Does habitat specialization shape the evolutionary potential of wild bird populations?

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Abstract

Because specialist species evolved in more temporally and spatially homogeneous environments than generalist species, they are supposed to experience less fluctuating selection. For this reason, we expect specialists to show lower overall genetic variation as compared to generalists. We also expect populations from specialist species to be smaller and more fragmented, with lower neutral genetic diversity. We tested these hypotheses by investigating patterns of genetic diversity along a habitat specialization gradient in wild birds, based on estimates of heritability, coefficients of variation of additive genetic variance, and heterozygosity available in the literature. We found no significant effect of habitat specialization on any of the quantitative genetic estimators but generalists had higher heterozygosity. This effect was mainly a consequence of the larger population size of generalists. Our results suggest that evolutionary potential does not differ at the population level between generalist and specialist species, but the trend observed in heterozygosity levels and population sizes may explain their difference in susceptibility to extinction.

Introduction

Native specialist species are becoming less abundant in disturbed landscape to the benefit of generalist species (Shultz et al. 2005, Le Viol et al. 2012). There is some evidence that climate (Davey et al. 2013) and land use (Devictor et al. 2008a, b) changes are driving this decline of specialization in wild communities, leading to a functional biotic homogenization (Clavel et al. 2011). The higher sensitivity of specialists to global changes is expected to result from their narrower ecological niche, which is associated with smaller and more fragmented populations, more vulnerable to the destruction of their habitat. The persistence of species will ultimately depend upon two mechanisms: range shift or adaptation to environmental changes, through phenotypic plasticity or microevolution (Lynch and Lande 1993). Anthropogenic changes are now considered as the greatest evolutionary force (Palumbi 2001, Steffen et al. 2011) and it therefore becomes crucial to determine how specialist and generalist species differ in their ability to respond to these changes. Assessing whether generalist and specialist species differ in terms of evolutionary potential should give valuable information on their respective ability to defer extinction through evolution.

The two alternative strategies (specialist vs generalist) are generally thought to arise depending on fitness trade-offs between alternate phenotypes across environments (Richmond et al. 2005, Poisot et al. 2011): spatially and temporally variable environments should favour generalist strategies, because generalists can achieve higher average performance than specialists across multiple environments. In turn, stable environments should favour specialists which are able to exploit more efficiently a single resource (see Moran 1992 for theoretical evidence, and Kassen 2002 for experimental evidence). Expressed in terms of selection pressures, heterogeneous environments generate fluctuating selection, while in a homogeneous or stable environment, selection is more likely to be stabilising, or persistently directional (Keightley and Hill 1988). Additionally, generalist strategies may become less

73 profitable under high levels of local stabilizing selection, because trade-offs for the

74 performance in different niches become accordingly strong (Svardal et al. 2014). Specialists

75 can therefore be expected to evolve under stronger and more consistent selection pressures

76 that could deplete overall genetic variability. In contrast, the exposure of generalists to a

77 variety of environments, and to spatially and temporally fluctuating selection, could help

78 maintain a higher genetic diversity. For these reasons, we expect to find higher evolutionary

79 potential in generalist species than in specialist ones, which could partly explain the highest

80 sensitivity of specialists to environmental changes.

81   Only a scarce number of empirical studies support this prediction so far. Hägele and

82 Rowell-Rahier (2000) showed in a herbivorous insect genera that host specialist species have

83 a lower heritability (and thus a lower evolutionary potential) of growth rate than host

84 generalists. A review of selection experiments in bacteria by Kassen (2002) also suggests that

85 environmental heterogeneity may be driving both the quantity of genetic variation in a

86 population and the niche width of individuals, resulting in the evolution of generalists and the

87 maintenance of genetic variation in heterogeneous environments. However, the link between

88 specialization and evolutionary potential is largely unknown in wild populations.

89

90   Here, we review available estimates of evolutionary potential in relation to habitat

91 specialisation and population size in wild bird populations. As emphasised in the univariate

92 breeder's equation, $R = h^2 S$ (Lande 1979), the predicted evolutionary response (R) depends on

93 the selection gradient (S) and on the evolutionary potential of a trait, measured as its heritability

94 (h^2, the ratio between the amount of genetic additive variance and total phenotypic variance). We

95 thus mainly focused on estimates of heritability and additive genetic variance as they also

96 represent the most widely reported estimates of evolutionary potential for quantitative traits

97 (Postma 2014). We predict higher genetic variance for generalist species (heritability,

98   hereafter h², and the additive genetic coefficient of variation, hereafter CV_A, are the two

99   standardized estimates of genetic variance we used).

100   We also reviewed estimates of heterozygosity (hereafter Hz), a widely available

101   measure of genetic diversity known to depend on demographic processes such as inbreeding

102   level, drift and population size (Soulé 1976, Frankham et al. 2002). Hz is not a direct

103   estimator of evolutionary potential, as it does not relate to additive genetic variance, but rather

104   a proxy for overall genetic diversity, which is often considered in conservation study as an

105   indicator of population health. More specifically, Hz has been correlated with extinction risks

106   (Evans and Sheldon 2008) and population fitness (Reed and Frankham 2003). On this topic

107   again, little empirical work can be found, but a study carried out on the bark beetle (Kelley et

108   al. 2000) indicated that specialist sister-species indeed had reduced levels of Hz when

109   compared to generalist ones. Simply because of a narrower ecological niche, specialist species

110   have access to a more limited range of habitats than generalist ones. For this reason,

111   populations of specialists may be smaller and more fragmented which is likely to negatively

112   impact genetic diversity by limiting effective population size and gene flow (Whitlock and

113   Barton 1997). We therefore predict that specialists should have lower Hz than generalists,

114   mainly as a result of smaller population size.

115

116

Material & Methods

Data collection

Habitat specialization indexes

Assessing specialization by categorizing habitat types has been criticized as too subjective and unrealistic (Bazzaz 1991, Thompson et al. 1998, Fridley et al. 2007). Therefore, we used two different indices based on independent methods: The Species Specialization Index (SSI), as defined by Julliard et al. (2006) and the relative niche width measurement (θ) as introduced in plants by Fridley et al (2007) and in birds by Ducatez et al. (2014). Both indices use different approaches and are therefore not strongly correlated, but rather represent the diversity of methods available to measure habitat specialisation.

The SSI is defined as the coefficient of variation of a species abundance across a set of predefined habitats (Julliard et al. 2004). A high SSI thus implies that a species abundance varies strongly across habitats. Specialist species have higher values of SSI, generalists have lower values. SSI was calculated for 234 species at the European scale, the territory being partitioned into 98 habitat categories defined in the EUNIS database (see Le Viol et al., 2012 for details). Affinity of each species for nesting and foraging in a given habitat is coded by experts on three levels (3: primary habitats; 2: secondary; 1: others). Note that because the coefficient of variation is the standard deviation scaled to the mean, SSI does not depend on population size.

The niche width (Θ) is based on the expectation that a generalist species occurs in a range of habitat categories that vary considerably in species composition, whereas a specialist species is found in habitats that contain a consistent suite of other species. The idea of using the compositional diversity of species that co-occur with a target species to measure the degree of specialization was introduced by Colwell and Futuyma (1971). Specialist species have lower values of θ, generalists have higher values. To avoid a bias due to differences in species range, this index is based on habitat co-occurrence (rather than realized species co-

143   occurrence), meaning that two species that occupy the same habitat type in different places

144   are considered as co-occurring, even if their range does not overlap, e.g. this avoids island

145   species to be automatically considered as specialists. The niche width was estimated using

146   species co-occurrence data within each of the 82 IUCN habitat subcategories, and considering

147   all extant 9870 species listed by the IUCN (see Ducatez et al., 2014 for details). For a given

148   species, habitat width was measured as $\theta = \gamma / \mu(\alpha)$, where γ is the cumulative number of

149   species in the habitats used by a given species and $\mu(\alpha)$ is the mean habitat species richness

150   calculated over the different habitats inhabited by that species. This specialization index is

151   positively correlated with population size (Pearson's product-moment correlation $\rho = 0.25$, 95

152   % Confidence Interval [0.044, 0.43], p-value = 0.02, see supplementary material S1 for the

153   correlation of both specialization indexes with population size).

154   Habitat specialization was chosen over other available specialization indices as it

155   gathers the greatest number of niche axes in one parameter and is consequently the most

156   integrative. Indeed, temperature and food availability depend on habitat, which makes habitat

157   specialization linked with thermic and food specialization (Barnagaud et al. 2012). Our

158   dataset of quantitative estimates of evolutionary potential (i.e. quantitative genetic

159   parameters) includes species that cover a range of 3.1 in SSI (from 2.3 to 5.4) and of 6.4 in

160   niche width (from 1.58 to 8), and the neutral diversity data (i.e. Hz) covers a range of 4.6 in

161   SSI (from 2.3 to 6.9) and of 10.6 in niche width (from 1 to 10.6), when the total range

162   available for SSI is 8, ranging from 1.8 to 9.9 and the total range for niche width is 13.54,

163   ranging from 1 to 14.54. The distributions of both specialization index for each of our datasets

164   can be found in supplementary figure S2.

165

166 ***Population size***

167 Information on local population size was not available so the population size data we used

168 was extracted from the BirdLife International website in May 2014 (*http://www.birdlife.org/*).

169 Population sizes correspond to the total number of individuals in the world according to the

170 censuses published by BirdLife (2005, 2008).

171

172 ***Quantitative data: heritability and coefficient of additive genetic variance***

173 We chose the bird taxon because it gathers the greatest number of quantitative estimators

174 across all taxa (Postma, 2014). In order to gather estimates of evolutionary potential (h^2 and

175 CV_A) in bird populations, we performed a search in the *Web Of Knowledge* research engine.

176 We used the key-words: Topic= (« bird* ») AND (« heritabil* » OR « genetic* estimate* »)

177 and the search was performed in February 2013. When studies aimed at quantifying the

178 response of quantitative parameters to different environmental conditions (e.g. food quality),

179 only parameters estimated under natural conditions were used. These references were further

180 checked against the list gathered by Postma (2014), in order to maximize the number of

181 references providing estimates of heritability and coefficients of additive genetic variance. h^2

182 and CV_As can be estimated with two different methods: the parent offspring regression and

183 the animal model. The former is the earliest method and has been used since the end of the

184 19th century. It estimates heritability by the phenotypic correlation between parents and

185 offspring (Lynch and Walsh 1998). The latter, the *animal model*, has been applied in ecology

186 for merely more than a decade. The animal model is a mixed model using information about

187 relatedness among individuals to infer the part of phenotypic variance due to additive genetic

188 variance (Henderson 1973, Kruuk 2004). Because parent offspring regression may

189 overestimate heritability (shared environments increase the resemblance between parents and

190 offspring), the method used to estimate quantitative parameters was specified in our dataset

191 and subsequent analyses.

192   Only life-history and morphological traits (See supplementary material, table S3 for

193   trait classification) were kept, as for behavioural traits the type of traits were extremely

194   heterogeneous and for physiological traits, data were available for only four traits from two

195   studies. We considered here that pooling heritabilities or CV_As from different traits measured

196   in a population is relevant, as we were not looking for an accurate estimate of evolutionary

197   potential, but for an estimate of the general level of additive genetic variance in the

198   population. Both h² and CV_A represent standardised measures of additive genetic variance,

199   respectively to the total phenotypic variance and to the mean.

200

201   ***Genetic diversity***

202   We used the heterozygosity (Hz) data published by Evans and Sheldon (2008). They collected

203   Hz values measured at microsatellite loci for wild bird species in the literature and used

204   expected Hz because it is less sensitive to sample size (Nei 1978) and the occurrence of null

205   alleles (Callen et al. 1993). When multiple studies were available for one species, Evans &

206   Sheldon (2008) kept the study with the largest sample size and the highest number of

207   microsatellites loci used to estimate Hz. Thus, while the quantitative genetics estimates are

208   available for several populations in some species, the estimates for Hz are only available for

209   one population per species. We used the Hz values for the 54 species that matched our SSI

210   specialization index and for the 183 species in their dataset that matched our estimation of the

211   niche width (*θ*).

212

213   ***Phylogeny***

214   To account for the non-independence of species, we used species relatedness extracted from

215   phylogenetic trees. Phylogenetic trees were obtained from the website *www.birdtree.org* that

216   provides subsets of the first complete bird phylogeny (Jetz et al. 2012). Each model was run

217   with 100 alternative trees.

218

Statistical analyses

To assess the effect of habitat specialization on evolutionary potential (h^2, CV_A) or neutral genetic diversity (Hz) we used linear mixed models. Ideally, models should include as fixed effects population size (log-transformed) and an estimator of habitat specialization (SSI or niche width Ө). However, for h^2 and CV_A, population size was only available for few species, resulting in a too small sample size to run our models. We thus included population size in models considering Hz but not in models considering h^2 and CV_A. In terms of random variables, a phylogeny effect was included in all models to account for species non-independence.

Because of a more complex data structure, analyses of h^2 and CV_A included several additional fixed and random effects compared to models run for heterozygosity. First, we expected systematic differences between certain types of traits (morphological or life history traits, Postma, 2014). Consequently, we added "Type of trait" as a fixed effect in models with two levels, "morphological" and "life-history". Similarly, as the method used to estimate heritabilities (animal model or parent-offspring regression) entails a systematic difference, we added an "Estimation method" fixed effect in models investigating heritability.

Second, h^2 and CV_A estimates are trait and population specific because they are based on observations of some characteristics of individuals sampled from a given population. Therefore it was necessary to include in the models two additional random effects: "population identity" and "trait", with a nested structure. "Trait" was nested within "population identity" and "population identity" within "phylogeny". The MCMCglmm R package (Hadfield 2013) does not model nested effects, but the variables were designed in order to account for this nested structure: each species/population/trait combination was given a unique ID allowing to take into account each level in a meaningful way (phylogeny

243　(species), population within species, trait within population within species). Some species

244　(e.g. *Fulica atra*) were represented by one estimator for only one population when others (e.g.

245　*Passer domesticus*) were represented by multiple populations, and multiple traits for each

246　population. The random effects "population identity" and "trait" allow taking this lack of

247　balance into account.

248　　　　Finally, the standard error associated with heritability estimates was included as a

249　random effect to account for measurement error. Unfortunately, this was not possible with

250　CV_A, due to the paucity of errors reported, nor with heterozygosity for which standard errors

251　were not available. The random effects were assumed to follow normal distributions with a

252　mean of 0 and a variance equal to $\sigma_a^2 \mathbf{A}$ for the phylogeny (where σ_a^2 is the phylogenetic

253　variance and **A** is the phylogenetic relatedness matrix), a variance equal to $\sigma_m^2 \mathbf{M}$ for the error

254　effect (where σ_m^2 is the measurement error variance and **M** is a diagonal matrix containing the

255　square standard error of the published estimates; we fixed the variance σ_m^2 to 1 as the sampling

256　variances are known, see Hadfield & Nakagawa 2009 for details) and variances equal to $\sigma^2 \mathbf{I}$

257　for the remaining effects (where σ^2 represents the population variance within species, the trait

258　variance within population within species or the residual variance; **I** is the identity matrix).

259　　　　These models were run using Bayesian methods as implemented in the MCMCglmm

260　R package. 1 000 000 iterations of each model were run. The first 50 000 iterations were used

261　to initiate the chain, not to estimate parameters, and the thinning interval was set to 10. The

262　amount of iterations was considered sufficient as autocorrelations were low (<0.06) for fixed

263　and random effects.

264　　　　An inverse-gamma prior for random effects was used (V = 1 and nu = 0.002), in order

265　to minimise the effect of prior information on posterior distribution. To assess prior

266　sensitivity, the same models were run using a parameter expanded prior (V = 1, nu = 1,

267   alpha.mu = 0, alpha.V = 10000) and a weakly informative prior (V = σ/4, n = 1 where σ is the

268   total variance of the dependent variable). Using different priors did not affect the results

269   (Supplementary Table S5 and S6).

270   To account for phylogeny uncertainty, each model was run with each of the 100

271   alternative trees provided by Jetz et al. (2012), and the estimates presented in the result

272   section represent the average over the 100 models.

Results

Available data for quantitative genetics estimates

275   For the analysis using the SSI index, 520 estimates of h² and 150 estimates of CV_A from

276   respectively 64 and 13 studies were gathered, with an average of 3.52 traits per study for h²

277   and 6.62 per studies for CV_A. Variance among studies in number of estimates is large, ranging

278   from 1 to 48 for h² and from 1 to 14 for CV_A. The number of estimates calculated from parent

279   offspring regression is 363 for h² against 157 from "animal model" and 39 for CV_A against

280   111 from "animal model". Only life-history and morphological traits were kept, with

281   respectively 132 and 388 estimates for h², and 43 and 107 for CV_A.

282   For the analysis using the niche width measurement (*θ*), a total of 923 h² and 190 CV_A

283   estimates from respectively 64 and 20 studies were gathered, with an average of 2.6 traits per

284   study for h² and 5.7 per study for CV_A. Variance among studies in the number of estimates

285   was large, ranging from 1 to 48 for h² and from 1 to 14 for CV_A. 707 h² estimates came from

286   parent-offspring regressions and 216 from "animal models". For CV_A, 52 were estimated

287   from parent offspring regression and 139 from "animal models". Only life-history and

288   morphological traits were kept in the analyses (due to the low number of physiological and

289   behavioural traits), with respectively 176 and 747 estimates for h², and 61 and 129 for CV_A.

290

Effect of specialization on additive genetic variance (h^2, CVA)

Heritability was not predicted by specialization, whether considering the SSI (Table 1, posterior mean = 0.054, 95% CI [-0.022, 0.14], pMCMC = 0.13, Fig 2a) or the niche width (θ, Table 2, posterior mean = -0.018 95% CI [-0.057, 0.023], pMCMC = 0.36, Fig 3a) as indices of habitat specialization. Morphological traits had higher heritability than life-history traits in both data sets (Table1 & Table 2), and estimates from the animal model were lower than estimates from parent-offspring regressions for the SSI data (Table1).

Similarly, CV_A was not predicted by either the SSI (posterior mean = 0.66, 95% CI [-1.3, 2.7], pMCMC = 0.48, Fig 2b) or the niche width (θ) (Table2, posterior mean = -0.26, 95% CI [-1.9, 1.5], pMCMC = 0.71, Fig 3b).

Effect of specialization and population size on genetic diversity (Hz)

Heterozygosity was not predicted by either the SSI (Table 3, posterior mean=0.014, 95% CI [-0.025, 0.053], pMCMC = 0.48) or the niche width (Table 3, posterior mean=0.051, 95% CI [-0.021, 0.12], pMCMC = 0.16), but population size did have a significant effect on heterozygosity (Table 3, posterior mean=0.044, 95% CI [0.023, 0.064], P <0.001, and posterior mean=0.036, 95% CI [0.020, 0.054], P <0.001). Species with larger global population sizes had higher levels of heterozygosity. Because niche width and population size are positively correlated (Pearson's product-moment correlation=0.25, df=88, P=0.020), an effect of niche width on heterozygosity appears when population size is not part of the model (posterior mean=0.071, 95% CI [0.022, 0.12], pMCMC =0.0045). The SSI however was not correlated to population size (Pearson's product-moment correlation=-0.27, df=35, P=0.10)

Discussion

The ability of wild populations to persist in a changing environment depends largely on their evolutionary potential (Hoffmann and Sgrò 2011, Vander Wal et al. 2013). We expected a

316 higher evolutionary potential in generalists as compared to specialists, based on the different

317 selection pressures their ecology suggests they are exposed to. In contrast with this, across 36

318 wild bird populations and using two different specialization indexes, we found no significant

319 effect of specialization on evolutionary potential -as estimated by quantitative genetics

320 estimates, h^2 and CV_A. Specialization did not correlate with genetic diversity measured by Hz

321 either, but we found a significant positive relationship between population size and

322 heterozygosity. In turn, population size correlates positively with niche width (but not with

323 the SSI index), indicating that species with larger niches (generalists) also tend to exhibit

324 more genetic diversity, as a consequence of their larger population sizes. The fact that

325 populations of generalist species are larger than populations of specialist species can be

326 explained by several factors, such as larger available habitat patches, better connectivity

327 between patches, or higher dispersal rates (Kattan 1992, Stireman 2005). In turn, higher

328 genetic diversity in larger populations is in line with theoretical and empirical expectations

329 (Soulé 1976, Frankham 1996). Our results thus suggest that the effect of specialization on

330 genetic diversity results from demographic processes rather than evolutionary processes such

331 as long-term differences in selection pressures. Indeed, we found that specialization had an

332 effect on heterozygosity through population size, but not on quantitative genetic estimates:

333 neutral markers are tightly linked to demography, migration, drift and mutation while

334 selection is expected to shape variance of quantitative traits (Sgrò et al. 2011).

335 The prediction that specialists should have in general lower evolutionary potential than

336 generalists due to stronger and more consistent selection pressures was not confirmed by this

337 study. So far, the empirical support for this hypothesis was limited, to our knowledge, to two

338 local scale study in insects (Hagele & Rowell-Rahier 2000 and Kelley et al. 2000) and to

339 experimental evolution in bacteria, as reviewed by Kassen (2002). Several reasons (outlined

340   below) may explain the absence of pattern, but in any case, the generality of this result will

341   need to be confirmed (or infirmed) by more empirical studies from wild populations.

342   First, we know little about the origin of generalism. For example, if a species niche is

343   fully covered by specialized populations, each population exploiting a part of the niche only,

344   the species will be described as generalist. In this case, high genetic diversity is expected

345   among populations, but not necessarily within populations, making the pattern undetectable

346   when genetic parameters are sampled at the population level (as it is the case for h^2 and CV_A).

347   This particular genetic structure may have evolved under large spatial scale environmental

348   variation. The ability of populations to respond to new selection pressures may then depend

349   on the amount of gene flow among populations. To provide further insights in this direction,

350   an informative index would be the F_{ST}, which compares within population genetic variation to

351   among-population genetic variation, a core question in our investigation. Unfortunately,

352   estimating F_{ST} requires heterozygosity measures in multiple populations for each studied

353   species, which would be available only after implementing new field studies.

354   A second major issue is the definition of "evolutionary potential". Because it was the

355   most readily provided estimate of additive genetic variance in natural populations and because

356   of its central role in the breeder's equation, we used heritability. However, because it is a ratio

357   and because of its univariate definition, heritability can be a misleading estimate of

358   evolutionary potential. Heritability is a ratio of variances and as such its direction of variation

359   can be interpreted in multiple ways, i.e. higher heritability can be the result of either higher

360   additive genetic variance or lower environmental variance. This is of fundamental importance

361   here since environmental variance could be larger for generalist species dealing with more

362   heterogeneous environments than specialist species, hence masking any potential increase in

363   additive genetic variance. A solution around this issue is the use of coefficients of variation of

364   additive genetic variance rather than heritability (Houle 1992, Hansen et al. 2003, 2011,

365   Hansen and Houle 2008). Unfortunately, CV_A was reported for only 15 species, and often

366   published without associated standard errors. Moreover, 45% of those estimators are likely to

367   be biased (Garcia-Gonzalez et al. 2012). It was thus not possible to reliably assess the effect

368   of specialisation on CV_A but this is an avenue worthwhile pursuing in the future. Another

369   aspect through which heritability may not be a suitable estimate of evolutionary potential is its

370   univariate and trait specific nature as it may not reflect overall evolvability and constraints

371   (e.g. genetic correlations, Sih et al. 2004). Multivariate approaches are therefore be needed to

372   bring further light on these issues (Walsh and Blows 2009, Hansen et al. 2011, Teplitsky et al.

373   2014).

374   Third, on a more functional note, the absence of patterns for quantitative genetic

375   estimates in our study may also be explained by a lack of knowledge about the functionality

376   of the traits. Indeed, in the study of Hagele & Rowell-Rahier (2000), growth rate heritability

377   was related to a diet specialization index. As a selection pressure resulting from food

378   availability is expected to directly impact growth rate, the niche parameter used to assess

379   specialization index was thus tightly linked to the trait for which evolutionary potential was

380   measured. In this way, the effect of selection pressure is more likely to be detected when

381   measuring heritability. However, this would not mean overall lower evolutionary potential in

382   specialists, but only for a subset of traits closely associated to the specialization parameter. In

383   our case, with the dataset obtained from the literature, such a clear functional link between

384   traits and habitat specialization is not available: we chose a integrative specialization

385   parameters and investigated the additive genetic variance for all available traits together.

386   However, a population can be submitted to strong selection pressures, for instance on wing

387   size (Hall et al. 2004) or beak shape (Grant, B., Grant 2003), that would reduce genetic

388   variance for these traits, a pattern that would not be detected in our analyses because we

389   pooled genetic variance estimates irrespectively of the traits' function. In the case of reduced

390   overall evolutionary potential, we would expect a decreased genetic variance in traits closely

391   associated to fitness. We thus tried to restrict the data to heritability estimates related to

392   fitness traits (e.g. clutch size, breeding success) but the sample size was drastically reduced in

393   this case (90 heritabilities for 24 species), which didn't allow us to estimate effects properly.

394   In conclusion, our study indicates that there is no detectable effect of habitat

395   specialization on evolutionary potential in birds, at least when considering estimates of

396   additive genetic variance currently available in the literature. However, this does not mean

397   that specialist and generalist species stand the same chances when facing environmental

398   changes: our study suggests that species with narrower habitat niches have smaller

399   populations with reduced levels of neutral genetic diversity, which indicate increased

400   extinction risks (Evans and Sheldon 2008). In the close future, new estimates of additive

401   genetic variance for wild populations may be available, such as multivariate ones, allowing

402   for further exploration of the relationship between specialization and evolutionary potential.

403

404

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Supporting information

S1 Correlation between both specialization indexes and population size.

S2 Specialization indexes distributions

S3 Trait Classification

S4 Phylogenetic trees

S5 Results with weakly informative priors

S6 Results with parameter expanded priors

S7 References for heritability

S8 References for CV_As

S9 List of species taken from Evans &Sheldon (2007)

S10 Visualization for heritability data

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References

Barnagaud, J. Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Viol, I. and Archaux, F. 2012. Relating habitat and climatic niches in birds. - PLoS One 7: e32819.

Bazzaz, F. A. 1991. Habitat Selection in Plants. - Am. Nat. 137: S116–S130.

BirdLife, F. 2005. Birds in Europe: population estimates, trends and conservation status. - Br. Birds 98: 269–271.

Callen, D. F., Thompson, a D., Shen, Y., Phillips, H. a, Richards, R. I., Mulley, J. C. and

428   Sutherland, G. R. 1993. Incidence and origin of "null" alleles in the (AC)n microsatellite

429   markers. - Am. J. Hum. Genet. 52: 922–927.

430   Clavel, J., Julliard, R. and Devictor, V. 2011. Worldwide decline of specialist species: Toward

431   a global functional homogenization? - Front. Ecol. Environ. 9: 222–228.

432   Colwell, R. and Futuyma, D. 1971. On the measurement of niche breadth and overlap.pdf. -

433   Ecology 52: 567–576.

434   Davey, C., Devictor, V. and Jonzen, N. 2013. Impact of climate change on communities:

435   revealing species' contribution. - J. Anim. Ecol. 82: 551–561.

436   Devictor, V., Julliard, R., Couvet, D. and Jiguet, F. 2008a. Birds are tracking climate

437   warming, but not fast enough. - Proc. R. Soc. London B Biol. Sci. 275: 2743–2748.

438   Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, a and Couvet, D. 2008b. Functional

439   biotic homogenization of bird communities in disturbed landscapes. - Glob. Ecol.

440   Biogeogr. 17: 252–261.

441   Ducatez, S. D., Ingley, R. T. and SHine, R. 2014. Using species co-occurrence patterns to

442   quantify relative habitat breadth in terrestrial vertebrates. - Ecosphere 5: 1–12.

443   Evans, S. R. and Sheldon, B. C. 2008. Interspecific patterns of genetic diversity in birds:

444   correlations with extinction risk. - Conserv. Biol. 22: 1016–25.

445   Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. - Conserv.

446   Biol. 10: 1500–1508.

447   Frankham, R., Ballou, J. D. and Briscoe, D. A. 2002. Introduction to Conservation Genetics.

448   Fridley, J. D., Vandermast, D. B., Kuppinger, D. M., Manthey, M. and Peet, R. K. 2007. Co-

449   occurrence based assessment of habitat generalists and specialists: A new approach for

450   the measurement of niche width. - J. Ecol. 95: 707–722.

451   Garcia-Gonzalez, F., Simmons, L. W., Tomkins, J. L., Kotiaho, J. S. and Evans, J. P. 2012.

452   Comparing evolvabilities: Common errors surrounding the calculation and use of

453 coefficients of additive genetic variation. - Evolution (N. Y). 66: 2341–2349.

454 Grant, B., Grant, P. 2003. What Darwin's Finches can Teach Us about the Evolutionary
455   Origin and Regualtion of Biodiversity. - Bioscience 53: 965–975.

456 Hadfield, A. J. 2013. Package " MCMCglmm ." in press.

457 Hägele, B. F. and Rowell-Rahier, M. 2000. Choice, performance and heritability of
458   performance of specialist and generalist insect herbivores towards cacalol and
459   seneciphylline, two allelochemicals of Adenostyles alpina (Asteraceae). - J. Evol. Biol.
460   13: 131–142.

461 Hall, K. S. S., Ryttman, H., Fransson, T. and Stolt, B. O. 2004. Stabilising selection on wing
462   length in reed warblers Acrocephalus scirpaceus. - J. Avian Biol. 35: 7–12.

463 Hansen, T. F. and Houle, D. 2008. Measuring and comparing evolvability and constraint in
464   multivariate characters. - J. Evol. Biol. 21: 1201–19.

465 Hansen, T. F., Armbruster, W., Carlson, M. and Pelabon, C. 2003. Evolvability and genetic
466   constraints in Dalechampia Blossoms: genetic correlations and conditional evolvability. -
467   J. Evol. Biol. 16: 754–766.

468 Hansen, T. F., Pélabon, C. and Houle, D. 2011. Heritability is not Evolvability. - Evol. Biol.
469   38: 258–277.

470 Henderson, C. R. 1973. Sire evaluation and genetic trends. - Proc. Anim. Breed. Genet. Symp.
471   Honour J.L. Lush.: 10–41.

472 Hoffmann, A. and Sgrò, C. 2011. Climate change and evolutionary adaptation. - Nature 470:
473   479–485.

474 Houle, D. 1992. Comparing evolvability and variability of quantitative traits. - Genetics 130:
475   195–204.

476 International, B. 2008. State of the World's Birds - indicators for our changing world. -
477   Database

478   Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, a O. 2012. The global

479   diversity of birds in space and time. - Nature 491: 444–8.

480   Julliard, R., Jiguet, F. and Couvet, D. 2004. Common birds facing global changes: What

481   makes a species at risk? - Glob. Chang. Biol. 10: 148–154.

482   Julliard, R., Clavel, J., Devictor, V., Jiguet, F. and Couvet, D. 2006. Spatial segregation of

483   specialists and generalists in bird communities. - Ecol. Lett. 9: 1237–44.

484   Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance

485   of diversity. - J. Evol. Biol. 15: 173–190.

486   Kattan, G. H. 1992. Rarity and vulnerability: the birds of the cordilheira central of Colombia.

487   - Conserv. Biol. 6: 64–70.

488   Keightley, P. D. and Hill, W. G. 1988. Quantitative genetic variability maintained by

489   mutation-stabilizing selection balance in finite populations. - Genet. Res. 54: 33–43.

490   Kelley, S. T., Farrell, B. D. and Mitton, J. B. 2000. Effects of specialization on genetic

491   differentiation in sister species of bark beetles. Heredity 84: 218 Ð227. - Heredity

492   (Edinb). in press.

493   Kruuk, L. 2004. Estimating genetic parameters in natural populations using the "animal

494   model." - Philos. Trans. R. Soc. London B Biol. Sci. 359: 873–890.

495   Lande, R. 1979. Quantitative Genetic Analysis of Multivariate Evolution, Applied to Brain:

496   Body Size Allometry. - Genet. Anal. 33: 402–416.

497   Lynch, M. and Lande, R. 1993. Evolution and extinction in response to envrionmental

498   change. - In: Biotic interactions and global change. pp. 234–250.

499   Lynch, M. and Walsh, B. 1998. Genetics and analysis of quantitative traits.

500   Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. - Am. Nat. 139:

501   971–989.

502   Nei, M. 1978. Estimation of Average Heterozygosity and genetice distance from a small

503   number of individuals. - Genetics 89: 583–590.

504   Palumbi, S. R. 2001. Evolution - Humans as the world's greatest evolutionary force. -
505   Science (80-.). 293: 1786–1790.

506   Poisot, T., Bever, J. D., Nemri, A., Thrall, P. H. and Hochberg, M. E. 2011. A conceptual
507   framework for the evolution of ecological specialization. - Ecol. Lett. 14: 841–851.

508   Postma, E. 2014. Four decades of estimating heritabilities in wild vertebrate populations:
509   Improved methods, more data, better estimates? - In: Quantitative Genetics in the Wild.
510   pp. 16–33.

511   Reed, D. H. and Frankham, R. 2003. Correlations between fitness and genetic diversity. -
512   Conserv. Biol. 17: 230–237.

513   Richmond, C., Breitburg, D. L. and Rose, K. A. 2005. The role of environmental generalist s
514   ecies in ecosystem function. - Ecol. Modell. 188: 279–295.

515   Sgrò, C. M., Lowe, A. J. and Hoffmann, A. A. 2011. Building evolutionary resilience for
516   conserving biodiversity under climate change: {Conserving} biodiversity under climate
517   change. - Evol. Appl. 4: 326–337.

518   Shultz, S., Bradbury, R. and Evans, K. 2005. Brain size and resource specialization predict
519   long-term population trends in British birds. - Proc. R. Soc. London B Biol. Sci. 272:
520   2305–2311.

521   Sih, A., Bell, A. and Johnson, J. 2004. Behaviroal syndroms: an ecological and evolutionary
522   overview. - Trends Ecol. Evol. 19: 372–378.

523   Soulé, M. 1976. Allozyme variation, its determinants in space and time. - In: Ayala, F. (ed),
524   Molecular evolution. Sinauer Associates, Sunderland, Massachusetts., pp. 60–77.

525   Steffen, W., Persson, Å., Deutsch, L. and Zalasiewicz, J. 2011. The Anthropocene: From
526   Global Change to Planetary Stewardship. - Ambio 19: 142–151.

527   Stireman, J. O. 2005. The evolution of generalization? Parasitoid flies and the perils of

528   inferring host range evolution from phylogenies. - J. Evol. Biol. 18: 325–336.

529   Svardal, H., Rueffler, C. and Doebeli, M. 2014. Organismal complexity and the potential for

530   evolutionary diversification. - Evolution (N. Y). 68: 3248–3259.

531   Teplitsky, C., Robinson, M. R. and Merilä, J. 2014. Evolutionary potential and constraints in

532   wild populations. - In: Quantitative genetics in the wild. pp. 190–208.

533   Thompson, K., Hodgson, J. G. and Gaston, K. J. 1998. Abundance-range size relationships in

534   the herbaceous flora of central England. - J. Ecol. 86: 439–448.

535   Vander Wal, E., Garant, D., Festa-Bianchet, M. and Pelletier, F. 2013. Evolutionary rescue in

536   vertebrates: evidence, applications and uncertainty. - Philos. Trans. R. Soc. Lond. B.

537   Biol. Sci. 368: 20120090.

538   Viol, I. Le, Jiguet, F. and Brotons, L. 2012. More and more generalists: two decades of

539   changes in the European avifauna. - Biol. Lett. 8: 780–782.

540   Walsh, B. and Blows, M. W. 2009. Abundant Genetic Variation + Strong Selection =

541   Multivariate Genetic Constraints: A Geometric View of Adaptation. - Annu. Rev. Ecol.

542   Evol. Syst. 40: 41–59.

543   Whitlock, M. C. and Barton, N. H. 1997. The effective size of subdivided population. -

544   Genetics 146: 427–441.

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552 **Table1. Effect of Species Specialization Index (SSI) on two quantitative estimates of evolutionary potential: heritability and coefficient of variation of**

553 **additive genetic variance (CV$_A$).**. Estimates of effects are given by posterior means (Post. Mean) and their associated 95% confidence intervals (CI 95%). pMCMC

554 values are also given for fixed effects. For the effect of type of trait, the reference level is 'life history' as compared to 'morphological'. For the effect of the

555 estimation method, the reference level is 'animal model' as compared to 'parent offspring regression'.

Explanatory var.		Heritability			CV$_A$		
	Effect	Post. mean	CI 95%	Pc	Post.mean	CI 95%	Pc
Fixed	Intercept	0.0299	-0.261/0.281	0.866	9.81	2.79/16.5	0.013[**]
	SSI	0.0535	-0.0218/0.139	0.128	0.664	-1.31/2.67	0.479
	Type of trait: morphological	0.192	0.130/0.252	<0.001[***]	-8.25	-11.3/-5.03	<0.001[***]
	Estimation method: regression	0.0452	0.00283/0.0871	0.036[*]	-0.848	3.71/1.96	0.549
Random	Phylogeny	0.004	0.000/0.017		4.07	0.000/18.7	
	Population	0.002	0.000/0.013		0.677	0.000/3.39	
	Trait	0.021	0.016/0.029		17.3	8.25/30.7	
	Residual	0.004	0.003/0.006		25.8	19.0/36.0	

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557 **Table2 Effect of species niche width Index (θ) on two estimates of genetic variance: heritability and coefficient of variation of additive genetic variance (CV$_A$).**

558 Estimates of effects are given by posterior means (Post. Mean) and their associated 95% confidence intervals (CI 95%). pMCMC values are also given for fixed effects. For the

559 effect of type of trait, the reference level is 'life history' as compared to 'morphological'. For the effect of the estimation method, the reference level is 'animal model' as

560 compared to 'parent offspring regression'.

Explanatory var.		Heritability			CVa		
	Effect	Post.mean	CI 95%	Pc	Post.mean	CI 95%	Pc
Fixed	Intercept	0.34	0.086 / 0.59	0.011	12	4 / 20	0.012
	Ө	-0.018	-0.057 / 0.023	0.36	-0.26	-1.9 / 1.5	0.71
	Type of trait : Morphological	0.21	0.17 / 0.25	<0.001	-7.0	-10 / -4.0	<0.001
	Estimation method : regression	-0.00097	-0.045 / 0.044	0.97	-1.5	-5.4 / 2.2	0.44
Random	Phylogeny	0.040	0.012 / 0.074		3.8	0.00013 / 19	
	Population	0.0060	0.0026 / 0.0096		1.7	0.00012 / 8.1	
	Trait	0.0061	0.0020 / 0.011		4.8	0.00014 / 21	
	Residual	0.017	0.014 / 0.021		74	54 / 93	

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563 **Table3. Effect of species niche width (θ) and Species Specialization Index (SSI) on heterozygosity (Hz).** Estimates of effects are given by posterior means (Post.

564 Mean) and their associated 95% confidence intervals (CI 95%). pMCMC values are also given for fixed effects. The second model includes population size as a fixed effect.

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|	Explanatory var.	Heterozygosity			Response var.	Heterozygosity		
	Effect	Post.mean	CI 95%	Pc	Effect	Post.mean	CI 95%	Pc
Fixed	Intercept	0.047	-0.21 / 0.29	0.71	Intercept	0.058	-0.28 / 0.39	0.72
	θ	0.051	-0.021 / 0.12	0.16	SSI	0.014	-0.025 / 0.053	0.48
	Log Population size	0.044	0.023 / 0.064	<0.001	Log Population size	0.036	0.020 / 0.054	<0.001
Random	Phylogeny	0.0047	0.00023 / 0.012		Phylogeny	0.010	0.00020 / 0.030	
	Residual	0.020	0.014 / 0.028		Residual	0.014	0.0044 / 0.024	

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571 **Fig1** Distribution of coefficients of variation of genetic additive variance (CV_A, a), heritabilities (b) and heterozygosity (c) along gradient of

572 habitat specialization (SSI).

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574 **Fig2** Distribution of coefficients of variation of genetic additive variance (CV_A, a), heritabilities (b) and heterozygosity (c) along gradient of

575 habitat niche width (θ).

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Fig 1 Distribution of coefficient of additive genetic variance (a), heritability (b), and heterozygosity (c) along a habitat specialization gradient. Each SSi value represents a species which name appears below
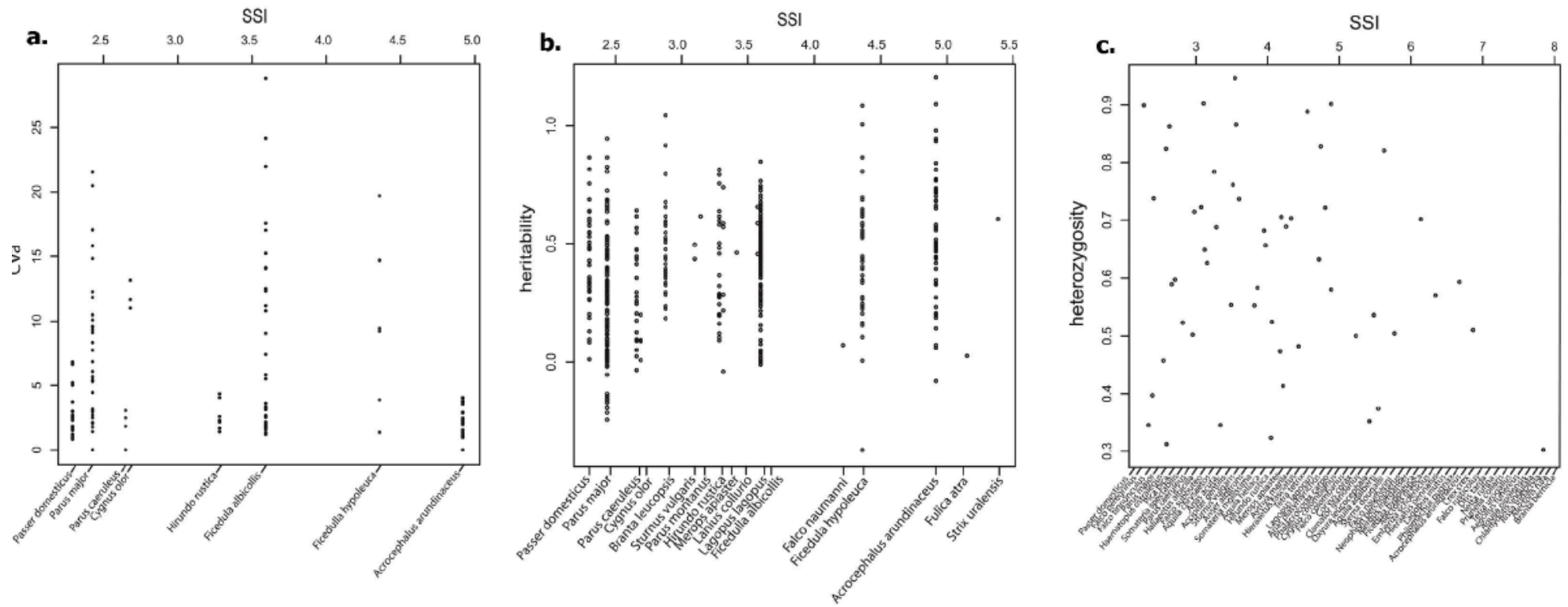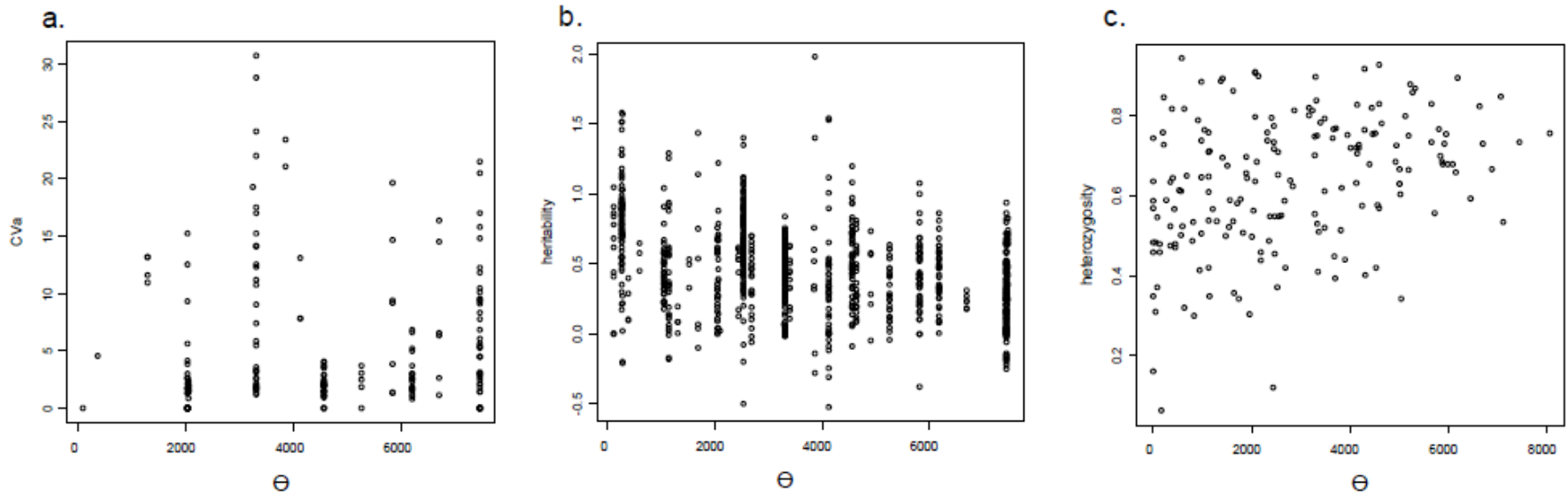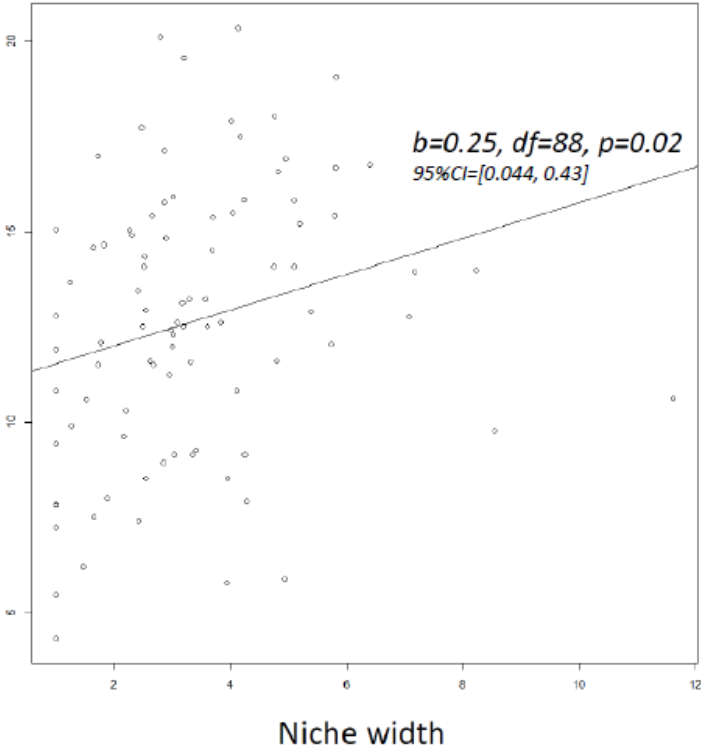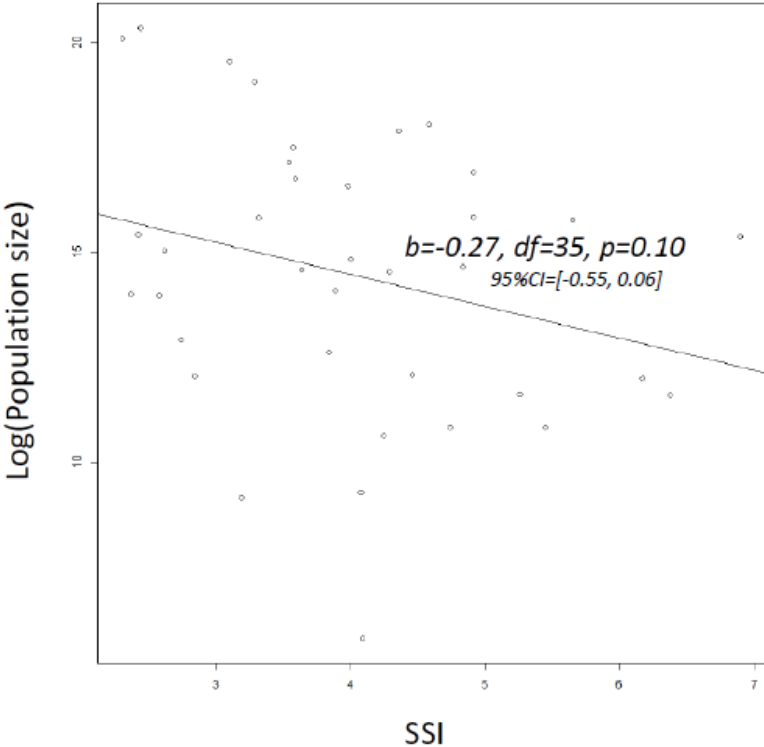

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Fig 2 Distribution of coefficient of additive genetic variance (a), heritability (b), and heterozygosity (c) along a habitat niche width gradient. Each Θ value represents a species.

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S1. Pearson's product-moment correlation of both the Species Specialization Index and Niche width with population size

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S2. Distribution of specialization indexes, SSI and niche width, for available data.
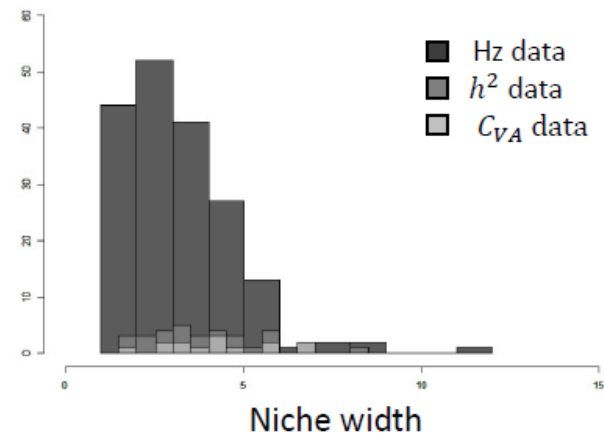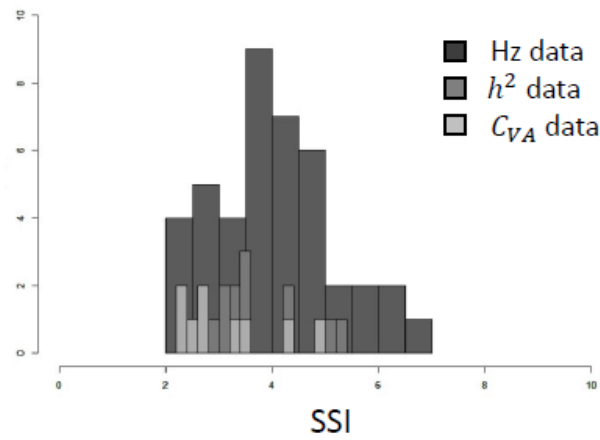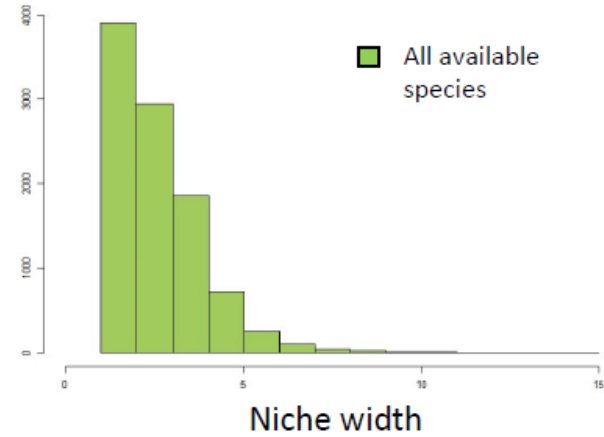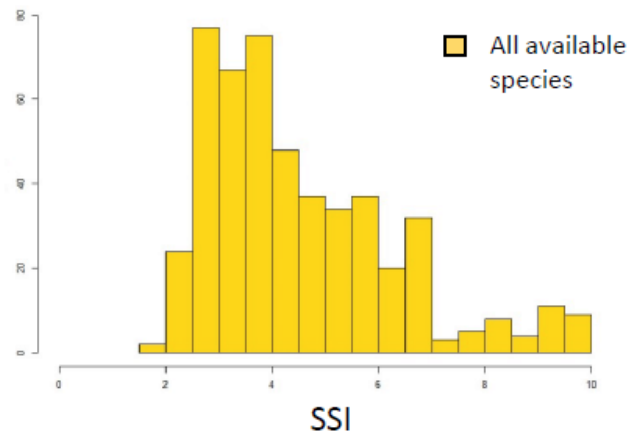
Table S3. List of traits for heritability and coefficient of additive genetic variance data sorted in "life-history" and "morphology" trait categories.

| Life-history (h^2)		
actual egg weight	female first-year recruits	mean chroma (egg colour trait)
actual egg weight adjusted for annual variation	female life span	mean egg size
adult survival probability	female lifetime fledging success	mean egg weight
age at first reproduction	female lifetime reproductive success	mean lightness (egg colour trait)
age at last reproduction	first egg volume	median egg size
anual productivity	hatch date	nr of eggs fledged
arrival date	hatch weight	nr of eggs hatched
breeding time	laying date	number of fledglings
calendar hatching date	laying date elevation	number of nesting attempts per year
clutch size	laying date plasticity	relative hatching date
clutch size adjusted for annual variation	life span	SD chroma (egg colour trait)
delay before breeding	lifetime fledgling production	SD lightness (egg colour trait)
egg breadth	lifetime reproductive success	settling date
egg length	lifetime reproductive success	sex ratio at 6 days old
egg mass	log10-transformed recruiting age	sex ratio at independence
egg shape	longevity	standardized laying date
egg size	male annual fitness	start of wing moult
egg volume	male extra-pair reproductive success	time of laying
elevation of the laying date-temperature reaction norm	male first-year fledging success	total number of eggs laid per year
estimated egg weight	male first-year recruits	total number of young raised to 30 days of age
estimated egg weight adjusted for annual variation	male life span	total number of young raised to 6 days of age
femal annual fitness	male lifetime fledging success	.
female annual fitness	male lifetime reproductive success	.
female extra-pair paternity rate	max chroma (egg colour trait)	.
female first-year fledging success	max lightness (egg colour trait)	.

Morphology (h²)			
Backcolour	culmen depth	head-length poor condition	PC2-bill (excl. Extra pair youngs)
badge size	culmen length	height of white patch	PC2-body
bill depth	culmen width	male bill depth	PC2-body (excl. Extra pair youngs)
bill depth (excl. Extra pair youngs)	Drostian colour	male bill length	skull length
bill length	fat breeding season	male body condition index	tail length
bill length (excl. Extra pair youngs)	fat winter	male body mass	tail white
bill length . fall-spring	feather growth bar width	male nestling mass	tarsus length
bill length . summer	female bill depth	male tarsus length	tarsus length (excl. Extra pair youngs)
bill length at 2 days	female bill length	male wing length	tarsus length . fall-spring
bill width	female body condition index	mate's forehead patch size	tarsus length . summer
bill width (at a depth of 4mm)	female body mass	muscle breeding season	tarsus length at day 10
bill width (excl. Extra pair youngs)	female nestling mass	muscle insertion length left	tarsus length at day 5
bill width . fall-spring	female tarsus length	muscle insertion length right	total badge size (black throat badge; sexual ornament)
bill width . summer	female wing length	muscle winter	UV/bluevsGreen/Red
body condition index	first primary length	nestling mass	UVvsBlue
body mass	flattened wing chord	nestling tarsus length	visible badge size
body mass . fall-spring	forehead patch size	offspring condition	weight
body mass . summer	forehead patch size old	outer tail length	Weight (excl. Extra pair youngs)
body mass at day 10	forehead patch size young	patch heigth	width of white patch
body mass at day 5	forhead patch size of a female's mate	patch width	Wing
Brownness scores	GreensvsRed	PC1-bill	Wing (excl. Extra pair youngs)
Capcolour	head length	PC1-bill (excl. Extra pair youngs)	wing length
central tail length	head size	PC1-body	wing patch size old
Chestcolour	head-length good condition	PC1-body (excl. Extra pair youngs)	wing patch size young
chick condition	head-length normal condition	PC2-bill	wing projection

Life-history (C_{Va})		
age at first reproduction	egg laying date standardized spring temperature 1	lifetime reproductive success
age at last reproduction	egg laying date standardized spring temperature -1	lifetime reproductive success
annual fitness	egg mass	log10-transformed recruiting age
annual reproductive success	female fitness	longevity
breeding time	female mate choice	male extra-pair reproductive success
clutch size	first egg volume	male fitness
clutch size standardized spring temperature 0	first-year fledging success	mean egg weight
clutch size standardized spring temperature 1	first-year recruits	nr of eggs fledged
clutch size standardized spring temperature -1	laying date	nr of eggs hatched
clutch size standardized spring temperature NA	life span	nr of seasons bred
egg laying date	lifetime fledging success	.
egg laying date standardized spring temperature 0	lifetime fledgling production	.

Morphology (C_{Va})		
adult body mass	forehead patch size	SD lightness (egg colour trait)
adult tarsus length	head-length good condition	skull length
bill depth	head-length normal condition	tail length
bill length	head-length poor condition	tarsus length
bill width	max chroma (egg colour trait)	total badge size (black throat badge; sexual ornament)
body mass	max lightness (egg colour trait)	visible badge size
culmen depth	mean chroma (egg colour trait)	weight
culmen length	mean lightness (egg colour trait)	wing length
culmen width	nestling mass	wing patch size
feather growth bar width	patch heigh	wing projection
first primary length	patch width	
fledgling mass	SD chroma (egg colour trait)	
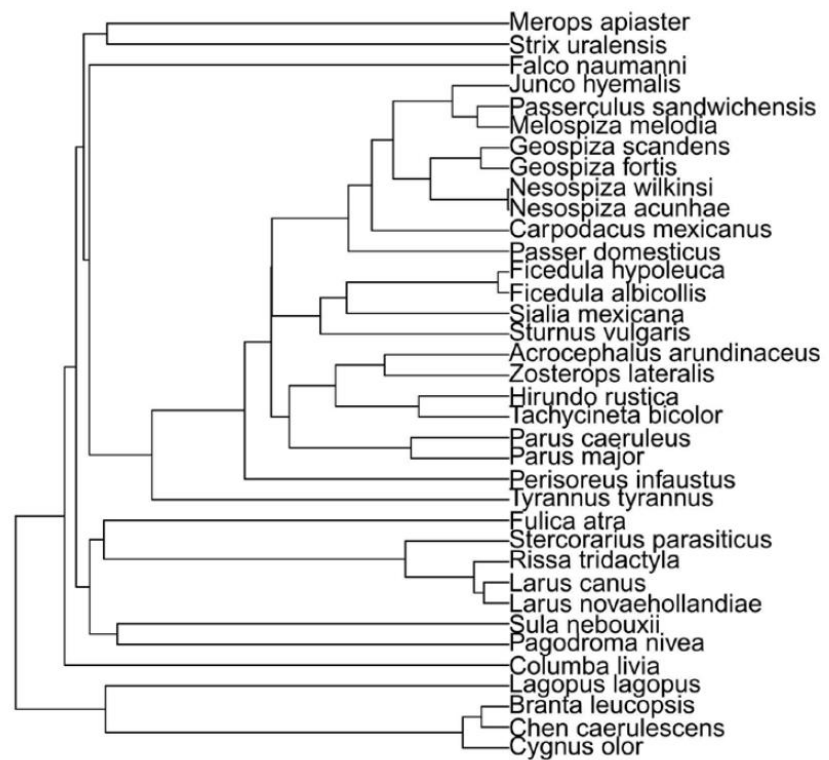
S4.a   **Phylogenetic tree for heritability data**

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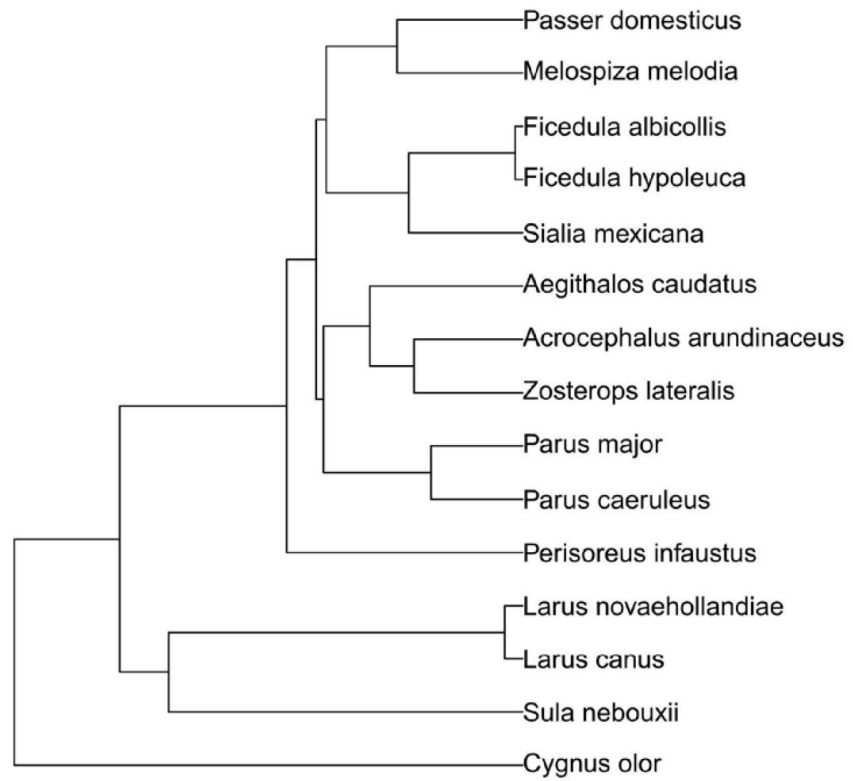
S4.b **Phylogenetic tree for coefficient of additive genetic variance data**

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594 **Table S3** Estimators (Post.mean), confidence intervals (CI) and critical probabilities (Pc) for the fixed and random effects of the three mixed

595 models corresponding to each estimator of evolutionary potential: heritability, CVa and Heterozygosity. **For weakly informative priors.**

	Response var.	Heritability			CVa			Heterozygosity		
	Effect	Post.mean	CI 95%	pMCMC	Post.mean	CI 95%	Pc	Post.mean	CI 95%	pMCMC
Fixed	Intercept	0.050	-0.210/0.309	0.680	9.21	-1.63/20.1	0.088[**]	0.657	0.419/0.887	<10[-5***]
	SSI	0.046	-0.023/0.117	0.139	0.740	-2.24/3.82	0.607	-0.003	-0.047/0.041	0.158
	Type of Trait : morphologique	0.198	0.140/0.256	<10[-5***]	-7.77	-11.28/-4.24	2.10[-5***]			
	Calcul method : regression	0.046	0.005/0.088	0.030[*]	-1.40	-4.36/1.61	0.355			
Random	Phylogeny	0.008	0.001/0.021		13.7	1.01/39.7		0.025	0.000/0.072	
	Population	0.007	0.001/0.014		5.75	1.02/13.53				
	Trait	0.021	0.015/0.027		18.74	8.18/30.12				
	Residual	0.004	0.003/0.006		27.19	19.1/36.2		0.016	0.015/0.031	

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Table S4 Estimators (Post.mean), confidence intervals (CI) and critical probabilities (Pc) for the fixed and random effects of the three mixed

models corresponding to each estimator of evolutionary potential: heritability, CVa and Heterozygosity. For parameter expanded prior.

	Response var.	Heritability			CVa			Heterozygosity		
	Effect	Post.mean	CI 95%	pMCMC	Post.mean	CI 95%	Pc	Post.mean	CI 95%	pMCMC
Fixed	Intercept	0.053	-0.162/0.270	0.579	9.59	-0.194/19.9	0.057.	0.695	0.411/0.980	$<10^{-5***}$
	SSI	0.044	-0.018/0.103	0.136	0.656	--2.05/3.37	0.583	-0.012	-0.078/0.052	0.704
	Type of trait : morphological	0.198	0.142/0.255	$<10^{-5***}$	-7.93	-11.2/-4.49	$<10^{-5***}$			
	Estimation method : regression	0.048	0.007/0.090	0.022^{*}	--1.17	-4.05/1.74	0.426			
Random	Phylogeny	0.004	0.000/0.017		14.8	0.000/55.8		0.007	0.000/0.026	
	Population	0.005	0.000/0.013		2.03	0.000/7.81				
	Trait	0.022	0.015/0.028		19.6	9.03/31.6				
	Résidual	0.004	0.002/0.006		26.6	18.8/35.3		0.052	0.030/0.077	

Fig S7. References for heritability data

Akesson, M., Bensch, S., & Hasselquist, D. (2007). Genetic and phenotypic associations in morphological traits : a long term study of great reed warblers Acrocephalus arundinaceus. Journal of Avian Biology, 38, 58–72. doi:10.1111/j.2007.0908-8857.03669.x

Alatalo, R,Lundberg, A, (1989) Heritability and selection on tarsus length in the Pied Flycatcher (Ficedula hypoleuca). Evolution, 40(3), 574-583.

Alatalo, R. V., Gustafsson, L., & Lundberg, A. (1990). Phenotypic Selection on Heritable Size Traits : Environmental Variance and Genetic Response. The American Naturalist, 135(3), 464–471.

Barbraud . C. (2000). Natural selection on body size traits in a long-lived bird, the snow petrel Pagodroma nivea. Journal of Evolutionary Biology (13). 81–88. Retrieved from http://www.jstor.org/stable/2409649

Björklund, M. (1997). Variation in growth in the blue tit (Parus caeruleus). Journal of Evolutionary Biology, 10, 139 – 155.

Boag . P. T. (1983). The Heritability of External Morphology in Darwin's Ground Finches (Geospiza) on Isla Daphne Major . Galapagos. Evolution . 37(5) . 877.

Bonneaud, C., Sinsheimer, J. S., Richard, M., Chastel, O., & Sorci, G. (2009). Mhc polymorphisms fail to explain the heritability of phytohaemagglutinin-induced skin swelling in a wild passerine. Biology letters, 5(6), 784–7. doi:10.1098/rsbl.2009.0435

Boulinier . T. . Sorci . G. . Monnat . J.-Y. . & Danchin . E. (1997). Parent–offspring regression suggests heritable susceptibility to ectoparasites in a natural population of kittiwake. Journal of Evolutionary Biology . 10(1) . 77. Retrieved from http://apps.webo

Brommer, J. E., Merilä, J., Sheldon, B. C., & Gustafsson, L. (2005). Natural selection and genetic variation for reproductive reaction norms in a wild bird population. Evolution; international journal of organic evolution, 59(6), 1362–71.

Brommer . J. E. . & Rattiste . K. (2008). "Hidden" reproductive conflict between mates in a wild bird population. Evolution; international journal of organic evolution . 62(9) . 2326–33. doi:10.1111/j.1558-5646.2008.00451.x

Caro, S. P., Charmantier, A., Lambrechts, M. M., Blondel, J., Balthazart, J., & Williams, T. D. (2009). Local adaptation of timing of reproduction: females are in the driver's seat. Functional Ecology, 23(1), 172–179. doi:10.1111/j.1365-2435.2008.01486.x

Charmantier, A., & Réale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild ? Molecular Ecology, 14, 2839–2850. doi:10.1111/j.1365-294X.2005.02619.x

Charmantier . A. . Keyser . A. J. . & Promislow . D. E. L. (2007). First evidence for heritable variation in cooperative breeding behaviour. Proceedings. Biological sciences / The Royal Society . 274(1619) . 1757–61. doi:10.1098/rspb.2007.0012

Charmantier, A., Kruuk, L. E. B., & Lambrechts, M. M. (2004). PARASITISM REDUCES THE POTENTIAL FOR EVOLUTION IN A WILD BIRD POPULATION. Evolution, 58(1), 203–206.

Charmantier, A., Perrins, C., McCleery, R. H., & Sheldon, B. C. (2006). Evolutionary response to selection on clutch size in a long-term study of the mute swan. The American naturalist, 167(3), 453–65. doi:10.1086/499378

Cuervo, J.J., Moller, A.P., De Lope, F., (2007), Haematocrit is weakly related to condition in nestling Barn Swallow Hirundo rustica,Ibis,149, 128-134.

Dhondt, A. A. (1982). Heritability of Blue Tit Tarsus Length from Normal and Cross-Fostered Broods. Evolution, 36(2), 418. doi:10.2307/2408064

Duckworth . R. a . & Kruuk . L. E. B. (2009). Evolution of genetic integration between dispersal and colonization ability in a bird. Evolution; international journal of organic evolution . 63(4) . 968–77. doi:10.1111/j.1558-5646.2009.00625.x

Findlay . C. S. . & Cooke . F. (1982). Breeding Synchrony in the Lesser Snow Goose (Anser caerulescens caerulescens). I. Genetic and Environmental Components of Hatch Date Variability and their Effects on Hatch Synchrony. Evolution . 36(2) . 342. doi:10.2307/2

Findlay . C. S. . & Cooke . F. (1983). Genetic and Environmental Components of Clutch Size Variance in a Wild Population of Lesser Snow Geese (Anser caerulescens caerulescens). Evolution . 37(4) . 724–734.

656 Flux . J. E. C. . & Flux . M. M. (1982). Artificial selection and gene flow in wild starlings . Sturnus
657 vulgaris. Naturwissenschaften . 69(2) . 96–97. doi:10.1007/BF00441236
658 Freeman-Gallant . C. . & Rothstein . M. (1999). Apparent heritability of parental care in Savannah
659 Sparrows. Auk . 116(4) . 1132–1136. Retrieved from http://apps.webofknowledge.com/full
660 record.do?product=UA&search mode=CitingArticles&qid=41&SID=N2kchoHKHEHl5ja
661 Frentiu . F. D. . Clegg . S. M. . Blows . M. W. . & Owens . I. P. F. (2007). Large body size in an
662 island-dwelling bird: a microevolutionary analysis. Journal of evolutionary biology . 20(2) . 639–49.
663 doi:10.1111/j.1420-9101.2006.01242.x
664 Garant, D., Sheldon, B. C., & Gustafsson, L. (2004). CLIMATIC AND TEMPORAL EFFECTS ON
665 THE EXPRESSION OF SECONDARY SEXUAL CHARACTERS : GENETIC AND
666 ENVIRONMENTAL COMPONENTS. Evolution, 58(3), 634–644.
667 Garant, D., Hadfield, J. D., Kruuk, L. E. B., & Sheldon, B. C. (2008). Stability of genetic variance and
668 covariance for reproductive characters in the face of climate change in a wild bird population.
669 Molecular ecology, 17(1), 179–88. doi:10.1111/j.1365-2
670 Garant, D., Kruuk, L. E. B., McCleery, R. H., & Sheldon, B. C. (2004). Evolution in a changing
671 environment: a case study with great tit fledging mass. The American naturalist, 164(5), E115–29.
672 doi:10.1086/424764
673 Garant, D., Kruuk, L. E. B., Wilkin, T. a, McCleery, R. H., & Sheldon, B. C. (2005). Evolution driven
674 by differential dispersal within a wild bird population. Nature, 433(7021), 60–5.
675 doi:10.1038/nature03051
676 Gibbs . H. L. (1988). Heritability and Selection on Clutch Size in Darwin's Medium Ground Finches
677 (Geospiza fortis). Evolution . 42(4) . 750–762.
678 Gienapp, P., Postma, E., & Visser, M. E. (2006). WHY BREEDING TIME HAS NOT RESPONDED
679 TO SELECTION FOR EARLIER BREEDING IN A SONGBIRD POPULATION. Evolution, 60(11),
680 2381–2388.
681 Gosler, A. G., & Harper, D. G. C. (2000). Assessing the heritability of body condition in birds: a
682 challenge exemplified by the great tit Parus major L. (Aves). Biological Journal of the Linnean
683 Society, 71(1), 103–117.
684 Grant . P. R. . & Grant . B. R. (1995). Predicting Microevolutionary Responses to Directional
685 Selection on Heritable Variation. Evolution . 49(2) . 241. doi:10.2307/2410334
686 Griffith, SC Owens, IPF Burke, T. (1999). Environmental determination of a sexually selected trait.
687 Nature, 400(6742), 358–560. doi:10.1038/22536
688 Gustafsson, L. (1986). Lifetime Reproductive Success and Heritability: Empirical Support for Fisher's
689 Fundamental Theorem. The American Naturalist, 128(5), 761. doi:10.1086/284601
690 Hadfield, J.D, Nutall,A., Osorio,D., Owens, I.P.F., (2006), Testing the phenotypic gambit: phenotypic,
691 genetic and environmental correlations of colour, European society for evolutionary biology, 20, 549-
692 557.
693 Hadfield, J.D., Owens,I.P.F., (2006), strong environmental determination of carotenoid-based plumage
694 trait is not mediated by carotenoid availability, european society for evolutionary biology, 19, 1104-
695 1114.
696 Hasselquist, D., Bensch, S., & Schantz, T. V. (1995). Estimating cuckoldry in birds : the heritability
697 method and DNA fingerprinting give different results. Oikos, 72(2), 173–178.
698 Hegyi, G., Herényi, M., Wilson, A. J., Garamszegi, L. Z., Rosivall, B., Eens, M., & Török, J. (2010).
699 Breeding experience and the heritability of female mate choice in collared flycatchers. PloS one,
700 5(11), e13855. doi:10.1371/journal.pone.0013855
701 Husby, A., Hille, S. M., & Visser, M. E. (2011). Testing mechanisms of Bergmann's rule: phenotypic
702 decline but no genetic change in body size in three passerine bird populations. The American
703 naturalist, 178(2), 202–13. doi:10.1086/660834
704 Jakober, H., Stauber,W., (2000) Werden die neutöter (Lanius collurio) kleiner?, J.Ornithol, 141, 408-
705 417.
706 Jensen, H., Steinsland, I., Ringsby, T. H., & Saether, B.-E. (2008). Evolutionary dynamics of a sexual
707 ornament in the house sparrow (Passer domesticus): the role of indirect selection within and between
708 sexes. Evolution;

709 Jensen, H., Saether, B.-E., Ringsby, T. H., Tufto, J., Griffith, S. C., & Ellegren, H. (2003). Sexual
710 variation in heritability and genetic correlations of morphological traits in house sparrow (Passer
711 domesticus). Journal of Evolutionary Biology, 16(6),
712 Johnson . S. G. . & Johnston . R. F. (1990). Environmental variation and quantitative genetic
713 parameters in the feral pigeon . Columba livia. Biological Journal of the Linnean Society . 40(4) .
714 321–332. doi:10.1111/j.1095-8312.1990.tb00542.x
715 Keller . L. F. . Grant . P. R. . Grant . B. R. . & Petren . K. (2001). Heritability of morphological traits
716 in Darwin ' s Finches : misidenti ® ed paternity and maternal effects. Heredity . 87 . 325–336.
717 Kim . S.-Y. . Drummond . H. . Torres . R. . & Velando . a. (2011). Evolvability of an avian life history
718 trait declines with father's age. Journal of evolutionary biology . 24(2) . 295–302. doi:10.1111/j.1420-
719 9101.2010.02165.x
720 Kontiainen, P., Brommer, J.E., Karell, P., Pieieäinen, H., (2007), Heritability, plasticity and
721 canalization of Ural owlegg size in a cyclic environment, Journal of Evolutionary Biology, 21, 88-97.
722 Kvalnes, T., Ringsby, T.H., Jensen, H., Saether, B.-E., (2013) Correlates of egg size variation in a
723 population of house sparrow Passer domesticus, Oecologia, 171(2), 391-402.
724 Larsson, K., & Forslund, P. (1992). Genetic and Social Inheritance of Body and Egg Size in the
725 Barnacle Goose (Branta leucopsis). Evolution, 46(1), 235–244.
726 Larsson . K. . Rattiste . K. . & Lilleleht . V. (1997). Heritability of head size in the common gull Larus
727 canus in relation to environmental conditions during offspring growth. Heredity . 79 . 201–207.
728 Larsson, K. (1993). Inheritance of body size in the Barnacle Goose under different environmental
729 conditions. Journal of Evolutionary Biology, 6(2), 195–208
730 Lessells . C. M. . Cooke . F. . & Rockwell . R. F. (1989). Is there a trade-off between egg weight and
731 clutch size in wild Lesser Snow Geese (Anser c . caerulescens)? Journal of Evolutionary Biology . 2 .
732 457–472.
733 Lessells, C. M., & Ovenden, G. N. (1989). Heritability of Wing Length and Weight in European Bee-
734 Eaters (Merops apiaster). The Condor, 91(1), 210. doi:10.2307/1368167
735 Liedvogel, M., Cornwallis, C. K., Sheldon, B.C., (2012) Integrating candidate gene and quantitative
736 genetic approaches to understand variation in timing of breeding in wild tit populations, Journal of
737 evolutionary Biology, 25(5), 813-823
738 Lifjeld, T., Slagsvold, T., (1990) Manipulations of male parental investment in polygynous pied
739 flycatchers, Ficedula hypoleuca, Behavioral Ecology, 1(1), 48-54.
740 McCleery, R. H., Pettifor, R. a, Armbruster, P., Meyer, K., Sheldon, B. C.,
741
742
743

744 ## Fig S8. List of References for C_{Va} data.

745 Akesson, M., Bensch, S., Hasselquist, D., Tarka, M., & Hansson, B. (2008). Estimating heritabilities and
746 genetic correlations: comparing the "animal model" with parent-offspring regression using data from
747 a natural population. PloS one, 3(3), e1739. doi:1
748 Akesson, M., Bensch, S., & Hasselquist, D. (2007). Genetic and phenotypic associations in
749 morphological traits : a long term study of great reed warblers Acrocephalus arundinaceus. Journal of
750 Avian Biology, 38, 58–72. doi:10.1111/j.2007.0908-8857.03669.x
751 MacColl, A. D. C., & Hatchwell, B. J. (2003). HERITABILITY OF PARENTAL EFFORT IN A PASSERINE BIRD.
752 Evolution, 57(9), 2191. Retrieved from
753 http://apps.webofknowledge.com/full_record.do?product=UA&search_mode
754 =GeneralSearch&qid=3&SID=U2A@flBJ8oI6n889kJf&page
755 Charmantier, A., Kruuk, L. E. B., & Lambrechts, M. M. (2004). PARASITISM REDUCES THE POTENTIAL
756 FOR EVOLUTION IN A WILD BIRD POPULATION. Evolution, 58(1), 203–206.
757 Nilsson, J., Akesson, M., & Nilsson, J. F. (2009). Heritability of resting metabolic rate in a wild
758 population of blue tits. Journal of evolutionary biology, 22(9), 1867–74. doi:10.1111/j.1420-
759 9101.2009.01798.x

760 Charmantier, A., Perrins, C., McCleery, R. H., & Sheldon, B. C. (2006). Quantitative genetics of age at
761 reproduction in wild swans: support for antagonistic pleiotropy models of senescence. Proceedings
762 of the National Academy of Sciences of the United States.
763 Charmantier, A., Keyser, A. J., & Promislow, D. E. L. (2007). First evidence for heritable variation in
764 cooperative breeding behaviour. Proceedings. Biological sciences / The Royal Society, 274(1619),
765 1757–61. doi:10.1098/rspb.2007.0012
766 Charmantier, A., Perrins, C., McCleery, R. H., & Sheldon, B. C. (2006). Evolutionary response to
767 selection on clutch size in a long-term study of the mute swan. The American naturalist, 167(3), 453–
768 65. doi:10.1086/499378 Merilä, J., & Sheldon, B. (2000). Lifetime Reproductive Success and
769 Heritability in Nature. The American naturalist, 155(3), 301–310. doi:10.1086/303330
770 Qvarnström, A., Brommer, J. E., & Gustafsson, L. (2006). Testing the genetics underlying the co-
771 evolution of mate choice and ornament in the wild. Nature, 441(7089), 84–6.
772 doi:10.1038/nature04564
773 Garant, D., Sheldon, B. C., & Gustafsson, L. (2004). CLIMATIC AND TEMPORAL EFFECTS ON THE
774 EXPRESSION OF SECONDARY SEXUAL CHARACTERS : GENETIC AND ENVIRONMENTAL COMPONENTS.
775 Evolution, 58(3), 634–644.
776 Tschirren, B., Sendecka, J., Groothuis, T. G. G., Gustafsson, L., & Doligez, B. (2009). Heritable variation
777 in maternal yolk hormone transfer in a wild bird population. The American naturalist, 174(4), 557–64.
778 doi:10.1086/605379
779 Morales, J., Kim, S.-Y., Lobato, E., Merino, S., Tomás, G., Martínez-de la Puente, J., & Moreno, J.
780 (2010). On the heritability of blue-green eggshell coloration. Journal of evolutionary biology, 23(8),
781 1783–91. doi:10.1111/j.1420-9101.2010.02044.x
782 Brommer, J. E., Rattiste, K., & Wilson, a. (2010). The rate of ageing in a longlived bird is not heritable.
783 Heredity, 104(4), 363–70. doi:10.1038/hdy.2009.125
784 Larsson, K., Rattiste, K., & Lilleleht, V. (1997). Heritability of head size in the common gull Larus canus
785 in relation to environmental conditions during offspring growth. Heredity, 79, 201–207.
786 Teplitsky, C., Mills, J. a, Yarrall, J. W., & Merilä, J. (2009). Heritability of fitness components in a wild
787 bird population. Evolution; international journal of organic evolution, 63(3), 716–26.
788 doi:10.1111/j.1558-5646.2008.00581.x
789 Reid, J. M., Arcese, P., Sardell, R. J., & Keller, L. F. (2011). Additive genetic variance, heritability, and
790 inbreeding depression in male extra-pair reproductive success. The American naturalist, 177(2), 177–
791 87.
792 doi:10.1086/657977
793 Husby, A., Hille, S. M., & Visser, M. E. (2011). Testing mechanisms of Bergmann's rule: phenotypic
794 decline but no genetic change in body size in three passerine bird populations. The American
795 naturalist, 178(2), 202–13.
796 doi:10.1086/660834
797 Husby, A., Nussey, D. H., Visser, M. E., Wilson, A. J., Sheldon, B. C., & Kruuk, L. E. B. (2010).
798 Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (Parus major)
799 populations. Evolution; international journal of organic
800 Garant, D., Hadfield, J. D., Kruuk, L. E. B., & Sheldon, B. C. (2008). Stability of genetic variance and
801 covariance for reproductive characters in the face of climate change in a wild bird population.
802 Molecular ecology, 17(1), 179–88. doi:10.1111/j.1365-2
803 McCleery, R. H., Pettifor, R. a, Armbruster, P., Meyer, K., Sheldon, B. C., & Perrins, C. M. (2004).
804 Components of variance underlying fitness in a natural population of the great tit Parus major. The
805 American naturalist, 164(3), E62–
806 72. doi:10.1086/42266
807 Garant, D., Kruuk, L. E. B., Wilkin, T. a, McCleery, R. H., & Sheldon, B. C. (2005).
808 Evolution driven by differential dispersal within a wild bird population. Nature, 433(7021), 60–5.
809 doi:10.1038/nature03051

810   Garant, D., Kruuk, L. E. B., McCleery, R. H., & Sheldon, B. C. (2004). Evolution in a changing
811   environment: a case study with great tit fledging mass. The American naturalist, 164(5), E115–29.
812   doi:10.1086/424764
813   Jensen, H., Steinsland, I., Ringsby, T. H., & Saether, B.-E. (2008). Evolutionary dynamics of a sexual
814   ornament in the house sparrow (Passer domesticus): the role of indirect selection within and
815   between sexes. Evolution; international journal of organic
816   Jensen, H., Saether, B.-E., Ringsby, T. H., Tufto, J., Griffith, S. C., & Ellegren, H.
817   (2003). Sexual variation in heritability and genetic correlations of morphological traits in house
818   sparrow (Passer domesticus). Journal of Evolutionary Biology, 16(6),
819   Gienapp, P., & Merilä, J. (2010). Genetic and environmental effects on a condition-dependent trait:
820   feather growth in Siberian jays. Journal of evolutionary biology, 23(4), 715–23. doi:10.1111/j.1420-
821   9101.2010.01949.x
822   Duckworth, R. a, & Kruuk, L. E. B. (2009). Evolution of genetic integration between dispersal and
823   colonization ability in a bird. Evolution; international journal of organic evolution, 63(4), 968–77.
824   doi:10.1111/j.15585646.2009.00625.x
825   Kim, S.-Y., Drummond, H., Torres, R., & Velando, a. (2011). Evolvability of an avian life history trait
826   declines with father's age. Journal of evolutionary biology, 24(2), 295–302. doi:10.1111/j.1420-
827   9101.2010.02165.x
828   Frentiu, F. D., Clegg, S. M., Blows, M. W., & Owens, I. P. F. (2007). Large body size in an island-
829   dwelling bird: a microevolutionary analysis. Journal of evolutionary biology, 20(2), 639–49.
830   doi:10.1111/j.1420-9101.2006.01242.x
831
832
833
834
835
836
837
838
839
840
841
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846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861

Fig S9. List of references from Evans & Sheldon (2008)

Abbott, C. L., and M. C. Double. 2003. Genetic structure, conservation genetics and evidence of speciation by range expansion in shy and white-capped albatrosses. Molecular Ecology 12: 2953-2962.

Adcock, G. J., and R. A. Mulder. 2002. Polymorphic microsatellite loci for paternity analysis in the Madagascar paradise flycatcher (*Terpsiphone mutata* : Aves). Molecular Ecology Notes 2: 287-289.

Adcock, G. J., N. E. Langmore, R. A. Mulder, and R. M. Kilner. 2005. Microsatellite loci for population and behavioural studies of Horsfield's bronzecuckoo (*Chalcites basalis* : Aves). Molecular Ecology Notes 5: 619-621.

Akst, E. P., P. D. Boersma, and R. C. Fleischer. 2002. A comparison of genetic diversity between the Galapagos Penguin and the Magellanic Penguin. Conservation Genetics 3: 375-383.

Asai, S., C. Shimoda, I. Nishiumi, K. Eguchi, and S. Yamagishi. 1999. Isolation of microsatellite loci for paternity testing in the rufous vanga *Schetba rufa*. Molecular Ecology 8: 513-514.

Bardeleben, C. 2004. Isolation of polymorphic tetranucleotide microsatellite markers for the little greenbul (*Andropadus virens*). Molecular Ecology Notes 4: 698-700.

Bardeleben, C., and M. M. Gray. 2005. Isolation of polymorphic tetranucleotide microsatellite markers for the pygmy kingfisher *Ceyx picta*. Molecular Ecology Notes 5: 478-480.

Bardeleben, C., R. L. Moore, J. A. Nicholls, J. J. Austin, and T. E. Robson. 2005. Isolation of polymorphic tetranucleotide microsatellite markers in the satin bowerbird, *Ptilonorhynchus violaceus*. Molecular Ecology Notes 5: 305-307.

Bardeleben, C., M. M. Gray, J. Austin, and I. A. do Rosario. 2005. Isolation of polymorphic tetranucleotide microsatellite for the large-billed scrubwren (*Sericomis magnirostris*). Molecular Ecology Notes 5: 143-145.

Bardeleben, C., K. S. Delaney, J. Austin, and R. L. Moore. 2005. Isolation of polymorphic tetranucleotide microsatellite markers for the grey-headed robin (*Poecilodryas albispecularis*). Molecular Ecology Notes 5: 146-148.

Beck, N., R. Peakall, and R. Heinsohn. 2003. Isolation and characterization of polymorphic microsatellite markers in the white-winged chough (*Corcorax melanorhamphos*). Molecular Ecology Notes 3: 586-588.

Benson, D. P. 2002. Low extra-pair paternity in White-tailed Ptarmigan. Condor 104:192-197.

Blanchard, L., and J. S. Quinn. 2001. The characterization of microsatellite loci in the communally breeding smooth-billed ani (*Crotophaga ani*). Molecular Ecology Notes 1: 152-154.

Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, J. D. Brawn, and K. N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the Greater Prairie Chicken. Conservation Biology 12: 836-843.

Bouzat, J. L., and K. Johnson. 2004. Genetic structure among closely spaced leks in a peripheral population of lesser prairie-chickens. Molecular Ecology 13: 499505.

Bulgin, N. L., H. L. Gibbs, P. Vickery, and A. J. Baker. 2003. Ancestral polymorphisms in genetic markers obscure detection of evolutionarily distinct populations in the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*). Molecular Ecology 12: 831-844.

Burg, T. M. 1999. Isolation and characterization of microsatellites in albatrosses. Molecular Ecology 8: 338-341.

Burg, T. M., A. J. Gaston, K. Winker, and V. L. Friesen. 2005. Rapid divergence and postglacial colonization in western North American Steller's jays (*Cyanocitta stelleri*). Molecular Ecology 14: 3745-3755.

Burgess, S. L., and R. C. Fleischer. 2006. Isolation and characterization of polymorphic microsatellite loci in the Hawaiian flycatcher, the elepaio (*Chasiempis sandwichensis*). Molecular Ecology Notes 6: 14-16.

912 Busch, J. D., T. E. Katzner, E. Bragin, and P. Keim. 2005. Tetranucleotide microsatellites for aquila and
913 haliaeetus eagles. Molecular Ecology Notes 5: 3941.
914 Byers, B. E., H. L. Mays, I. R. K. Stewart, and D. F. Westneat. 2004. Extrapair paternity increases
915 variability in male reproductive success in the chestnutsided warbler (*Dendroica pensylvanica*), a
916 socially monogamous songbird. Auk 121: 788-795.
917 Cabe, P. R., and K. E. Marshall. 2001. Microsatellite loci from the house wren (*Troglodytes aedon*).
918 Molecular Ecology Notes 1: 155-156.
919 Caizergues, A., O. Ratti, P. Helle, L. Rotelli, L. Ellison, and J. Y. Rasplus. 2003. Population genetic
920 structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. Molecular
921 Ecology 12: 2297-2305.
922 Caizergues, A., A. Bernard-Laurent, J. F. Brenot, L. Ellison, and J. Y. Rasplus. 2003. Population genetic
923 structure of rock ptarmigan *Lagopus mutus* in Northern and Western Europe. Molecular Ecology 12:
924 2267-2274.
925 Caparroz, R., C. Y. Miyaki, and A. J. Baker. 2003. Characterization of microsatellite loci in the Blue-
926 and-gold Macaw, *Ara ararauna* (Psittaciformes : Aves). Molecular Ecology Notes 3: 441-443.
927 Cathey, J. C., J. A. DeWoody, and L. M. Smith. 1998. Microsatellite markers in Canada geese (*Branta
928 canadensis*). Journal of Heredity 89: 173-175.
929 Chbel, F., D. Broderick, Y. Idaghdour, A. Korrida, and P. McCormick. 2002. Characterization of 22
930 microsatellites loci from the endangered Houbara bustard (*Chlamydotis undulata undulata*).
931 Molecular Ecology Notes 2: 484-487.
932 Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable
933 isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's
934 warbler (*Wilsonia pusilla*). Molecular Ecology 12: 819-830.
935 Dasmahapatra, K. K., C. M. Lessells, A. C. Mateman, and W. Amos. 2004. Microsatellite loci in the
936 European bee-eater, *Merops apiaster*. Molecular Ecology Notes 4: 500-502.
937 Dawson, D. A., O. Hanotte, C. Greig, I. R. K. Stewart, and T. Burke. 2000. Polymorphic microsatellites
938 in the blue tit *Parus caeruleus* and their crossspecies utility in 20 songbird families. Molecular Ecology
939 9: 1941-1944.
940 Dawson, D. A., F. M. Hunter, J. Pandhal, R. Buckland, A. Parham, I. L. Jones, M.
941 Bradshaw, R. Jehle, and T. Burke. 2005. Assessment of 17 new whiskered auklet (*Aethia pygmaea*)
942 microsatellite loci in 42 seabirds identifies 5-15 polymorphic markers for each of nine Alcinae species.
943 Molecular Ecology Notes 5: 289-297. Delaney, K. S., and R. K. Wayne. 2005. Adaptive units for
944 conservation:
945 Population distinction and historic extinctions in the Island Scrub-Jay.
946 Conservation Biology 19: 523-533.
947 Denk, A. G., B. Gautschi, K. Carter, and B. Kempenaers. 2004. Seven polymorphic microsatellite loci
948 for paternity assessment in the mallard (*Anas platyrhynchos*). Molecular Ecology Notes 4: 506-508.
949 Doerr, E. D. 2005. Characterization of microsatellite loci in the brown treecreeper (*Climacteris
950 picumnus*) and cross-species amplification in the white-throated treecreeper (*Cormobates
951 leucophaeus*). Molecular Ecology Notes 5: 654-656.
952 Dowling, D. K., J. Adcock, and R. A. Mulder. 2003. Novel polymorphic microsatellite markers for
953 paternity analysis in the red-capped robin (*Petroica goodenovii* : Aves). Molecular Ecology Notes 3:
954 517-519.
955 Duval, E. H., and K. J. Nutt. 2005. Isolation and characterization of polymorphic microsatellite loci in
956 the lance-tailed manakin (*Chiroxiphia lanceolata*). Molecular Ecology Notes 5: 112-114.
957 Eggert, L. S., and R. C. Fleischer. 2004. Isolation of polymorphic microsatellite loci in the Hawaii
958 amakihi (*Hemignathus virens*) and their use in other honeycreeper species. Molecular Ecology Notes
959 4: 725-727.
960 Estoup, A., and S. M. Clegg. 2003. Bayesian inferences on the recent island colonization history by the
961 bird *Zosterops lateralis lateralis*. Molecular Ecology 12: 657-674.
962 Fields, R. L., and K. T. Scribner. 1997. Isolation and characterization of novel waterfowl microsatellite
963 loci: Cross-species comparisons and research applications. Molecular Ecology 6: 199-202.

964 Francisco, M. R., P. M. Galetti, and L. Gibbs. 2004. Isolation and characterization of microsatellite loci
965 in the blue manakin, *Chiroxiphia caudata* (Aves, Pipridae). Molecular Ecology Notes 4: 758-760.
966 Galbusera, P., M. Githiru, L. Lens, and E. Matthysen. 2004. Genetic equilibrium despite habitat
967 fragmentation in an Afrotropical bird. Molecular Ecology 13: 1409-1421.
968 Gautschi, B., I. Tenzer, J. P. Muller, and B. Schmid. 2000. Isolation and characterization of
969 microsatellite loci in the bearded vulture (*Gypaetus barbatus*) and cross-amplification in three Old
970 World vulture species. Molecular Ecology 9: 2193-2195.
971 Gautschi, B., M. K. Arter, R. E. Husi, W. Wettstein, and B. Schmid. 2002. Isolation and characterization
972 of microsatellite loci in the globally endangered Corncrake, *Crex crex* Linne. Conservation Genetics 3:
973 451-453.
974 Gay, L., P. D. Du Rau, J. Y. Mondain-Monval, and P. A. Crochet. 2004.
975 Phylogeography of a game species: the red-crested pochard (*Netta rufina*) and consequences for its
976 management. Molecular Ecology 13: 1035-1045.
977 Gibbs, H. L., L. M. Tabak, and K. Hobson. 1999. Characterization of microsatellite DNA loci for a
978 neotropical migrant songbird, the Swainson's thrush (*Catharus ustulatus*). Molecular Ecology 8: 1551-
979 1552.
980 Gibbs, H. L., R. J. G. Dawson, and K. A. Hobson. 2000. Limited differentiation in microsatellite DNA
981 variation among northern populations of the yellow warbler: evidence for male-biased gene flow?
982 Molecular Ecology 9: 2137-2147.
983 Goetz, J. E., K. P. McFarland, and C. C. Rimmer. 2003. Multiple paternity and multiple male feeders in
984 Bicknell's Thrush (*Catharus bicknelli*). Auk 120: 10441053.
985 Gonzalez, E. G., A. M. Castilla, and R. Zardoya. 2005. Novel polymorphic microsatellites for the red-
986 legged partridge (*Alectoris rufa*) and cross-species amplification in Alectoris graeca. Molecular
987 Ecology Notes 5: 449-451.
988 Grant, P. R., B. R. Grant, J. A. Markert, L. F. Keller, and K. Petren. 2004. Convergent evolution of
989 Darwin's finches caused by introgressive hybridization and selection. Evolution 58: 1588-1599.
990 Griffith, S. C., I. R. K. Stewart, D. A. Dawson, I. P. F. Owens, and T. Burke. 1999. Contrasting levels of
991 extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is
992 there an 'island effect'? Biological Journal of the Linnean Society 68: 303-316.
993 Guay, P. J., and R. A. Mulder. 2005. Isolation and characterization of microsatellite markers in musk
994 duck (*Biziura lobata* : Aves), and their application to other waterfowl species. Molecular Ecology
995 Notes 5: 249-252. Haavie, J., G. P. Saetre, and T. Moum. 2000. Discrepancies in population
996 differentiation at microsatellites, mitochondrial DNA and plumage colour in the pied flycatcher -
997 inferring evolutionary processes. Molecular Ecology 9: 11371148.
998 Hale, A. M., and C. R. Hughes. 2003. Characterization of polymorphic microsatellite loci in a
999 neotropical wood-quail, *Odontophorus leucolaemus*. Molecular Ecology Notes 3: 508-510.
1000 Hamao, S., and D. S. Saito. 2005. Extrapair fertilization in the black-browed reed warbler
1001 (*Acrocephalus bistrigiceps*): Effects on mating status and nesting cycle of cuckolded and cuckolder
1002 males. Auk 122: 1086-1096.
1003 Hammond, E. L., A. J. Lymbery, G. B. Martin, D. Groth, and J. D. Wetherall. 2002. Microsatellite
1004 analysis of genetic diversity in wild and farmed emus (Dromaius *novaehollandiae*). Journal of
1005 Heredity 93: 376-380.
1006 Hanotte, O., C. Zanon, A. Pugh, C. Greig, A. Dixon, and T. Burke. 1994. Isolation and Characterization
1007 of Microsatellite Loci in a Passerine Bird - the Reed Bunting *Emberiza schoeniclus*. Molecular Ecology
1008 3: 529-530.
1009 Hansson, B., H. Westerdahl, D. Hasselquist, M. Akesson, and S. Bensch. 2004. Does linkage
1010 disequilibrium generate heterozygosity-fitness correlations in great reed warblers? Evolution 58:
1011 870-879.
1012 Hasegawa, O., Y. Ishibashi, and S. Abe. 2000. Isolation and characterization of microsatellite loci in
1013 the red-crowned crane *Grus japonensis*. Molecular Ecology 9: 1677-1678.
1014 Hasegawa, O., Y. Ishibashi, and S. Abe. 2005. Polymorphic microsatellite DNA markers for the
1015 rhinoceros auklet (*Cerorhinca monocerata*). Molecular Ecology Notes 5: 637-638.

1016   Hawley, D. M. 2005. Isolation and characterization of eight microsatellite loci from the house finch
1017   (*Carpodacus mexicanus*). Molecular Ecology Notes 5: 443445.
1018   Hille, S. M., M. Nesje, and G. Segelbacher. 2003. Genetic structure of kestrel populations and
1019   colonization of the Cape Verde archipelago. Molecular Ecology 12: 2145-2151.
1020   Hsu, Y.-C., Severinghaus, L. L., Lin, Y.-S. & Li, S.-H. 2003. Isolation and characterization of
1021   microsatellite DNA markers from the Lanyu scops owl (*Otus elegans botelensis*). Molecular Ecology
1022   Notes 3: 595-597.
1023   Huang, Y. J., C. S. Chen, and S. H. Li. 2004. Polymorphic tetranucleotide microsatellite loci in the
1024   Hwamei (*Garrulax canorus canorus*) (Timaliidae).
1025   Molecular Ecology Notes 4: 170-172.
1026   Hughes, C. R., and D. M. Deloach. 1997. Developing microsatellites when they are rare: Trinucleotide
1027   repeat loci in the northern mockingbird *Mimus polyglottos*. Molecular Ecology 6: 1099-1102.
1028   Hughes, C. R., and T. R. Robinson. 2001. Characterization of microsatellite loci developed for song
1029   wrens *Cyphorhinus phaeocephalus*. Molecular Ecology Notes 1: 165-167.
1030   Hughes, J. M., P. B. Mather, A. Toon, J. Ma, I. Rowley, and E. Russell. 2003. High levels of extra-group
1031   paternity in a population of Australian magpies *Gymnorhina tibicen*: evidence from microsatellite
1032   analysis. Molecular Ecology 12: 3441-3450.
1033   Ishibashi, Y., O. Mikami, and S. Abe. 2000. Isolation and characterization of microsatellite loci in the
1034   Japanese marsh warbler *Locustella pryeri*. Molecular Ecology 9: 373-375.
1035   Jeffery, K. J., L. F. Keller, P. Arcese, and M. W. Bruford. 2001. The development of microsatellite loci
1036   in the song sparrow, *Melospiza melodia* (Aves) and genotyping errors associated with good quality
1037   DNA. Molecular Ecology Notes 1: 11-13.
1038   Ji, Y. J., Y. D. Liu, C. Q. Ding, and D. X. Zhang. 2004. Eight polymorphic microsatellite loci for the
1039   critically endangered crested ibis, *Nipponia nippon* (Ciconiiformes : Threskiornithidae). Molecular
1040   Ecology Notes 4: 615-617.
1041   Johnson, P. C. D., M. K. Fowlie, and W. Amos. 2005. Isolation of microsatellite loci from the common
1042   buzzard, *Buteo buteo* (Aves : Accipitridae). Molecular Ecology Notes 5: 208-211.
1043   King, T. L., M. S. Eackles, A. P. Henderson, C. I. Bocetti, D. Currie, and J. M. Wunderle. 2005.
1044   Microsatellite DNA markers for delineating population
1045   structure and kinship among the endangered Kirtland's warbler (*Dendroica kirtlandii*). Molecular
1046   Ecology Notes 5: 569-571.
1047   Koopman, M. E., N. A. Schable, and T. C. Glenn. 2004. Development and optimization of
1048   microsatellite DNA primers for boreal owls (*Aegolius funereus*). Molecular Ecology Notes 4: 376-378.
1049   Kraaijeveld, K., P. J. Carew, T. Billing, G. J. Adcock, and R. A. Mulder. 2004. Extra-pair paternity does
1050   not result in differential sexual selection in the mutually ornamented black swan (*Cygnus atratus*).
1051   Molecular Ecology 13:
1052   1625-1633.
1053   Kretzmann, M. B., N. Capote, B. Gautschi, J. A. Godoy, J. A. Donazar, and J. J. Negro. 2003. Genetically
1054   distinct island populations of the Egyptian vulture (*Neophron percnopterus*). Conservation Genetics 4:
1055   697-706.
1056   Lambert, D. M., T. King, L. D. Shepherd, A. Livingston, S. Anderson, and J. L. Craig. 2005. Serial
1057   population bottlenecks and genetic variation: Translocated populations of the New Zealand
1058   Saddleback (*Philesturnus carunculatus rufusater*). Conservation Genetics 6: 1-14.
1059   Latch, E. K., E. J. Smith, and O. E. Rhodes. 2002. Isolation and characterization of microsatellite loci in
1060   wild and domestic turkeys (*Meleagris gallopavo*). Molecular Ecology Notes 2: 176-178.
1061   Li, S. H., Y. J. Huang, and J. L. Brown. 1997. Isolation of tetranucleotide microsatellites from the
1062   Mexican jay *Aphelocoma ultramarina*. Molecular Ecology 6: 499-501.
1063   Lieckfeldt, D., A. Schmidt, and C. Pitra. 2001. Isolation and characterization of microsatellite loci in
1064   the great bustard, *Otis tarda*. Molecular Ecology Notes 1: 133-134.
1065   Loyau, A., B. Moureau, M. Richard, P. Christe, P. Heeb, and G. Sorci. 2005. Cross-amplification of
1066   polymorphic microsatellites reveals extra-pair paternity and brood parasitism in *Sturnus vulgaris*.
1067   Molecular Ecology Notes 5: 135-139.

1068   Maak, S., K. Wimmers, S. Weigend, and K. Neumann. 2003. Isolation and characterization of 18
1069   microsatellites in the Peking duck (*Anas platyrhynchos*) and their application in other waterfowl
1070   species. Molecular Ecology Notes 3: 224-227.
1071   MacDougall-Shackleton, E. A., and S. A. MacDougall-Shackleton. 2001. Cultural and genetic evolution
1072   in mountain white-crowned sparrows: Song dialects are associated with population structure.
1073   Evolution 55: 2568-2575.
1074   Mank, J. E., J. E. Carlson, and M. C. Brittingham. 2004. A century of hybridization: Decreasing genetic
1075   distance between American black ducks and mallards. Conservation Genetics 5: 395-403.
1076   Martinez, J. G., T. Burke, D. Dawson, J. J. Soler, M. Soler, and A. P. Moller. 1998. Microsatellite typing
1077   reveals mating patterns in the brood parasitic great spotted cuckoo (*Clamator glandarius*). Molecular
1078   Ecology 7: 289-297.
1079   Martinez, J. G., J. J. Soler, M. Soler, A. P. Moller, and T. Burke. 1999.
1080   Comparative population structure and gene flow of a brood parasite, the great spotted cuckoo
1081   (*Clamator glandarius*), and its primary host, the magpie (*Pica pica*). Evolution 53: 269-278.
1082   Martinez-Cruz, B., V. A. David, J. A. Godoy, J. J. Negro, S. J. O'Brien, and W. E. Johnson. 2002. Eighteen
1083   polymorphic microsatellite markers for the highly endangered Spanish imperial eagle (*Aquila*
1084   *adalberti*) and related species. Molecular Ecology Notes 2: 323-326.
1085   Maurer, G., M. L. Hale, M. H. Verduijn, and K. Wolff. 2005. Polymorphic microsatellite loci in
1086   pheasant coucal (*Centropus phasianinus*). Molecular Ecology Notes 5: 337-339.
1087   McDonald, D. B., and W. K. Potts. 1994. Cooperative Display and Relatedness among Males in a Lek-
1088   Mating Bird. Science 266: 1030-1032.
1089   McGuire, H. L., and M. A. F. Noor. 2002. Microsatellite loci for great white herons and great blue
1090   herons (Aves, Ardeidae, *Ardea herodias*). Molecular Ecology Notes 2: 170-172.
1091   McInnes, L. M., I. R. Dadour, M. E. Stewart, W. G. F. Ditcham, P. Mawson, and P. B. S. Spencer. 2005.
1092   Characterization of polymorphic microsatellite markers for the Carnaby's cockatoo (*Calyptorhynchus*
1093   *latirostris*) and related black cockatoo species. Molecular Ecology Notes 5: 504-506.
1094   McRae, S. B., and W. Amos. 1999. Characterization of hypervariable microsatellites in the
1095   cooperatively breeding white-browed sparrow weaver *Plocepasser mahali*. Molecular Ecology 8: 903-
1096   904.
1097   McRae, S. B., S. T. Emlen, D. R. Rubenstein, and S. M. Bogdanowicz. 2005. Polymorphic mircosatellite
1098   loci in a plural breeder, the grey-capped social weaver *(Pseudonigrita arnaudi)*, isolated with an
1099   improved enrichment protocol using fragment size-selection. Molecular Ecology Notes 5: 16-20.
1100   Mira, S., C. Billot, T. Guillemaud, L. Palma, and M. L. Cancela. 2002. Isolation and characterization of
1101   polymorphic microsatellite markers in Eurasian vulture *Gyps fulvus*. Molecular Ecology Notes 2: 557-
1102   558.
1103   Mira, S., K. Wolff, and M. L. Cancela. 2005. Isolation and characterization of microsatellite markers in
1104   Bonelli's eagle (*Hieraaetus fasciatus*). Molecular Ecology Notes 5: 493-495.
1105   Muniz, L. S. B., R. H. F. Macedo, and J. Graves. 2003. Isolation and characterization of dinucleotide
1106   microsatellite loci in communally breeding Guira cuckoos (Aves : Cuculidae). Molecular Ecology Notes
1107   3: 209-211.
1108   Munoz-Fuentes, V., N. Gyllenstrand, J. J. Negro, A. J. Green, and C. Vila. 2005. Microsatellite markers
1109   for two stifftail ducks: the white-headed duck, Oxyura *leucocephala*, and the ruddy duck, *O.*
1110   *jamaicensis*. Molecular Ecology Notes 5: 263-265.
1111   Nesje, M., and K. H. Roed. 2000. Microsatellite DNA markers from the gyrfalcon (*Falco rusticolus*) and
1112   their use in other raptor species. Molecular Ecology 9: 1438-1440.
1113   Nesje, M., K. H. Roed, J. T. Lifjeld, P. Lindberg, and O. F. Steen. 2000. Genetic relationships in the
1114   peregrine falcon (*Falco peregrinus*) analysed by microsatellite DNA markers. Molecular Ecology 9: 53-
1115   60.
1116   Ost, M., E. Vitikainen, P. Waldeck, L. Sundstrom, K. Lindstrom, T. Hollmen, J. C. Franson, and M. Kilpi.
1117   2005. Eider females form non-kin brood-rearing coalitions. Molecular Ecology 14: 3903-3908.
1118   Otsuka, R., I. Nishiumi, and M. Wada. 2003. Characterization of 12 polymorphic microsatellite loci in
1119   the Japanese bush warbler *Cettia diphone*. Molecular Ecology Notes 3: 44-46.

1120 Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005.
1121 Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife
1122 Management 69: 630-637.
1123 Pearce, J. M., S. L. Talbot, B. J. Pierson, M. R. Petersen, K. T. Scribner, D. L. Dickson, and A. Mosbech.
1124 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. Condor 106: 229-
1125 240.
1126 Petren, K., P. R. Grant, B. R. Grant, and L. F. Keller. 2005. Comparative landscape genetics and the
1127 adaptive radiation of Darwin's finches: the role of peripheral isolation. Molecular Ecology 14: 2943-
1128 2957.
1129 Piertney, S. B., A. D. C. MacColl, P. J. Bacon, and J. F. Dallas. 1998. Local genetic
1130 structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers.
1131 Molecular Ecology 7: 1645-1654.
1132 Piertney, S. B., A. Goostrey, J. F. Dallas, and D. N. Carss. 1998. Highly polymorphic microsatellite
1133 markers in the great cormorant *Phalacrocorax carbo*. Molecular Ecology 7: 138-140.
1134 Piertney, S. B., L. Shorey, and J. Hoglund. 2002. Characterization of microsatellite DNA markers in the
1135 white-bearded manakin (*Manacus manacus*). Molecular Ecology Notes 2:504-505.
1136 Primmer, C. R., A. P. Moller, and H. Ellegren. 1995. Resolving GeneticRelationships with Microsatellite
1137 Markers - a Parentage Testing System for the Swallow *Hirundo rustica*. Molecular Ecology 4: 493-498.
1138 Proudfoot, G., R. Honeycutt, and R. D. Slack. 2005. Development and characterization of
1139 microsatellite DNA primers for ferruginous pygmy-owls (*Glaucidium brasilianum*). Molecular Ecology
1140 Notes 5: 90-92.
1141 Randi, E., Tabarroni, C., Rimondi, V. L. & Sfougaris, A. 2003. Phylogeography of the rock partridge
1142 (*Alectoris graeca*). Molecular Ecology 12: 2201-2214.
1143 Rasner, C. A., P. Yeh, L. S. Eggert, K. E. Hunt, D. S. Woodruff, and T. D. Price. 2004. Genetic and
1144 morphological evolution following a founder event in the dark-eyed junco, *Junco hyemalis thurberi*.
1145 Molecular Ecology 13: 671-681.
1146 Richardson, D. S., F. L. Jury, D. A. Dawson, P. Salgueiro, J. Komdeur, and T. Burke. 2000. Fifty
1147 Seychelles warbler (*Acrocephalus sechellensis*) microsatellite loci polymorphic in Sylviidae species and
1148 their cross-species amplification in other passerine birds. Molecular Ecology 9: 2226-2231.
1149 Roeder, A. D., R. K. Marshall, A. J. Mitchelson, T. Visagathilagar, P. A. Ritchie, D. R. Love, T. J. Pakai, H.
1150 C. McPartlan, N. D. Murray, N. A. Robinson, K. R. Kerry, and D. M. Lambert. 2001. Gene flow on the
1151 ice: genetic differentiation among Adelie penguin colonies around Antarctica. Molecular Ecology 10:
1152 1645-1656.
1153 Russello, M., D. Calcagnotto, R. DeSalle, and G. Amato. 2001. Characterization of microsatellite loci in
1154 the endangered St. Vincent Parrot, *Amazona guildingii*. Molecular Ecology Notes 1: 162-164.
1155 Sainsbury, J. P., E. S. Macavoy, and G. K. Chambers. 2004. Characterization of microsatellite loci in the
1156 Kaka, *Nestor meridionalis*. Molecular Ecology Notes 4: 623-625.
1157 Saito, D., I. Nishiumi, and M. Nakamura. 2001. Characterization of nine polymorphic microsatellite
1158 loci from the alpine accentor *Prunella collaris*. Molecular Ecology Notes 1:258-259.
1159 Saito, D. S., T. Saitoh, and I. Nishiumi. 2005. Isolation and characterization of microsatellite markers
1160 in Ijima's leaf warbler, *Phylloscopus ijimae* (Aves : Sylviidae). Molecular Ecology Notes 5: 666-668.
1161 Saladin, V., D. Bonfils, T. Binz, and H. Richner. 2003. Isolation and characterization of 16 microsatellite
1162 loci in the Great Tit *Parus major*. Molecular Ecology Notes 3: 520-522.
1163 Schable, N. A., B. C. Faircloth, W. E. Palmer, J. P. Carroll, L. W. Burger, L. A. Brennan, C. Hagen, and T.
1164 C. Glenn. 2004. Tetranucleotide and dinucleotide microsatellite loci from the northern bobwhite
1165 (*Colinus virginianus*). Molecular Ecology Notes 4:415-419.
1166 Schlosser, J. A., T. W. J. Garner, J. M. Dubach, and A. G. McElligott. 2003. Characterization of
1167 microsatellite loci in Humboldt penguin (*Spheniscus humboldti*) and cross-amplification in other
1168 penguin species. Molecular Ecology Notes 3: 62-64.
1169 Scribner, K. T., M. R. Petersen, R. L. Fields, S. L. Talbot, J. M. Pearce, and R. K. Chesser. 2001. Sex-
1170 biased gene flow in spectacled eiders (anatidae): Inferences from molecular markers with contrasting
1171 modes of inheritance. Evolution 55: 2105-2115.

1172 Sefc, K. M., R. B. Payne, and M. D. Sorenson. 2001. Characterization of microsatellite loci in village
1173 indigobirds *Vidua chalybeata* and cross-species amplification in estrildid and ploceid finches.
1174 Molecular Ecology Notes 1: 252254.
1175 Segelbacher, G., R. J. Paxton, G. Steinbruck, P. Trontelj, and I. Storch. 2000.
1176 Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). Molecular Ecology 9:1934-
1177 1935.
1178 Strausberger, B. M., and M. V. Ashley. 2003. Breeding biology of brood parasitic brown-headed
1179 cowbirds (*Molothrus ater*) characterized by parent-offspring and sibling-group reconstruction. Auk
1180 120: 433-445.
1181 Szczys, P., C. R. Hughes, and R. V. Kesseli. 2005. Novel microsatellite markers used to determine the
1182 population genetic structure of the endangered Roseate Tern*, Sterna dougallii*, in Northwest Atlantic
1183 and Western Australia. Conservation Genetics 6: 461-466.
1184 Tarof, S. A., L. M. Ratcliffe, and P. T. Boag. 2001. Polymorphic microsatellite loci for assigning
1185 parentage in least flycatchers (*Empidonax minimus*). Molecular Ecology Notes 1:146-148.
1186 Tarr, C. L., S. Conant, and R. C. Fleischer. 1998. Founder events and variation at microsatellite loci in
1187 an insular passerine bird, the Laysan finch (*Telespiza cantans*). Molecular Ecology 7: 719-731.
1188 Tarr, C. L., and R. C. Fleischer. 1999. Population boundaries and genetic diversity in the endangered
1189 Mariana crow (*Corvus kubaryi*). Molecular Ecology 8: 941-949.
1190 Thuman, K. A., F. Widemo, and S. B. Piertney. 2002. Characterization of polymorphic microsatellite
1191 DNA markers in the ruff (*Philomachus pugnax*). Molecular Ecology Notes 2: 276-277.
1192 Tirard, C., F. Helfenstein, and E. Danchin. 2002. Polymorphic microsatellites in the black-legged
1193 kittiwake *Rissa tridactyla*. Molecular Ecology Notes 2: 431433.
1194 Tomasulo-Seccomandi, A. M., N. A. Schable, A. L. Bryan, I. L. Brisbin, S. N. Del Lama, and T. C. Glenn.
1195 2003. Development of microsatellite DNA loci from the wood stork (Aves, Ciconiidae, *Mycteria*
1196 *americana*). Molecular Ecology Notes 3:563-566.
1197 Topinka, J. R., and B. May. 2004. Development of polymorphic microsatellite loci in the northern
1198 goshawk (*Accipiter gentilis*) and cross-amplification in other raptor species. Conservation Genetics 5:
1199 861-864.
1200 Van Dongen, W. F. D., and R. A. Mulder. 2005. Isolation and characterization of microsatellite
1201 markers for paternity assessment in the golden whistler (*Pachycephala pectoralis*: Aves). Molecular
1202 Ecology Notes 5: 4-6.
1203 Van Treuren, R., R. Bijlsma, J. M. Tinbergen, D. Heg, and L. Van de Zande. 1999. Genetic analysis of
1204 the population structure of socially organized oystercatchers (*Haematopus ostralegus*) using
1205 microsatellites. Molecular Ecology 8: 181-187.
1206 Veit, M. L., R. J. Robertson, P. B. Hamel, and V. L. Friesen. 2005. Population genetic structure and
1207 dispersal across a fragmented landscape in cerulean warblers (*Dendroica cerulea*). Conservation
1208 Genetics 6: 159-174.
1209 Wang, M. T., Y. C. Hsu, C. T. Yao, and S. H. Li. 2005. Isolation and characterization of 12
1210 tetranucleotide repeat microsatellite loci from the greenbacked tit (*Parus monticolus*). Molecular
1211 Ecology Notes 5: 439-442.
1212 Watson, C. J. W., A. A. Beheler, and O. E. Rhodes. 2002. Development of hypervariable microsatellite
1213 loci for use in eastern phoebes (*Sayornis phoebe*) and related Tyrannids. Molecular Ecology Notes 2:
1214 117-118.
1215 Westneat, D. F., and H. L. Mays. 2005. Tests of spatial and temporal factors influencing extra-pair
1216 paternity in red-winged blackbirds. Molecular Ecology 14: 2155-2167.
1217 Williams, D. A., E. C. Berg, A. M. Hale, and C. R. Hughes. 2004. Characterization of microsatellites for
1218 parentage studies of white-throated magpie-jays (*Calocitta formosa*) and brown jays (*Cyanocorax*
1219 *morio*). Molecular Ecology Notes 4: 509-511.
1220 Williams, C. L., A. M. Fedynich, D. B. Pence, and O. E. Rhodes. 2005. Evaluation of allozyme and
1221 microsatellite variation in Texas and Florida Mottled Ducks. Condor 107: 155-161.

1222 Winker, K., T. C. Glenn, and G. R. Graves. 1999. Dinucleotide microsatellite loci in a migratory wood
1223 warbler (Parulidae : *Limnothlypis swainsonii*) and amplification among other songbirds. Molecular
1224 Ecology 8: 1553-1556.
1225 Wright, T. F., A. M. Rodriguez, and R. C. Fleischer. 2005. Vocal dialects, sexbiased dispersal, and
1226 microsatellite population structure in the parrot *Amazona auropalliata*. Molecular Ecology 14: 1197-
1227 1205.
1228 Yeung, C., Y. J. Huang, and S. H. Li. 2004. Development of polymorphic microsatellite markers for the
1229 Steere's Liocichla (*Liocichla steerii*). Molecular Ecology Notes 4: 420-422.
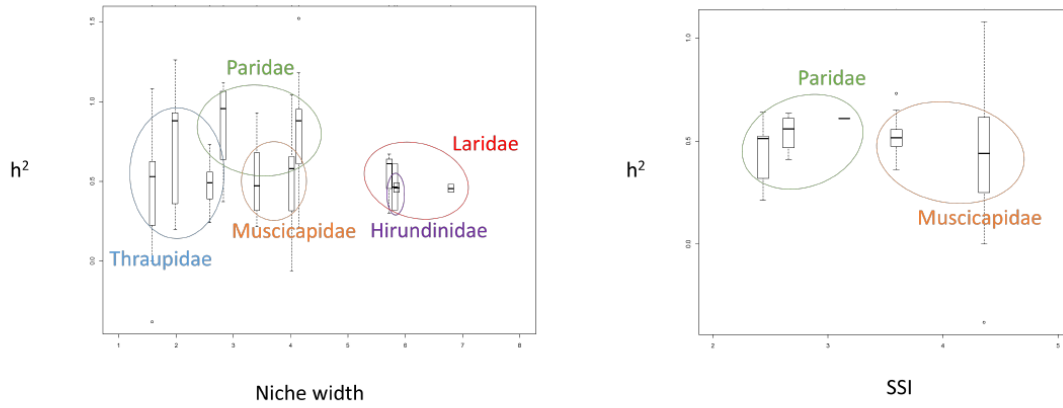1230 Yodogawa, Y., I. Nishiumi, D. Saito, and K. Okanoya. 2003. Characterization of eight polymorphic
1231 microsatellite loci from the Bengalese finch (*Lonchura striata* var. *domestica*). Molecular Ecology
1232 Notes 3: 183-185.
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S10. Data visualisation: heritability of body mass and tarsus length as a function of SSI and Niche width

In this figure we present heritability of tarsus length and body mass, the two most represented traits in our dataset, for families that had more than one species represented. Species belonging to the same family are linked by hand-drawn ellipses.

Heritability of Tarsus length

Heritability of Body mass

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