

1 **Biological Sciences: Population Biology**

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3 **Consistent scaling of inbreeding depression in space and time**

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26 Abstract

27

28 Inbreeding may increase the extinction risk of small populations. Yet, studies using modern
29 genomic tools to investigate inbreeding depression in nature have been limited to single
30 populations, and little is known about the dynamics of inbreeding depression in subdivided
31 populations over time. Natural populations often experience different environmental conditions and
32 differ in demographic history and genetic composition; characteristics that can affect the severity of
33 inbreeding depression. We utilised extensive long-term data on more than 3100 individuals from
34 eight islands in an insular house sparrow metapopulation to examine the generality of inbreeding
35 effects. Using genomic estimates of realised inbreeding, we discovered that inbred individuals had
36 lower survival probabilities and produced fewer recruiting offspring than non-inbred individuals.
37 Inbreeding depression, measured as the decline in fitness related traits per unit inbreeding, did not
38 vary appreciably among populations or with time. As a consequence, populations with more
39 resident inbreeding (due to their demographic history) paid a higher total fitness cost, evidenced by
40 a larger variance in fitness explained by inbreeding within these populations. Our results are in
41 contrast to the idea that effects of inbreeding generally depend on ecological factors and genetic
42 differences among populations, and expand the understanding of inbreeding depression in natural
43 subdivided populations.

44 Significance statement

45

46 Inbreeding often causes negative effects that, according to theory, may vary in severity with
47 population size or harshness of the environment. Studying this in wild vertebrates has been
48 prevented by the difficulty of collecting long-term data on multiple populations. We used genomic
49 estimates of inbreeding to investigate its effects on fitness components and morphological traits in
50 bird populations. Inbred individuals had lower survival, and produced fewer offspring compared to
51 non-inbred individuals. Inbreeding depression was constant across populations with differing
52 environments and population sizes. Consequently, populations with more resident inbreeding
53 suffered higher total loss of fitness due to inbreeding. Our results highlight the importance of
54 considering inbreeding in conservation and management of populations with a wide range of
55 characteristics.

56 Introduction

57

58 Inbreeding depression manifests in life-history and morphological traits and has widespread
59 consequences at both individual and population levels (1). The most severe effects are commonly
60 found in fitness related traits (1–4). Reductions in survival and reproductive success due to
61 inbreeding can be substantial and eventually lead to extinction of a population (5–7).

62 At the population level, inbreeding can be defined, in a narrow sense, as mating between
63 relatives that occurs more often than expected under random mating. More broadly, inbreeding also
64 includes any mating between relatives (whether random or non-random at population level) and the
65 loss of heterozygosity caused by genetic drift (1). As parental relatedness varies, also individual
66 inbreeding varies within a population; a heterogeneity that can be captured by individual estimates
67 of inbreeding. Such estimates can be extracted from individual pedigrees (1, 8). Until recently, the
68 effects of inbreeding have been challenging to study in natural populations due to the lack of deep
69 and accurate pedigrees. However, as individual inbreeding always results in higher genomic
70 homozygosity, it can be directly quantified based on genomic data (9). Here we use realised
71 estimates of inbreeding that are based on genome-wide homozygosity caused by both mating
72 between relatives and genetic drift. Genomic inbreeding estimates have enabled quantification of
73 realised inbreeding levels without bias caused by shallow or incomplete pedigree information,
74 however, empirical studies in natural populations are still rare (9–13).

75 Population demography has profound consequences on inbreeding levels and potentially on
76 the strength of inbreeding depression (see SI Appendix, Table S1 for theoretical expectations). In
77 large populations, selection against deleterious alleles is more efficient, due to weaker genetic drift.
78 Also, a slow rate of inbreeding due to low probability of mating with relatives contributes to
79 maintaining heterozygosity at overdominant loci (14, 15). In contrast, small populations experience
80 higher inbreeding levels that result in a higher proportion of homozygous loci. This exposes

81 recessive deleterious alleles to selection and eventually to purging in small populations (14, 16). In
82 addition, genetic drift drives alleles either to fixation or loss at a higher rate in small than in large
83 populations, and recessive alleles with deleterious effects may, consequently, drift to fixation.
84 Therefore, when a population is at mutation-selection-drift equilibrium, the mean fitness of a large
85 population is expected to be higher than the mean fitness of a small population, but inbreeding
86 depression is expected to be stronger in a large population (14). The quantitative importance of the
87 effect of population size on inbreeding depression is highly dependent on the architecture of the
88 genetic load; especially important are the level of dominance at relevant loci and the number of
89 deleterious alleles within the effect size range (i.e. selection coefficient close to $1/(4N_e)$ (17), where
90 N_e is effective population size) that could cause differences in inbreeding depression between
91 populations of differing sizes (18, 19). However, natural populations are rarely at equilibrium
92 (19) and the actual importance of purging in nature is controversial (1, 5, 14). For instance, purging
93 may be counteracted by dispersal in subdivided populations, because dispersal increases effective
94 population size, and introduces both beneficial and harmful alleles through gene flow (20, 21).
95 Dispersal may also generate heterosis (i.e. hybrid vigour), that is, increased fitness of offspring
96 produced by parents from different populations, caused by masking of negative inbreeding effects
97 (22).

98 Environmental heterogeneity is also expected to cause variation in inbreeding effects
99 between and within populations (23–26). Harsher environments have been documented to lead to
100 stronger selection and inbreeding depression, especially in laboratory conditions (27). However, due
101 to the difficulty of collecting appropriate data, testing whether inbreeding by environment
102 interactions are important in the wild is challenging (28, 29).

103 Studies on spatio-temporal variation in inbreeding depression of natural vertebrate
104 populations are lacking. In addition, we know little about how the total impact of inbreeding
105 changes due to variation in inbreeding depression and variation in the amount of inbreeding; effects

106 which can go in opposite directions (e.g. small populations can experience more inbreeding, but less
107 inbreeding depression than large ones) - resulting in an uncertain outcome at the population level.
108 To fill this knowledge gap, it is crucial to quantify the heterogeneity in inbreeding depression and
109 inbreeding levels within and among wild subdivided populations with different environmental and
110 demographic characteristics. Here we used data on more than 3100 adult individuals to study
111 inbreeding depression in multiple island populations of house sparrows (*Passer domesticus*) in
112 northern Norway that have been monitored since 1993 (30–32) (Fig. 1). To estimate pedigree
113 inbreeding coefficients and recruit production, we constructed a metapopulation pedigree using
114 single nucleotide polymorphism (SNP) data (33). First, we compared pedigree (F_{PED}) and genomic
115 inbreeding coefficients (F_{GRM} , for genomic relatedness matrix, and F_{ROH} , for runs of homozygosity)
116 based on 183k SNPs, and examined whether the level of inbreeding varied between populations and
117 years. Second, we quantified the effect of realised genomic inbreeding on annual and lifetime
118 reproductive success, survival, and morphology. Third, we examined whether inbreeding effects on
119 individual fitness and morphology varied across years and populations. In our system, this spatio-
120 temporal variation reflects differences in e.g. habitat type (34, 35) (SI Appendix, Table S2),
121 population size (32) (SI Appendix, Fig. S1), and environmental conditions such as climate and
122 weather (30, 34).

123

124 Results

125

126 *Spatio-temporal variation in genomic inbreeding*

127 Levels of inbreeding differed between islands (Fig. 2a and SI Appendix, Table S3) and years (Fig.
128 2a), with strong correlations between F_{GRM} , F_{ROH} and F_{PED} at the individual level ($r > 0.8$; SI
129 Appendix, Fig. S2). Variation among islands accounted for 8.5% of the total variation in individual
130 inbreeding estimates (F_{GRM} ; i.e. islands differed in their mean values of inbreeding, calculated from

131 posterior modes; Table 1). In contrast, annual variation within islands (“island-year”) explained
 132 only 2.5% of the variance in inbreeding. Randomisation tests showed that both island and island-
 133 year variances in F_{GRM} were larger than expected under the null hypothesis that inbreeding varied
 134 randomly across islands and years (1000 replicates for mode of island: $p < 0.001$ and island-year: p
 135 = 0.006). Inbreeding levels were highest on the island Aldra, where the median F_{GRM} was 0.045
 136 (interquartile range (IQR) 0.022-0.118, median $F_{ROH} = 0.028$, IQR = 0.008-0.085; Fig. 2 and SI
 137 Appendix, Table S3). High inbreeding level in the Aldra population was likely caused by a rather
 138 recent colonisation event, small population size and lower immigration rates compared to other
 139 populations (36). In contrast, the median F_{GRM} in the largest population (Hestmannøy) was 0.015
 140 (IQR = 0.007-0.026, median $F_{ROH} = 0.005$, IQR = 0.000-0.011). The other islands showed more
 141 similar intermediate levels of inbreeding, and mean inbreeding level decreased when population
 142 size increased (Spearman's correlation coefficient $\rho = -0.833$, $p = 0.015$; Fig. 2). Among-island
 143 variation in mean inbreeding was not associated with broad scale habitat differences, since sparrows
 144 had similar inbreeding levels on farm islands (median $F_{GRM} = 0.017$, IQR = 0.007-0.030) and non-
 145 farm islands (median $F_{GRM} = 0.019$, IQR = 0.011-0.033; 95% Bayesian Credible Interval (BCI) for
 146 difference in means of standardised F_{GRM} from -0.735 to 0.471; SI Appendix, Table S4 and Fig.
 147 S3a).

148

149 **Table 1.** Partitioning of variance in standardised F_{GRM} into spatial (island) and temporal (island-year;
 150 years nested within islands) components. A linear mixed effects model was fitted with sex as a fixed
 151 factor, and random intercepts for island and island-year. Means and modes of parameter estimates
 152 are presented, along with 95% Bayesian credible intervals (BCI).

<i>Random variances</i>	Mean	Mode [95% BCI]
Island	0.147	0.086 [0.044, 0.405]
Island-year	0.032	0.025 [0.012, 0.065]
Residual variance	0.902	0.901 [0.855, 0.952]

154

155

156 To examine whether our data provided sufficient range of inbreeding levels to be able to detect
157 inbreeding depression within each population, we estimated identity disequilibrium (ID, quantified
158 as g_2 (37)) that measures the variance in inbreeding among individuals. ID was positive for all study
159 populations (SI Appendix, Fig. S4), showing there was potential to detect inbreeding effects within
160 all of them. Concordant to F_{GRM} levels, ID was highest on Aldra ($g_2 = 0.0049$, 95% Confidence
161 Interval (CI) from 0.0036 to 0.0061) and lowest on Hestmannøy ($g_2 = 0.0014$, 95% CI from 0.0010
162 to 0.0018).

163

164 *Strong and consistent inbreeding depression in fitness components across time and space*

165 To study the effect of inbreeding on reproductive success using animal models (38), we constructed
166 a SNP pedigree at the metapopulation level (for details, see SI Appendix, Supplementary Results).
167 Our results showed a strong negative effect of inbreeding on individual fitness across all island
168 populations: lifetime reproductive success (LRS) decreased when inbreeding increased (Fig. 3, Fig.
169 4, and SI Appendix, Fig. S5). For example, individuals with $F_{GRM} = 0.125$ produced on average 47%
170 (95% BCI from 40% to 57%) fewer offspring during their lifetime than individuals with $F_{GRM} = 0$.
171 For comparison, using F_{ROH} as the measure of inbreeding, the LRS of individuals with $F_{ROH} = 0.125$
172 was on average 61% (95% BCI from 50% to 72%) lower than individuals with $F_{ROH} = 0$ (SI
173 Appendix, Fig. S5). This strong and negative effect of inbreeding on lifetime reproductive success
174 was a consequence of both decreased adult survival and lower annual reproductive success (AR;
175 Fig. 3, Fig. 4, and SI Appendix, Fig. S5; for more details, see SI Appendix, Table S5). There was no
176 evidence that males and females differed with respect to effects of inbreeding on reproductive
177 success or adult survival (SI Appendix, Table S6).

178 We found no evidence for the effect of inbreeding on fitness components to vary with either
179 habitat type (farm vs. non-farm island) or population size, as indicated by the 95% BCIs of the
180 interactions between inbreeding and habitat type or annual population size for all fitness

181 components (Fig. 3b-c and SI Appendix, Table S6). To examine if inbreeding depression varied
182 spatio-temporally, we included two random slope terms in the mixed effect models: an inbreeding
183 by island interaction (i.e. $F_{GRM} \times \text{island}$) that captured spatial variation, and an inbreeding by island-
184 year interaction (i.e. $F_{GRM} \times \text{island-year}$) that captured temporal variation. These models indicated
185 that inbreeding depression on both annual and lifetime reproductive success was similar among the
186 islands (SI Appendix, Fig. S6a and Table S5), as well as between years within islands (SI Appendix,
187 Fig. S7 and Table S5). Accordingly, variation in inbreeding effects on reproductive success among
188 islands or among years within islands explained only small amounts of the variation in inbreeding
189 depression (e.g. $F_{GRM} \times \text{island}$ for LRS: mean $\sigma^2 = 0.030$, 95% BCI from 0.004 to 0.100; SI
190 Appendix, Table S5 and Fig. S7). To examine whether these variances were larger than expected by
191 chance, we conducted permutations randomising the island and island-year variables in our data.
192 These randomisation tests suggest that the variances in inbreeding depression between islands and
193 years were not larger than would be expected by chance given the data structure ($p > 0.05$ in all
194 tests for LRS and AR; SI Appendix, Table S7). Hence, we conclude that the strong inbreeding
195 depression in both annual and lifetime reproductive success was remarkably consistent across time
196 and space. Nevertheless, the proportion of variance in fitness components explained by inbreeding
197 was larger in smaller populations, as indicated by highly negative relationships between the
198 proportion of variance explained by F_{GRM} and population size (ρ between -0.881 and -0.710, and p -
199 values between 0.007 and 0.058; SI Appendix, Fig. S8), i.e., the relative effect of inbreeding on
200 fitness decrease was stronger when population size was smaller. This result is likely caused by
201 higher variance in inbreeding in smaller populations, which in turn is suggested by a negative
202 correlation between g_2 and population size ($\rho = -0.738$, $p = 0.046$).

203 The overall negative effect of inbreeding on survival probability was strong at the
204 metapopulation level ($\beta = -0.155$, 95% BCI from -0.179 to -0.051; Fig. 3, Fig. 4e, and SI Appendix,
205 Table S5). Furthermore, we found evidence for spatially homogeneous inbreeding depression in

206 survival across the islands (the 95% BCIs of all island x F interaction terms overlapped zero; Fig. 4f
207 and SI Appendix, Table S8). This result was also supported by lower deviance information criterion
208 (DIC) value of the model including island only as a fixed factor (DIC = 9555) compared to the
209 model including also an interaction term between inbreeding and island (DIC = 9678). Similarly,
210 inbreeding effects on survival were consistent through years, as indicated by the lower DIC value of
211 the model including year only as a fixed factor (DIC = 9780) than the model including also an
212 interaction term between inbreeding and year (DIC = 9801; SI Appendix, Table S9).

213 To further compare the inbreeding load among populations, we estimated number of lethal
214 equivalents, i.e. group of deleterious alleles that have a cumulative lethal effect when homozygous
215 (1, 39), for each fitness component on each island. The estimated number of lethal equivalents
216 ranged from 6.16 to 23.80 for LRS, from 8.84 to 15.97 for AR, and from 1.03 to 14.19 for survival
217 (SI Appendix, Table S10). The general pattern was that the number of lethal equivalents were higher
218 for LRS and AR than for survival, and relatively similar across islands for each fitness component
219 (all 95% BCIs overlapped among the islands).

220

221 *Weak evidence for inbreeding depression in morphological traits*

222 We found weak evidence that inbreeding affected house sparrow morphology: inbred individuals
223 tended to be lighter ($\beta = -0.14$ g/unit change in standardised F_{GRM} , 95% BCI from -0.32 to 0.04) and
224 have shorter bills ($\beta = -0.05$ mm/unit change in standardised F_{GRM} , 95% BCI from -0.12 to 0.017)
225 than non-inbred individuals (Fig. 3a, Fig. 4, and SI Appendix, Table S5). But wing length, bill
226 depth, tarsus length, and total and visible badge sizes did not show any effect of inbreeding (Fig. 3a
227 and SI Appendix, Table S5). Likewise, we found little spatial and temporal variation in the effects
228 of inbreeding on morphological traits; in general, there was no evidence that the effect differed
229 between islands or years within islands (SI Appendix, Table S5, Table S7 and Fig. S6). Only the
230 effect of inbreeding on wing length varied more across islands than expected by chance (mean $\sigma^2 =$

231 0.048, randomisation test: $p = 0.009$; SI Appendix, Table S5 and Table S7). Furthermore, the
232 variance among years within islands in the effect of inbreeding was larger than expected by chance
233 only for wing length (mean $\sigma^2 = 0.032$, randomisation test: $p = 0.003$) and bill depth (mean $\sigma^2 =$
234 0.003 , randomisation test: $p = 0.03$). However, island specific inbreeding effects on morphology
235 were generally weak (SI Appendix, Fig. S6).

236

237 Discussion

238

239 Contrary to theoretical predictions (14, 16, 23, 25, 26), the negative inbreeding effects on fitness
240 components of wild house sparrow populations were consistent both in space and time - despite the
241 large variation in inbreeding levels, population sizes and environmental conditions. Thus, after
242 accounting for differences in mean fitness of our study populations, a given proportion of
243 autozygous loci caused a strikingly similar reduction in fitness of inbred individuals relative to non-
244 inbred individuals across environments. Our results differ from more common studies conducted on
245 single populations of mammals (28) and birds (29, 40), which have found inbreeding effects to vary
246 over time. Although only few other studies have been able to compare inbreeding depression in
247 natural environments across populations within the same species, our results add to the current
248 empirical evidence suggesting that inbreeding depression in fitness related traits may not be
249 strongly dependent on ecological conditions (5, 41). Here, we conducted temporal and spatial
250 analyses that capture the combined environmental differences among habitat types, islands and
251 years within islands, and thus broad inbreeding by environment interactions (I x E). Further studies
252 are needed to study the effects of, for example, more specific weather phenomena or small scale
253 ecological differences on inbreeding depression.

254 Population size explained only a small proportion of the variance in inbreeding depression
255 across the metapopulation (Fig. 3c). This implies that our range of local population sizes (N_e),

256 which is approximately between 10 and 100 (32, 42), did not result in measurable differences in the
257 strength of selection against inbred individuals via the processes of purging or fixation of
258 deleterious alleles. There may be several reasons why the expected decrease in inbreeding
259 depression in small populations was not observed. First, in isolated populations at mutation-
260 selection-drift equilibrium, the impact of effective population size depends on the genetic
261 architecture of the load; only deleterious alleles with a proportional effect on fitness near the range
262 of $1/4N_e$ (17) (here ca. 1/40-1/400) have a fate that varies with N_e ; they tend to either go to fixation
263 or be lost due to drift in small populations, while they remain at low frequencies and contribute to
264 inbreeding depression in large ones (18, 19). This category of large-effect alleles may be rare in our
265 study populations. If inbreeding depression is polygenic and mostly caused by deleterious alleles at
266 many loci where each allele has a small effect on fitness (2), the combined effect of all slightly
267 deleterious alleles could vary little among populations, even if there was spatial variation (due to
268 e.g. differences in N_e) in the relative frequencies of some of these small effect alleles. Second, the
269 populations are not isolated; the F_{ST} estimates between them are rather small (SI Appendix, Table
270 S11), and results from previous studies in the same metapopulation suggest that dispersal rates may
271 be relatively high (0.05-0.30 (34)), while variation in local effective size is approximately one order
272 of magnitude (table S4 in (32)). Thus, dispersal may be enough to homogenize the distribution of
273 deleterious alleles and ensure constant inbreeding depression at the metapopulation scale. Finally,
274 local populations may not be at equilibrium (19). For example, the most inbred population on Aldra
275 has a relatively small population size, but due to a recent founder effect, it is not at equilibrium and
276 there has possibly not yet been enough time to fix or efficiently purge deleterious alleles.
277 Consequently, inbreeding depression is as strong in Aldra as in other populations within the
278 metapopulation. However, Aldra still keeps the memory of the recent bottleneck in terms of a high
279 degree of resident inbreeding and high variance in inbreeding. Thus, this population pays a larger
280 total cost of inbreeding than expected from its size, since a larger proportion of variance in fitness

281 traits is due to losses caused by inbreeding (SI Appendix, Fig. S8). This illustrates that although
282 metapopulation dynamics may maintain a similar inbreeding depression among local populations,
283 some of them may still experience stronger total impact of inbreeding, due to their demographic
284 history.

285 Inbreeding depression may vary with the environmental conditions, which could result in
286 not only spatial variation but also variation among years within local populations. The actual
287 developmental and physiological effects of inbreeding in the studied house sparrow metapopulation
288 are not known, but due to the temporally constant inbreeding depression (SI Appendix, Fig. S7 and
289 Table S7), our results suggest that these changes are not strongly affected by extrinsic factors. For
290 example, if inbreeding depression was caused by genes affecting energy metabolism (43),
291 environmental factors, such as extreme weather phenomena, could be expected to mediate even
292 stronger inbreeding depression (26). On the other hand, the strength of inbreeding depression
293 caused by genes affecting intrinsic factors, such as sperm (44) or egg quality (45, 46), would likely
294 be less affected by the environment. Nevertheless, laboratory studies have shown that inbreeding
295 depression can be more severe under stress caused by extrinsic factors, such as heat and
296 intraspecific competition, than under benign environmental conditions (27). Interactions between
297 environmental conditions and inbreeding may appear less important for the severity of inbreeding
298 depression in natural populations than in experimental studies, for example, because experiments
299 have manipulated the environmental variation outside the natural range of the study organism (28).
300 It is also possible that environmental factors could counteract each other, so that a closer
301 examination of ecological and genetic mechanisms would be required to understand why inbreeding
302 depression appears consistent. For example, in our study system, nestling and adult survival, and
303 population densities, increase with temperature (30, 34). In addition, inbred individuals may suffer
304 higher fitness costs of competition (14, 47) at higher population densities. Thus, the net effect of
305 temperature-dependent survival and differential costs of competition could be that we observe

306 similar inbreeding depression at different densities.

307 We found strong inbreeding depression in fitness components but weak inbreeding effects in
308 morphological traits. Traits with large directional dominance variance, such as reproductive success,
309 have also previously shown to exhibit more severe inbreeding depression than traits with less
310 directional dominance (1, 4, 48). The presence of small effects of inbreeding on morphology in
311 adult individuals can be difficult to detect. However, because some morphological traits have been
312 found to affect individual fitness in our study system (49), small effects in multiple traits may add
313 up to stronger inbreeding depression observed in fitness components. We examined inbreeding
314 effects only in adults, and it is possible that inbreeding has stronger effects on morphology during
315 development and growth (50). Such inbreeding depression may also translate into lower survival of
316 inbred juveniles that has been documented in our study system (36, 51).

317 We show that inbreeding has consistent negative fitness consequences in a natural
318 subdivided vertebrate population, in which subpopulations experience different environmental
319 conditions. Importantly, our study populations have sizes typical for natural populations of
320 conservation concern, and our results support previous evidence that purging cannot be relied upon
321 as a mechanism to aid conservation of small populations (5, 14, 41, 52). We found that inbreeding
322 has larger relative negative effect on fitness in small than in large populations, which is caused by
323 higher mean level of inbreeding and consequently larger variance in inbreeding in small
324 populations; this suggests higher total loss of fitness due to inbreeding in small populations. Our
325 results imply that conservation and management decisions should prioritise minimising inbreeding
326 in populations from diverse ecological and genetic backgrounds. Future studies should aim to utilise
327 the full power of genome-wide datasets and disentangle the extrinsic and intrinsic ecological and
328 genomic mechanisms causing such consistent inbreeding depression within and among populations.
329 Finding the genomic regions that account for inbreeding depression will help in managing
330 endangered populations by detecting the most homozygous regions with strongest deleterious

331 effects and targeting genetic rescue programs based on this information (53), and in answering
332 broader evolutionary questions about the maintenance of genetic variation in fitness related traits (2,
333 54).

334

335

336 Materials and Methods

337

338 *Study system*

339 The study system (Fig. 1) consists of two habitat types: i) farm islands, where the sparrows live in
340 colonies on dairy farms and nest primarily inside barns and cowsheds, with access to cattle feed and
341 shelter all year round, and ii) non-farm islands, where the sparrows live exclusively outdoor in
342 gardens and nest mostly in nest boxes. Thus, on non-farm islands, sparrows are more exposed to
343 variation in food availability and weather conditions (34, 35, 55). The discrete island populations
344 together with high resighting rates (mean 74%) allow estimating population sizes, inter-island
345 dispersal, individual survival and reproductive success with high accuracy (34, 56, 57). Adult
346 population sizes (N between 4 and 240 (32); SI Appendix, Fig. S1) and dispersal rates (34) differ
347 between the islands and years, which is known to cause low to moderate genetic population
348 differentiation (SI Appendix, Table S11; 27). The differences in demography, along with spatio-
349 temporal variation in the environment, suggest that inbreeding levels and the strength of inbreeding
350 depression may differ (36, 51).

351

352 *Samples and genotyping*

353 Blood samples from 3253 adult house sparrows were genotyped for 200 000 SNPs using a custom
354 house sparrow Affymetrix Axiom array (33) at CIGENE (Ås, Norway). Virtually all adult house
355 sparrows (~90% of adults annually) present on eight of the islands during the years 1998-2013 were

356 included in this study (SI Appendix, Table S2). The samples comprised five farm islands: Aldra,
357 Gjerøy, Hestmannøy, Indre Kvarøy and Nesøy. Due to sharp declines in population sizes on non-
358 farm islands in 2000 (32), only samples from adults present between 2003-2013 were included from
359 the islands Selvær and Træna, and between 2004-2013 from Myken. After quality control (SI
360 Appendix, Supplementary Methods) the final dataset consisted of 3116 house sparrow individuals
361 (1580 females and 1536 males) that had genotypes for 1626 Z chromosomal loci and 181 529
362 autosomal loci distributed across 28 autosomes (33, 58).

363

364 *Pedigree construction*

365 A metapopulation level pedigree was constructed for 3116 adult house sparrows from the Helgeland
366 archipelago using the R (59) package *sequoia* (60). A heavily pruned dataset of 605 highly
367 informative and independent SNPs was used for pedigree construction. Parenthoods in the new SNP
368 based pedigree (“SNP pedigree”) were compared to those in a previous MS pedigree that was
369 constructed using between eight and 13 microsatellite loci separately for each study island including
370 nestlings, fledged juveniles and adult individuals as described in previous studies (36, 61–63) (SI
371 Appendix, Supplementary Results, Table S12, and Fig. S9). To validate the new SNP pedigree,
372 correlations were estimated between pairwise relatedness estimates based on SNP pedigree, MS
373 pedigree and genomic relatedness (SI Appendix, Supplementary Methods, Supplementary Results,
374 and Fig. S10).

375

376 *Inbreeding analyses*

377 Individual inbreeding coefficients were estimated using pedigree and SNP based methods. Pedigree
378 based inbreeding coefficients (F_{PED}) were estimated from the SNP pedigree using the R package
379 *pedigree* (64). Only individuals with at least two full ancestral generations were included in further
380 analyses with F_{PED} , which reduced the sample size to 1241 individuals. Genome-wide

381 heterozygosity was estimated using all 181 529 autosomal SNPs. Two genomic inbreeding
382 coefficients, based on weighted average homozygosity over all loci (F_{GRM} , for genomic relatedness
383 matrix) (65) and runs of homozygosity (F_{ROH}) (66) were estimated using 118 810 autosomal loci not
384 in strong linkage disequilibrium. F_{GRM} was estimated using the GCTA (65) software for the whole
385 metapopulation simultaneously. PLINK was used to extract homozygous sequence blocks and F_{ROH}
386 was calculated as the proportion of SNP covered genome within these homozygous sequence blocks
387 (SI Appendix, Supplementary Methods). Pairwise correlation between the inbreeding estimates was
388 estimated using Pearson's correlation coefficient (r). Since all estimates correlated strongly (SI
389 Appendix, Fig. S2), only results for analyses including F_{GRM} are presented in the main text, whereas
390 key results for F_{ROH} are presented in the Supplementary Results.

391 To estimate the contribution of island and year nested within island (“island-year”) to
392 variance in inbreeding, variance partitioning was done for standardised (to variance equal to 1 and
393 centered to the metapopulation mean) F_{GRM} estimates using Bayesian mixed effect models that were
394 fitted with the R package *R-INLA* (67). Identity disequilibrium (ID) between SNP loci was
395 estimated using g_2 as implemented in the R package *inbreedR* (68) for each island population
396 separately. In addition, F -statistics (pairwise F_{ST} and population-specific F_{IS}) were estimated for
397 each population using the R package *hierfstat* (69).

398

399 *Phenotypic and life-history data used in the inbreeding depression analyses*

400 The effect of realised inbreeding on individual reproductive success, survival probability, and
401 morphology was estimated using slightly different datasets depending on the question. Individual
402 reproductive success was measured in two ways: i) the number of offspring produced that recruited
403 to the adult metapopulation per year (AR, annual reproductive success), and ii) the number of
404 offspring produced that recruited to the adult metapopulation during an individual's lifetime (LRS,
405 lifetime reproductive success). Recruits that hatched in the years 1998-2012 were included in these

406 analyses. However, since the sampling time periods differed between the islands, LRS was
407 estimated for adult individuals that hatched at earliest one year before the sampling of the adults on
408 an island started (SI Appendix, Table S2): 1997 on the farm islands (Aldra, Gjerøy, Hestmannøy,
409 Indre-Kvarøy, and Nesøy), 2002 on the non-farm islands Selvær and Træna, and 2003 on the non-
410 farm island Myken. In total, 2062 unique individuals were included in the LRS dataset, and 2739 in
411 the AR dataset (5267 records, SI Appendix, Supplementary Methods). The dataset used for survival
412 analyses included 2728 house sparrows that were observed as adults on one of the eight study
413 islands between May and December in a specific year. Individuals that hatched before 1997 were
414 excluded from the analyses.

415 The inbreeding effect on adult morphology was estimated for seven traits: body mass (g),
416 tarsus length (mm), wing length (mm), bill length (mm), bill depth (mm), visible badge size (mm²,
417 only males) and total badge size (mm², only males). For a more detailed description of the field
418 procedures, see previous publications from the study system (49, 62, 70). Each individual had been
419 measured a varying number of times during their lifetime and at different times of the year. To make
420 the measurements comparable, a general linear mixed-effects model using the R package *lme4* (71)
421 was fitted separately for each sex and trait (70) (SI Appendix, Supplementary Methods and Table
422 S13). Parameter estimates from the fitted models were used to adjust each measurement to May in
423 the second calendar year, before the mean phenotypic values were calculated for each individual
424 (70). The dataset used in the morphology analyses included 1786 birds (941 females and 845 males)
425 that hatched between 1997-2012 on the farm islands, 2002-2012 on Træna and Selvær, and 2003-
426 2012 on Myken. Measurements taken from these birds until 2016 were used.

427

428 *Inbreeding depression analyses*

429 The effect of realised inbreeding on individual survival, reproductive success and morphology was
430 investigated using standardised (to variance equal to 1 and centered to metapopulation mean)

431 genomic inbreeding estimates F_{GRM} and F_{ROH} . Because recapture rates varied between the islands
432 (72), the effect of inbreeding on survival probability was estimated using capture-mark-recapture
433 (CMR) models (73, 74). The model fitting options provided by the programming language BUGS
434 were used (75). The models were fitted in JAGS (76) (Version 3.2.0) using the R package jagsUI
435 (77). To study the effect of inbreeding on reproductive success and morphology, Bayesian animal
436 models (78) were fitted within the INLA (79) framework, using the R-INLA package in R. LRS
437 models were fitted with a zero-inflated Poisson distribution, AR models with a Poisson distribution,
438 and morphological trait models with a Gaussian distribution. Results from all models are given in
439 the Supplementary Results (SI Appendix, Table S5 and Table S6). The proportion of total variance
440 that was explained by inbreeding (F_{GRM}) in each fitness component was estimated for each island
441 using variance estimates from the inbreeding depression models fitted as explained above.

442 To produce estimates of inbreeding load that are directly comparable with other study
443 systems, we also estimated the number of lethal equivalents (39) for all fitness components (LRS,
444 AR and survival) within each island, using the inbreeding depression models described above. The
445 number of lethal equivalents were estimated as twice the negation of the regression slope (-2β) of
446 F_{ROH} on each fitness component (because the species is diploid; 76).

447 Since all individuals were measured for all traits (badge sizes only in males), the
448 measurements are not independent between traits. Furthermore, we know from previous studies that
449 the morphological traits are phenotypically and genetically correlated to various degrees (61, 62).
450 To account for such non-independence, multivariate animal models were also fitted for the
451 morphological data. Results were concordant between multivariate MCMCglmm analyses and
452 univariate INLA analyses (SI Appendix, Supplementary Results and Table S14). For simplicity,
453 only univariate results are presented in the main results. Details of all inbreeding depression models
454 are given in the SI Appendix, Supplementary Methods.

455

456 *Statistical inference from random effects estimates using permutation tests*

457 The statistical support for a non-zero value of the variance explained by spatio-temporal random
458 effects in our models testing for inbreeding depression in LRS, AR, and morphological traits was
459 assessed separately. This was done because variance components are bound to be positive, and
460 because prior choice may influence the credible intervals derived from the posterior distribution
461 (81). We therefore determined the probability that the estimated variance explained by island
462 (spatial variation) and island-year (temporal variation) was different from a null expectation based
463 on permutation tests (78; details of permutation tests in SI Appendix, Supplementary Methods).

464

465 *Data availability*

466 Data and R scripts used in this study are deposited in Dryad
467 (<https://doi.org/10.5061/dryad.m0cfxpp10>) with two years embargo. During the embargo time, the
468 data are available from the authors on request.

469

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485

486

487 Contributions

488 AB, AKN, and HJ conceived the idea for the study. AB, AH, AMM, BES, BR, HH, HJ, HP, IJH,
489 PSR, SL, TK, and THR contributed to collecting and processing the field and/or genotype data. AB,
490 AKN, HH, HJ, SM, and YGAA analysed the data and interpreted the results. AKN wrote the
491 manuscript with input from all authors.

492

493 Competing interests

494 The authors declare no competing interests.

495

496 Supplementary information

497 Supplementary Methods, Supplementary Results, Supplementary Figures and Supplementary
498 Tables in SI Appendix.

499

500

501 References

502

- 503 1. L. F. Keller, D. M. Waller, Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**,
504 230–241 (2002).
- 505 2. D. Charlesworth, J. H. Willis, The genetics of inbreeding depression. *Nat. Rev. Genet.* **10**,
506 783–796 (2009).
- 507 3. P. Crnokrak, D. A. Roff, Inbreeding depression in the wild. *Heredity* **83**, 260–270 (1999).
- 508 4. M. A. DeRose, D. A. Roff, A comparison of inbreeding depression in life-history and
509 morphological traits in animals. *Evolution* **53**, 1288–1292 (1999).
- 510 5. I. Saccheri, M. Kuussaari, M. Kankare, P. Vikman, I. Hanski, Inbreeding and extinction in a
511 butterfly metapopulation. *Nature* **392**, 491–494 (1998).
- 512 6. R. Frankham, Genetics and extinction. *Biol. Conserv.* **126**, 131–140 (2005).
- 513 7. J. J. O’Grady, *et al.*, Realistic levels of inbreeding depression strongly affect extinction risk
514 in wild populations. *Biol. Conserv.* **3**, 42–51 (2006).
- 515 8. S. Wright, Coefficients of inbreeding and relationship. *Am. Nat.* **56**, 330–338 (1922).
- 516 9. M. Kardos, H. R. Taylor, H. Ellegren, G. Luikart, F. W. Allendorf, Genomics advances the
517 study of inbreeding depression in the wild. *Evol. Appl.* **9**, 1205–1218 (2016).
- 518 10. M. Kardos, *et al.*, Genomic consequences of intensive inbreeding in an isolated wolf
519 population. *Nat. Ecol. Evol.* **2**, 124–131 (2018).
- 520 11. J. Huisman, L. E. B. Kruuk, P. A. Ellis, T. Clutton-Brock, J. M. Pemberton, Inbreeding
521 depression across the lifespan in a wild mammal population. *Proc. Natl. Acad. Sci. USA* **113**,
522 3585–3590 (2016).
- 523 12. C. Bérénos, P. A. Ellis, J. G. Pilkington, J. M. Pemberton, Genomic analysis reveals
524 depression due to both individual and maternal inbreeding in a free-living mammal
525 population. *Mol. Ecol.* **25**, 3152–3168 (2016).
- 526 13. N. Chen, E. J. Cosgrove, R. Bowman, J. W. Fitzpatrick, A. G. Clark, Genomic consequences
527 of population decline in the endangered Florida scrub-jay. *Curr. Biol.* **26**, 2974–2979 (2016).
- 528 14. P. W. Hedrick, A. Garcia-Dorado, Understanding inbreeding depression, purging, and genetic
529 rescue. *Trends Ecol. Evol.* **31**, 940–952 (2016).
- 530 15. D. Demontis, *et al.*, Efficiency of selection, as measured by single nucleotide polymorphism
531 variation, is dependent on inbreeding rate in *Drosophila melanogaster*. *Mol. Ecol.* **18**, 4551–
532 4563 (2009).
- 533 16. R. Lande, D. W. Schemske, The evolution of self-fertilization and inbreeding depression in
534 plants. 1. genetic models. *Evolution* **39**, 24–40 (1985).

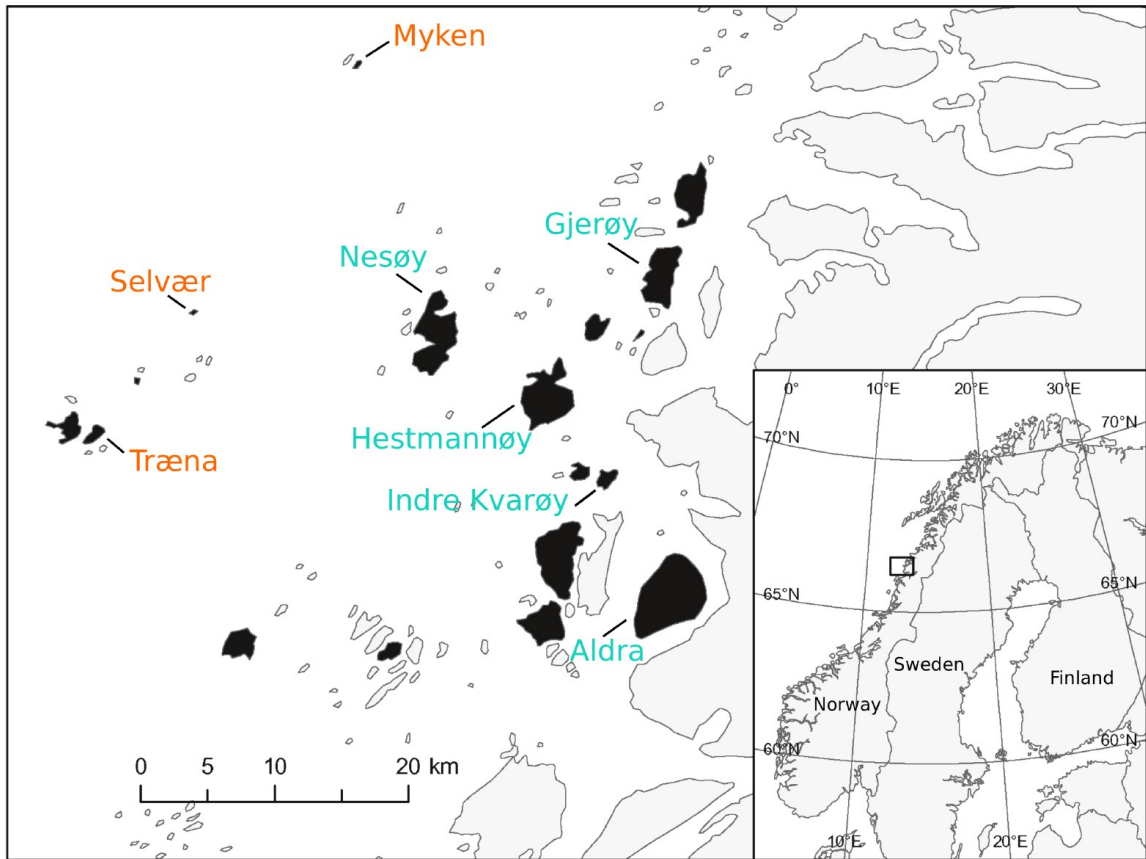
- 535 17. M. Kimura, *The neutral theory of molecular evolution*. (Cambridge University Press, 1983).
- 536 18. J. Wang, W. G. Hill, D. Charlesworth, B. Charlesworth, Dynamics of inbreeding depression
537 due to deleterious mutations in small populations: mutation parameters and inbreeding rate.
538 *Genet. Res.* **74**, 165–178 (1999).
- 539 19. B. Charlesworth, Mutational load, inbreeding depression and heterosis in subdivided
540 populations. *Mol. Ecol.* **27**, 4991–5003 (2018).
- 541 20. M. C. Whitlock, P. K. Ingvarsson, T. Hatfield, Local drift load and the heterosis of
542 interconnected populations. *Heredity* **84**, 452–457 (2000).
- 543 21. S. Glémin, J. Ronfort, T. Bataillon, Patterns of inbreeding depression and architecture of the
544 load in subdivided populations. *Genetics* **165**, 2193–2212 (2003).
- 545 22. T. Dobzhansky, Genetics of natural populations. xix. Origin of heterosis through natural
546 selection in populations of *Drosophila pseudoobscura*. *Genetics* **35**, 288–302 (1950).
- 547 23. P. W. Hedrick, S. T. Kalinowski, Inbreeding depression in conservation biology. *Annu. Rev.*
548 *Ecol. Evol. Syst.* **31**, 139–162 (2000).
- 549 24. P. Armbruster, D. H. Reed, Inbreeding depression in benign and stressful environments.
550 *Heredity* **95**, 235–242 (2005).
- 551 25. P. Cheptou, K. Donohue, Environment-dependent inbreeding depression: its ecological and
552 evolutionary significance. *New Phytol.* **189**, 395–407 (2011).
- 553 26. D. H. Reed, C. W. Fox, L. S. Enders, T. N. Kristensen, Inbreeding – stress interactions:
554 evolutionary and conservation consequences. *Ann. N. Y. Acad. Sci.* **1256**, 33–48 (2012).
- 555 27. C. W. Fox, D. H. Reed, Inbreeding depression increases with environmental stress: an
556 experimental study and meta-analysis. *Evolution* **65**, 246–258 (2011).
- 557 28. J. M. Pemberton, P. E. Ellis, J. G. Pilkington, C. Bérénos, Inbreeding depression by
558 environment interactions in a free-living mammal population. *Heredity*. **118**, 64–77 (2017).
- 559 29. A. B. Marr, P. Arcese, W. M. Hochachka, J. M. Reid, L. F. Keller, Interactive effects of
560 environmental stress and inbreeding on reproductive traits in a wild bird population. *J. Anim.*
561 *Ecol.* **75**, 1406–1415 (2006).
- 562 30. T. H. Ringsby, B.-E. Sæther, J. Tufto, H. Jensen, E. J. Solberg, Asynchronous spatiotemporal
563 demography of a house sparrow metapopulation in a correlated environment. *Ecology* **83**,
564 561–569 (2002).
- 565 31. H. Jensen, *et al.*, Genetic variation and structure of house sparrow populations: is there an
566 island effect? *Mol. Ecol.* **22**, 1792–1805 (2013).
- 567 32. H. T. Baalsrud, *et al.*, Effects of population characteristics and structure on estimates of
568 effective population size in a house sparrow metapopulation. *Mol. Ecol.* **23**, 2653–2668
569 (2014).

- 570 33. S. L. Lundregan, *et al.*, Inferences of genetic architecture of bill morphology in house
571 sparrow using a high density SNP array point to a polygenic basis. *Mol. Ecol.* **27**, 3498–
572 3514 (2018).
- 573 34. H. Pärn, T. H. Ringsby, H. Jensen, B.-E. Sæther, Spatial heterogeneity in the effects of
574 climate and density-dependence on dispersal in a house sparrow metapopulation. *Proc. R.*
575 *Soc. B Biol. Sci.* **279**, 144–152 (2012).
- 576 35. Y. G. Araya-ajoy, *et al.*, Characterizing morphological (co)variation using structural equation
577 models: Body size, allometric relationships and evolvability in a house sparrow
578 metapopulation. *Evolution* **73**, 452–466 (2019).
- 579 36. A. M. Billing, *et al.*, Evidence of inbreeding depression but not inbreeding avoidance in a
580 natural house sparrow population. *Mol. Ecol.* **21**, 1487–1499 (2012).
- 581 37. B. S. Weir, C. C. Cockerham, Mixed self and random mating at two loci. *Genet. Res.* **21**,
582 247–262 (1973).
- 583 38. A. J. Wilson, *et al.*, An ecologist’s guide to the animal model. *J. Anim. Ecol.* **79**, 13–26
584 (2010).
- 585 39. N. E. Morton, J. F. Crow, H. J. Muller, An estimate of the mutational damage in man from
586 data on consanguineous marriages. *Proc. Natl. Acad. Sci. USA* **42**, 855–863 (1956).
- 587 40. M. Szulkin, B. C. Sheldon, The environmental dependence of inbreeding depression in a wild
588 bird population. *PLoS One* **2**, e1027 (2007).
- 589 41. Y. Willi, J. Van Buskirk, M. Fischer, A threefold genetic Allee effect: population size affects
590 cross-compatibility, inbreeding depression and drift load in the self-incompatible *Ranunculus*
591 *reptans*. *Genetics* **169**, 2255–2265 (2005).
- 592 42. M. W. Stubberud, *et al.*, Sensitivity analysis of effective population size to demographic
593 parameters in house sparrow populations. *Mol. Ecol.* **26**, 2449–2465 (2017).
- 594 43. Z. Boratyński, E. Koskela, T. Mappes, E. Schroderus, Quantitative genetics and fitness
595 effects of basal metabolism. *Evol. Ecol.* **27**, 301–314 (2013).
- 596 44. P. Opatová, *et al.*, Inbreeding depression of sperm traits in the zebra finch *Taeniopygia*
597 *guttata*. *Ecol. Evol.* **6**, 295–304 (2016).
- 598 45. A. Sewalem, K. Johansson, M. Wilhelmson, K. Lillpers, Inbreeding and inbreeding
599 depression on reproduction and production traits of White Leghorn lines selected for egg
600 production traits. *Br. Poult. Sci.* **40**, 203–208, 20180231 (1999).
- 601 46. R. A. de Boer, M. Eens, W. Müller, Sex-specific effects of inbreeding on reproductive
602 senescence. *Proc. R. Soc. B Biol. Sci.* **285** (2018).
- 603 47. C. R. Haag, J. W. Hottinger, M. Riek, D. Ebert, Strong inbreeding depression in a *Daphnia*
604 metapopulation. *Evolution* **56**, 518–526 (2002).
- 605 48. D. M. Waller, J. Dole, A. J. Bersch, Effects of stress and phenotypic variation on inbreeding

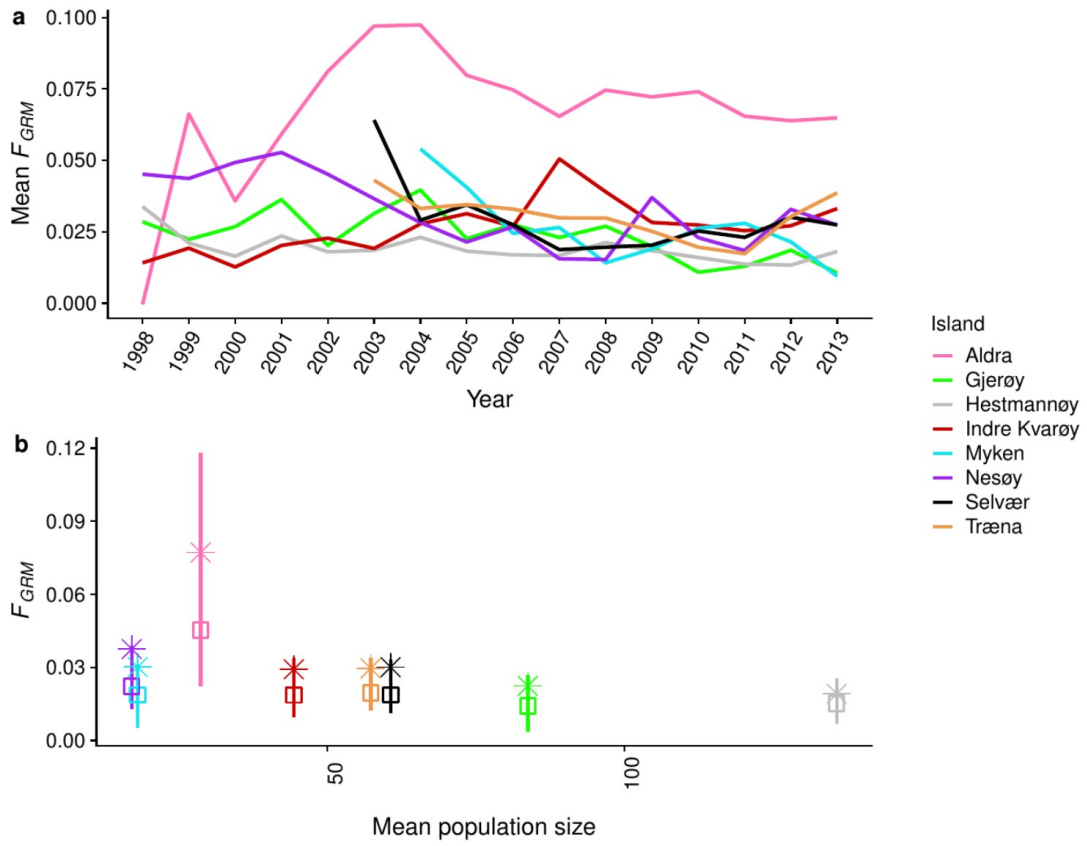
- 606 depression in *Brassica rapa*. *Evolution* **62**, 917–931 (2008).
- 607 49. H. Jensen, *et al.*, Lifetime reproductive success in relation to morphology in the house
608 sparrow *Passer domesticus*. *J. Anim. Ecol.* **73**, 599–611 (2004).
- 609 50. M. Olsson, A. Gullberg, H. Tegelström, Malformed offspring, sibling matings, and selection
610 against inbreeding in the sand lizard (*Lacerta agilis*). *J. Evol. Biol.* **9**, 229–242 (1996).
- 611 51. H. Jensen, E. M. Bremset, T. H. Ringsby, B.-E. Sæther, Multilocus heterozygosity and
612 inbreeding depression in an insular house sparrow metapopulation. *Mol. Ecol.* **16**, 4066–4078
613 (2007).
- 614 52. C. van Oosterhout, W. G. Zijlstra, M. K. van Heuven, P. M. Brakefield, Inbreeding
615 depression and genetic load in laboratory metapopulations of the butterfly *Bicyclus Anynana*.
616 *Evolution* **54**, 218–225 (2000).
- 617 53. M. A. Supple, B. Shapiro, Conservation of biodiversity in the genomics era. *Genome Biol.*
618 **19**, 1–12 (2018).
- 619 54. R. C. Lewontin, *The Genetic Basis of Evolutionary Change* (Columbia University Press,
620 1974).
- 621 55. H. Holand, *et al.*, Spatial variation in senescence rates in a bird metapopulation. *Oecologia*
622 **181**, 865–871 (2016).
- 623 56. H. Pärn, H. Jensen, T. H. Ringsby, B.-E. Sæther, Sex-specific fitness correlates of dispersal in
624 a house sparrow metapopulation. *J. Anim. Ecol.* **78**, 1216–1225 (2009).
- 625 57. J. Tufto, T. H. Ringsby, A. A. Dhondt, F. Adriaensen, E. Matthysen, A parametric model for
626 estimation of dispersal patterns applied to five passerine spatially structured populations. *Am.*
627 *Nat.* **165**, E13–E26 (2005).
- 628 58. T. O. Elgvin, *et al.*, The genomic mosaicism of hybrid speciation. *Sci. Adv.* **3**, 1–16 (2017).
- 629 59. R Core Team, R: A language and environment for statistical computing. (2019).
- 630 60. J. Huisman, Pedigree reconstruction from SNP data: parentage assignment, sibship clustering
631 and beyond. *Mol. Ecol. Resour.* **17**, 1009–1024 (2017).
- 632 61. H. Jensen, *et al.*, Sexual variation in heritability and genetic correlations of morphological
633 traits in house sparrow (*Passer domesticus*). *J. Evol. Biol.* **16**, 1296–1307 (2003).
- 634 62. H. Jensen, I. Steinsland, T. H. Ringsby, B.-E. Sæther, Evolutionary dynamics of a sexual
635 ornament in the house sparrow (*Passer domesticus*): The role of indirect selection within and
636 between sexes. *Evolution* **62**, 1275–1293 (2008).
- 637 63. M. W. Stubberud, *et al.*, Supporting Information, Sensitivity analysis of effective population
638 size to demographic parameters in house sparrow populations. *Mol. Ecol.* **26** (2017).
- 639 64. C. Albat, pedigree: pedigree functions. R package version 1.4. (2013).
- 640 65. J. Yang, S. H. Lee, M. E. Goddard, P. M. Visscher, GCTA: a tool for genome-wide complex

- 641 trait analysis. *Am. J. Hum. Genet.* **88**, 76–82 (2011).
- 642 66. R. McQuillan, *et al.*, Runs of homozygosity in European populations. *Am. J. Hum. Genet.* **83**,
643 359–372 (2008).
- 644 67. H. Rue, S. Martino, C. Nicolas, Approximate Bayesian inference for latent Gaussian models
645 by using integrated nested Laplace approximations. *J. R. Stat. Soc. Ser. B* **71**, 319–392
646 (2009).
- 647 68. M. A. Stoffel, *et al.*, inbreedR: an R package for the analysis of inbreeding based on genetic
648 markers. *Methods Ecol. Evol.* **7**, 1331–1339 (2016).
- 649 69. J. Goudet, T. Jombart, hierfstat: Estimation and tests of hierarchical F-statistics. R package
650 version 0.04-22. <https://CRAN.R-project.org/package=hierfstat> (2015).
- 651 70. T. Kvalnes, *et al.*, Reversal of response to artificial selection on body size in a wild passerine.
652 *Evolution* **71**, 2062–2079 (2017).
- 653 71. D. Bates, M. Mächler, B. M. Bolker, S. C. Walker, Fitting linear mixed-effects models using
654 lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
- 655 72. H. Holand, H. Jensen, J. Tufto, B.-E. Sæther, T. H. Ringsby, Temporal and spatial variation in
656 prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows (*Passer*
657 *domesticus*). *Parasitology* **140**, 1275–1286 (2013).
- 658 73. M. Kéry, M. Schaub, *Bayesian population analysis using WinBUGS: A Hierarchical*
659 *Perspective* (Academic Press, 2011).
- 660 74. J. Lebreton, K. P. Burnham, J. Clobert, D. R. Anderson, Modeling survival and testing
661 biological hypotheses using marked animals: a unified approach with case studies. *Ecol.*
662 *Monogr.* **62**, 67–118 (1992).
- 663 75. D. J. Lunn, A. Thomas, N. Best, D. Spiegelhalter, WinBUGS - a Bayesian modelling
664 framework: concepts, structure, and extensibility. *Stat. Comput.* **10**, 325–337 (2000).
- 665 76. M. Plummer, JAGS: A program for analysis of Bayesian graphical models using Gibbs
666 sampling in *Proceedings of the 3rd International Workshop on Distributed Statistical*
667 *Computing*, (2003), pp. 1–10.
- 668 77. K. F. Kellner, jagsUI: a wrapper around “rjags” to streamline “JAGS” analyses. R Package
669 version 1.5.0. Available from <http://CRAN.R-project.org/package=jagsUI>.
- 670 78. L. E. B. Kruuk, Estimating genetic parameters in natural populations using the “animal
671 model.” *Philos. Trans. R. Soc. B Biol. Sci.* **359**, 873–890 (2004).
- 672 79. A. M. Holand, I. Steinsland, S. Martino, H. Jensen, Animal models and Integrated Nested
673 Laplace Approximations. *G3 Genes, Genomes, Genet.* **3**, 1241–1251 (2013).
- 674 80. P. Nietlisbach, S. Muff, J. M. Reid, M. C. Whitlock, L. F. Keller, Nonequivalent lethal
675 equivalents: Models and inbreeding metrics for unbiased estimation of inbreeding load. *Evol.*
676 *Appl.* **12**, 266–279 (2019).

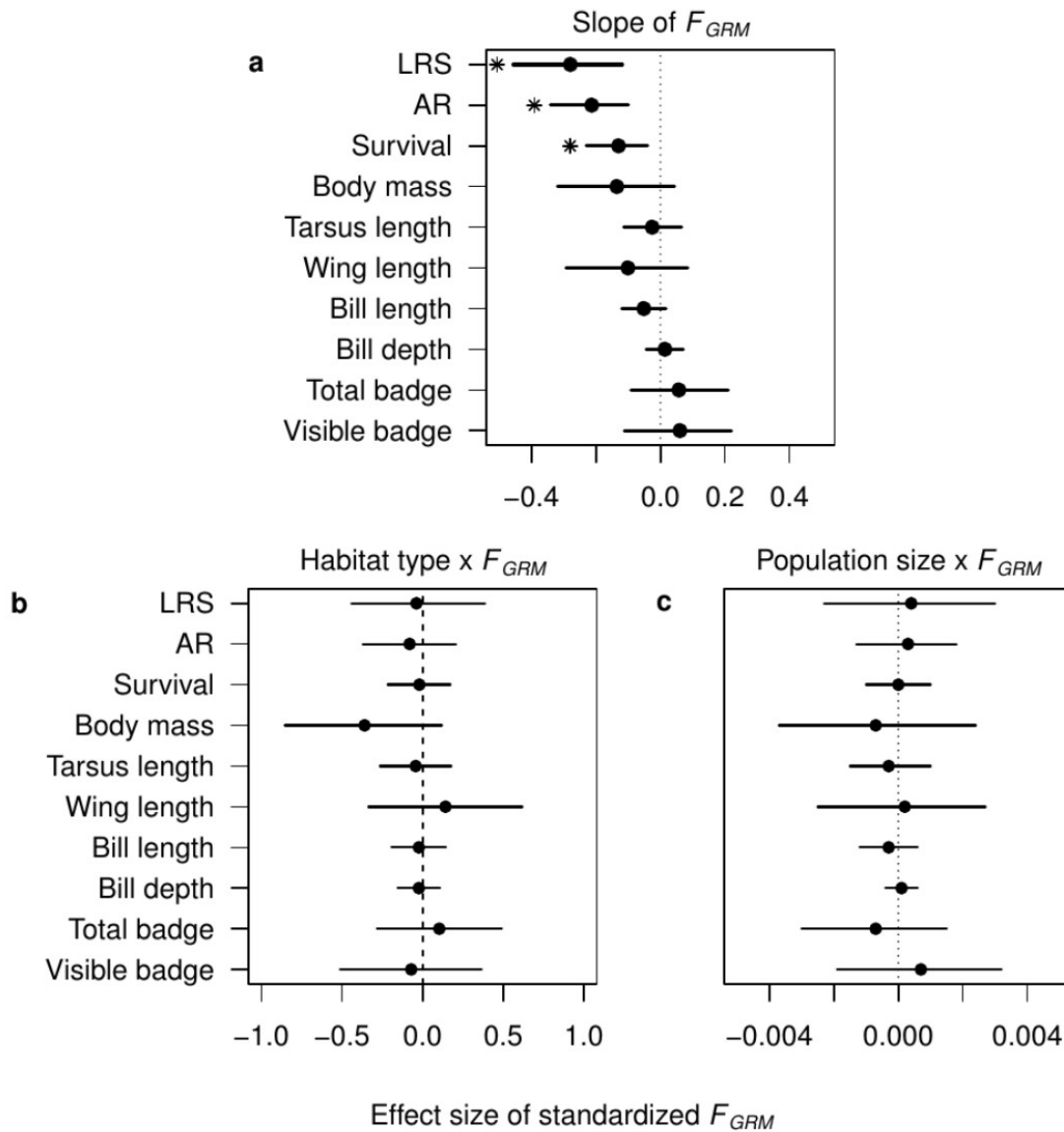
- 677 81. A. Gelman, *et al.*, *Bayesian data analysis* (Chapman & Hall/CRC Texts in Statistical
678 Science, 2013).
- 679 82. P. I. Good, *Permutation Tests: A practical guide to resampling methods for testing*
680 *hypotheses* (Springer-Verlag, 2000).
681



685 **Fig. 1** Map of the approximately 1600 km² house sparrow study system at the Helgeland coast in
686 Norway. The 18 islands in the study metapopulation are shown in black, and other islands (without
687 sparrows) and the mainland in grey. The eight islands included in the current study are indicated
688 with their names. The study system consists of two distinct habitat types: i) farm islands (turquoise
689 names), and ii) non-farm islands (orange names), where the sparrows live on dairy farms and in
690 gardens, respectively.

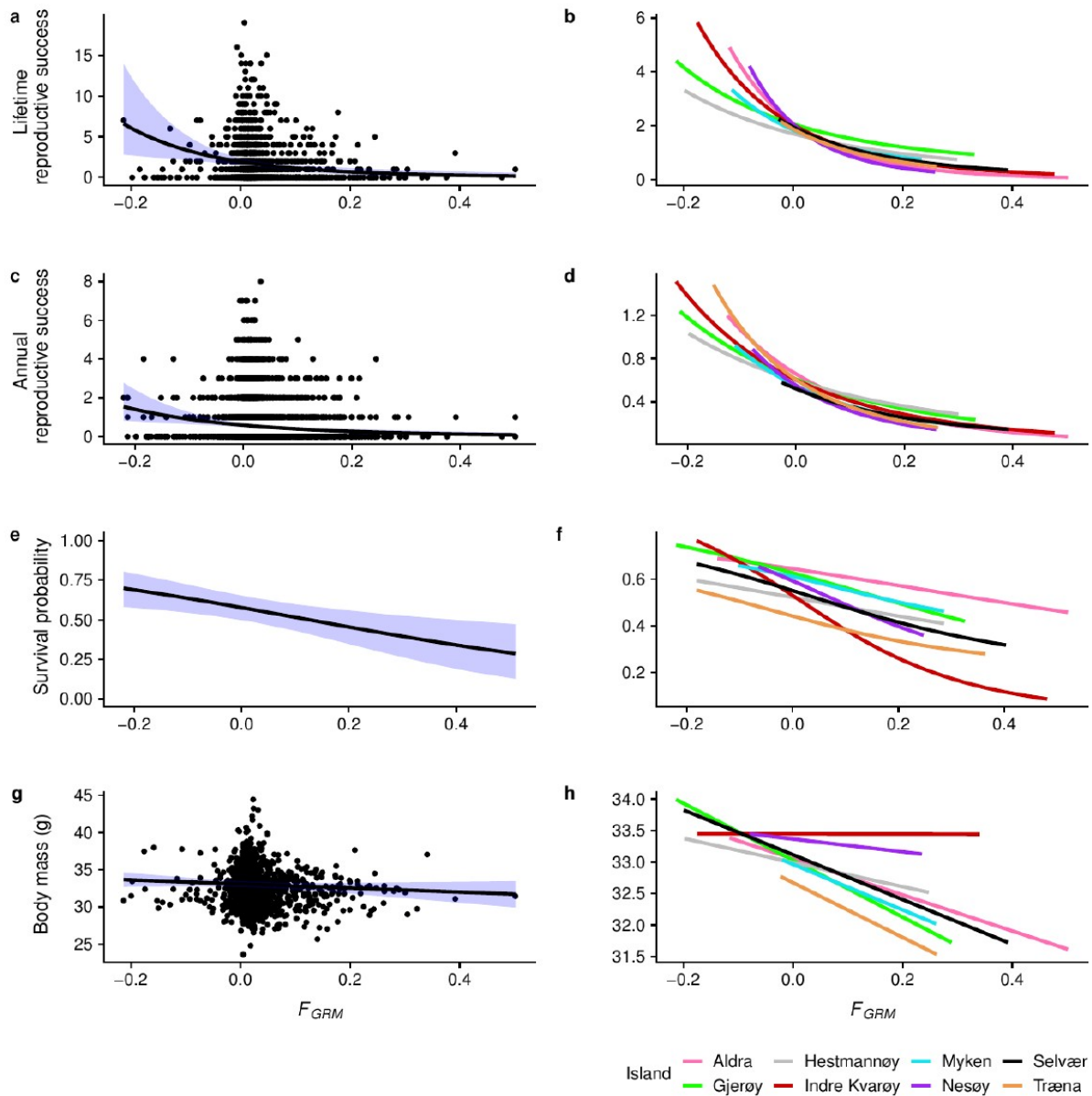


693 **Fig. 2** Inbreeding levels of adult individuals on each study island. **a**, Mean inbreeding coefficient
 694 (F_{GRM}) on each study island over the study period. **b**, The median (\square), interquartile range ($|$) and
 695 mean ($*$) of F_{GRM} on each island plotted against the mean population size over the study period.



697

698 **Fig. 3** Estimates of main effect of inbreeding and its interaction with environmental variables on
 699 life-history and morphological traits. **a**, Effect of inbreeding estimated with standardised F_{GRM} on
 700 survival probability, lifetime reproductive success (LRS), annual reproductive success (AR), and
 701 seven morphological traits. **b**, Interaction effect between F_{GRM} and habitat type (farm island as the
 702 baseline) on the same fitness components and morphological traits as in **a**. **c**, Interaction effect
 703 between F_{GRM} and annual population size on the studied traits. Results are from animal models fitted
 704 in INLA for LRS, AR and morphological traits, and from capture-mark-recapture models fitted in
 705 JAGS for survival probability. The interaction terms between habitat type, annual population size
 706 and sex with F_{GRM} were included in the models fitted for **b** and **c**, but not in the model fitted for **a**.
 707 Posterior mean effect size is indicated with a dot, and the corresponding 95% Bayesian credible
 708 interval (BCI) with a horizontal line. A strong effect, when the 95% BCI does not overlap zero, is
 709 indicated with an asterisk (*).



711 **Fig. 4** The effect of inbreeding on reproductive success, survival and body mass. In **a,c,e,** and **g**,
 712 lines are predicted mean effects of inbreeding (F_{GRM}) over the metapopulation system, shaded blue
 713 areas show 95% credible intervals, and individual observations are plotted as points (omitted from **e**
 714 for clarity). Panels **b, d, f,** and **h** show island specific predicted mean effects of inbreeding. Lifetime
 715 reproductive success (**a, b**) and annual reproductive success (**c, d**) were estimated as the number of
 716 offspring recruiting the adult population that an individual produced during its lifetime or per year,
 717 respectively. (**e, f**) The relationship between survival probability and inbreeding. Body mass (**g, h**)
 718 is based on all adult measurements and adjusted to trait value as one-year-old. The predicted lines
 719 were produced using animal models fitted in INLA (**a-d, g** and **h**), or capture-mark-recapture
 720 models in JAGS (**e** and **f**). The results of these models are presented in SI Appendix, Table S5.