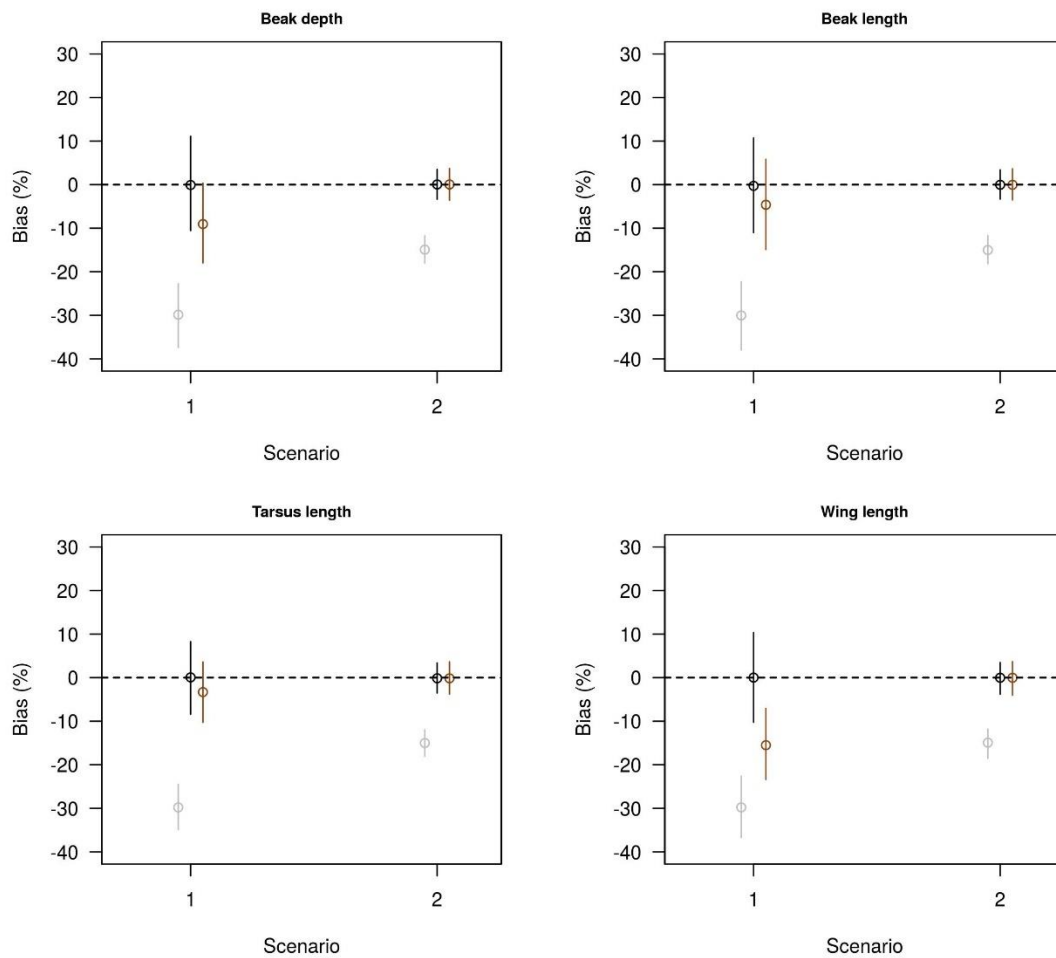
61 **Table S6.** Mean and 95% confidence intervals of the estimated slopes from the simulated data sets  
 62 where the size-independent variance and the allometric slopes of all traits were the same as in the  
 63 observed data. The estimates were obtained using bivariate regressions, bivariate regression with  
 64 correction factor  $k$ , PCA and SEM.

	Simulated	Bivariate regression	Bivariate regression $k$ corrected	PCA	SEM
Beak depth	0.37	0.26 (0.23, 0.29)	0.37 (0.33, 0.41)	0.34 (0.31, 0.37)	0.37 (0.33, 0.41)
Beak length	0.40	0.28 (0.25, 0.31)	0.40 (0.35, 0.45)	0.38 (0.34, 0.42)	0.40 (0.35, 0.45)
Tarsus length	0.70	0.49 (0.45, 0.53)	0.70 (0.64, 0.76)	0.69 (0.63, 0.73)	0.70 (0.64, 0.76)
Wing length	0.25	0.18 (0.16, 0.19)	0.25 (0.22, 0.28)	0.21 (0.19, 0.23)	0.25 (0.22, 0.28)

65

66 **Effects of the differences in size-independent variation in the different morphological traits.**

67 We also studied how the differences between the different traits in size-independent variation  
68 affected the estimation of the allometric slopes. We examined the bias in allometric slopes in a  
69 scenario where the size-independent variances are different versus a scenario where the size-  
70 independent variances are the same. We simulated two different scenarios one had the same  
71 allometric slopes and size-independent variance as in the studied house sparrow population,  
72 whereas in the other scenario the allometric slopes ( $b=1$ ) and size-independent variances ( $V_e=0.5$ )  
73 were the same for all traits. Figure 5 shows that when the size-independent variance and allometric  
74 slopes are the same in PCA and SEM then both approaches produce unbiased estimates, while  
75 bivariate regressions still underestimate the allometric slopes.



76  
77 **Figure S5.** Bias in the allometric slopes in two scenarios. Scenario 1 has the same allometric slopes and size-  
78 independent variance as in the studied house sparrow population, whereas in scenario 2 the allometric slopes and size-  
79 independent variance is the same for all traits. Bivariate regressions are depicted by grey lines, PCA by brown lines and  
80 SEM by black lines. Circles represent the mean estimate across simulations and error lines represent the 95%  
81 confidence intervals.

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**Table S2.** Parameter estimates for the hypothesized SEM (see Fig.1) applied to separate genetic covariance matrices for the inner farm (n=2793) versus outer non-farm (n=950) islands, and to males (n=1867) versus females (n=1876). We present A) the allometric relationships scaled to body mass, B) the size-independent correlation between beak depth and beak length, and C) the proportion of size-independent variance. Estimates are presented as the mean and 85% credible intervals (in parenthesis) of the SEM in order to compare the estimates between groups.

Relations	Farm	No-farm	Male	Female
<b>A) Allometric relationships</b>				
Beak depth	0.33 (0.24, 0.51)	0.38 (0.15, 0.72)	0.48 (-0.33, 1.19)	0.39 (0.27, 0.57)
Beak length	0.23 (0.12, 0.54)	0.13 (-0.22, 0.45)	0.89 (0.00, 3.75)	0.29 (0.15, 0.53)
Body mass	1 (1, 1)	1 (1, 1)	1 (1, 1)	1 (1, 1)
Tarsus length	0.41 (0.3, 0.67)	0.37 (0.13, 0.6)	0.68 (0.00, 2.69)	0.41 (0.28, 0.59)
Wing length	0.12 (0.07, 0.22)	0.23 (0.09, 0.41)	0.17 (-0.05, 0.67)	0.21 (0.14, 0.3)
<b>B) Size-independent correlation</b>				
	0.2 (0.06, 0.29)	0.19 (-0.15, 0.79)	0.08 (-0.21, 0.37)	0.19 (0.04, 0.32)
<b>C) Proportion of size-independent variance</b>				
Beak depth	0.76 (0.62, 0.86)	0.59 (0.09, 0.99)	0.87 (0.07, 1)	0.65 (0.45, 0.8)
Beak length	0.93 (0.77, 0.97)	0.96 (0.55, 1)	0.69 (-0.15, 0.95)	0.87 (0.7, 0.95)
Body mass	0.33 (0.1, 0.61)	0.26 (-10.14, 0.76)	0.73 (0.39, 1)	0.31 (0.08, 0.53)
Tarsus length	0.74 (0.55, 0.84)	0.75 (0.3, 1)	0.79 (0.36, 0.95)	0.7 (0.54, 0.83)
Wing length	0.93 (0.85, 0.97)	0.7 (0.32, 1)	0.96 (0.87, 1)	0.8 (0.69, 0.9)

**Table S3.** Parameter estimates for the hypothesized SEM (see Fig.1) applied to separate permanent environment covariance matrices for the inner farm (n=2793) versus outer non-farm (n=950) islands, and to males (n=1867) versus females (n=1876). We present A) the allometric relationships scaled to body mass, B) the size-independent correlation between beak depth and beak length, and C) the proportion of size-independent variance. Estimates are presented as the mean and 85% credible intervals (in parenthesis) of the SEM in order to compare the estimates between groups.

Relations	Farm	No-farm	Male	Female
<b>A) Allometric relationships</b>				
Beak depth	0.42 (0.31, 0.48)	0.47 (0.01, 1.28)	0.49 (0.28, 0.58)	0.23 (0.08, 0.5)
Beak length	0.49 (0.32, 0.55)	0.65 (0.22, 1.85)	0.39 (0.11, 0.48)	0.51 (0.3, 0.77)
Body mass	1 (1, 1)	1 (1, 1)	1 (1, 1)	1 (1, 1)
Tarsus length	1.11 (0.97, 1.28)	0.72 (0.27, 2.07)	0.98 (0.77, 1.16)	1.44 (0.81, 2.15)
Wing length	0.31 (0.26, 0.36)	0.29 (0, 0.58)	0.31 (0.2, 0.37)	0.28 (0.17, 0.39)
<b>B) Size-independent correlation</b>				
	0.1 (-0.06, 0.11)	0.17 (-0.34, 0.59)	0.12 (-0.1, 0.19)	0.09 (-0.25, 0.17)
<b>C) Proportion of size-independent variance</b>				
Beak depth	0.61 (0.55, 0.75)	0.71 (-0.87, 1)	0.46 (0.4, 0.72)	0.91 (0.59, 0.99)
Beak length	0.66 (0.61, 0.85)	0.64 (-2.91, 1)	0.69 (0.66, 0.92)	0.75 (0.5, 0.97)
Body mass	0.44 (0.34, 0.53)	0.6 (-0.09, 1)	0.27 (0.1, 0.38)	0.71 (0.39, 0.9)
Tarsus length	0.41 (0.33, 0.48)	0.64 (-1.78, 1)	0.36 (0.23, 0.46)	0.34 (-0.25, 0.67)
Wing length	0.51 (0.46, 0.61)	0.76 (0.38, 1)	0.49 (0.42, 0.67)	0.76 (0.5, 0.98)

**Table S4.** Genetic correlations for the two groups of islands (inner farm versus outer non-farm) estimated from separate animal models to the non-transformed measurements. We present the mean and 95% CIs.

Relations	Genetic		Environmental	
	Farm	Non-farm	Farm	Non-farm
Beak depth – beak length	0.33 (0.2, 0.45)	0.28 (-0.25, 0.59)	0.37 (0.14, 0.57)	0.69 (0.26, 0.94)
Beak depth - body mass	0.39 (0.25, 0.52)	0.83 (0.4, 0.99)	0.5 (0.27, 0.73)	0.07 (-0.7, 0.87)
Beak depth - tarsus length	0.21 (0.05, 0.35)	0.36 (-0.13, 0.96)	0.42 (0.28, 0.59)	0.38 (-0.31, 0.9)
Beak depth - wing length	0.07 (-0.05, 0.2)	0.55 (0.3, 0.76)	0.43 (0.17, 0.69)	0.36 (-0.54, 0.92)
Beak length - body mass	0.14 (0, 0.29)	0.17 (-0.46, 0.69)	0.35 (0.12, 0.59)	0.47 (-0.36, 0.93)
Beak length - tarsus length	0.24 (0.09, 0.38)	-0.51 (-0.95, 0.25)	0.42 (0.29, 0.55)	0.71 (0.23, 0.99)
Beak length - wing length	0.21 (0.09, 0.33)	0.26 (-0.03, 0.55)	0.31 (0.06, 0.57)	0.56 (-0.33, 0.97)
Body mass - tarsus length	0.42 (0.28, 0.55)	0.54 (-0.12, 0.96)	0.59 (0.47, 0.7)	0.54 (-0.07, 0.98)
Body mass - wing length	0.11 (-0.01, 0.23)	0.47 (0.21, 0.7)	0.94 (0.8, 1)	0.63 (-0.53, 0.99)
Tarsus length - wing length	0.11 (-0.02, 0.25)	0.31 (-0.28, 0.74)	0.71 (0.58, 0.84)	0.6 (-0.53, 0.99)