1 **Is basal metabolic rate associated with recruit production and survival in**

2 **free-living house sparrows?**

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15 Running headline: Fitness effects of BMR

Summary

1. Life history theory predicts that available energy is limited and needs to be allocated among different processes such as growth, reproduction and self-maintenance. Basal metabolic rate (BMR), a common measure of an animal's maintenance cost, is therefore believed to be a trait of ecological and evolutionary significance. However, although BMR is often assumed to be correlated with fitness, its association with individual variation in fitness in free-living populations is virtually unknown.

2. We examined the relationship between BMR in late winter prior to the breeding season and recruit production (number of offspring recorded the subsequent year), as well as adult survival, in two populations of house sparrow (*Passer domesticus*) on the islands Leka and Vega in northern Norway.

3. Number of recruits tended to be negatively related to BMR. However, analysing the data for each sex within the two populations revealed that the negative effect of BMR on recruit production was significant only for females on one of the islands.

4. Survival probability was associated with BMR, but the relationship differed both between sexes and populations. In the Leka population, we found evidence for stabilizing selection in the females and disruptive selection in the males. In contrast, there was no effect of BMR on survival in the Vega population.

5. Body mass influenced adult survival, but not recruit production. Furthermore, the relationship between BMR and fitness in females remained significant after controlling for body mass. Thus, the selection on BMR in females was not driven by a BMR-body mass correlation.

6. Basal metabolic rate was significantly related to fitness in both populations. However, the results in the present study show spatial variation as well as sex specific differences in the influence of BMR on fitness in house sparrows.

Introduction

Basal metabolic rate (BMR) is the lowest level of metabolic output of an endothermic organism in a normothermic state and represents an animal's maintenance cost (McNab 2002). This maintenance cost constitutes between 25 and 40 % of birds total energy expenditure in the field (Bryant 1997) and is therefore believed to be of ecological relevance. Basal metabolic rate shows great variation both between and within species, and the sources of variation have been extensively studied (Burton *et al*. 2011; Konarzewski & Książek 2013; White & Kearney 2013). Variation in BMR between species appears to be linked to basic life history characteristics. For example, tropical birds located at the slow end of the slow-fast continuum of life history variation (Sæther & Bakke 2000) are characterized by a low BMR compared to birds living in temperate environments belonging to the opposite end of the life-history continuum (Wiersma *et al*. 2007; Williams *et al*. 2010). At the intraspecific level common garden studies on passerine birds have shown differences in BMR between populations originating from different climates (e.g. Wikelski *et al*. 2003; Broggi *et al*. 2005; Maggini & Bairlein 2013), indicating an adaptive variation in BMR (Furness, 2003). Furthermore, avian (Rønning *et al*. 2007; Nilsson, Åkesson & Nilsson 2009; Tieleman *et al*. 2009; Bushuev, Kerimov & Ivankina 2011; Mathot *et al*. 2013) as well as mammalian (Konarzewski, Książek & Łapo 2005; Sadowska *et al*. 2005; Wone *et al*. 2009; Boratyński *et al*. 2013) studies provide growing evidence for significant additive genetic variance in this trait. These finding are further supported by the fact that BMR responds to artificial selection

62   (e.g. Książek, Konarzewski & Łapo 2004). However, in spite of being a trait that has been

63   found to exhibit additive genetic variation and been shown to respond to selection, the link

64   between BMR and fitness is still poorly understood.

65   The sign of the relationship between BMR and individual fitness, if any, is not obvious

66   and arguments have been put forward for either a positive or a negative relationship.

67   According to life history theory, available energy is limited and a fixed resource budget needs

68   to be allocated between various biological processes such as growth, reproduction and self-

69   maintenance (Gadgil & Bossert 1970; Roff 1992; Stearns 1992). Consequently, individuals

70   with low BMR should perform better because their lower self-maintenance cost enables them

71   to allocate more energy towards fitness-enhancing processes like growth and reproduction.

72   Hence, a negative relationship between BMR and reproduction should exist ('compensation'

73   hypothesis; Nilsson 2002). On the other hand, it has been argued that the ability to support a

74   high level of activity requires morphology with a high maintenance cost, i.e. high BMR (e.g.

75   Bennett & Ruben 1979; Hayes & Garland 1995). A high BMR is often associated with large

76   internal organs, including the alimentary tract (Lindström & Kvist 1995; Chappell, Bech &

77   Buttemer 1999). Individuals with high BMR may therefore have the capacity to eat more

78   food and convert it into usable energy at a higher rate. Basal metabolic rate has in turn been

79   found to correlate with total energy expenditure in free-living birds (Daan, Masman &

80   Groenewold 1990), but see Ricklefs, Konarzewski & Daan (1996). If BMR is functionally

81   linked to working capacity, a positive relationship between BMR and reproduction should be

82   expected ('increased intake' hypothesis; Nilsson 2002).

83   Although studies on the relationship between energy metabolism and fitness are few

84   (Burton *et al.* 2011), some evidence is now accumulating that BMR is related to differences

85   in reproductive success of birds. For instance, in male Leach's storm-petrels (*Oceanodroma*

86   *leucorhoa*) individuals with low BMR during the incubation period produced more offspring

87   by starting breeding earlier in the season (Blackmer *et al*. 2005). Conversely, Chastel,

88   Lacroix & Kersten (2003) found that house sparrows (*Passer domesticus*) with high pre-

89   breeding plasma triiodothyronine levels, a hormone related to BMR in the studied population,

90   raised more offspring. However, in great tits (*Parus major*) Bouwhuis *et al*. (2014) found no

91   evidence for directional selection on BMR when using the number of offspring produced

92   during the breeding season as a measure of fitness. Instead males with an average BMR

93   produced more offspring. Studies on laboratory rodents suggest that reproductive

94   performance is unrelated to BMR (Derting & McClure 1989; Hayes, Garland & Dohm 1992;

95   Johnson, Thomson & Speakman 2001; Johnston *et al*. 2007). To our knowledge only one

96   study has investigated the association between reproduction success and BMR in a free-living

97   mammal population, where Boratyński & Koteja (2010) found that BMR was positively

98   associated with overall reproductive success in the bank vole (*Myodes glareolus*).

99   In the only study investigating the association between BMR and survival in a free

100   living bird population; Bouwhuis *et al*. (2014) found no relationship between winter BMR

101   and survival in great tits. However, in mammals, Larivée *et al*. (2010) found evidence for

102   negative selection on resting metabolic rate, a trait closely related to BMR, in juvenile North

103   American red squirrel (*Tamiasciurus hudsonicus*), whereas selection in the opposite direction

104   has been found in short tailed voles (*Microtus agrestis*; Jackson, Trayhurn & Speakman

105   2001). Furthermore, BMR was found to affect over-winter survival in two geographically

106   separated bank vole populations, but the selection on BMR differed both between sexes and

107   seasons (Boratyński & Koteja 2009; Boratyński *et al.* 2010).

108   Results from studies investigating the relationship between variation in BMR and life

109   history and behavioural parameters important for individual fitness provide inconclusive

110   evidence for BMR as an important fitness-related trait (Biro et al. 2010; Burton *et al*. 2011;

111   Šíchová et al. 2014). Furthermore, much of our knowledge is based on studies conducted on

112   animals in captivity which may not be representative of free-living animals, which most

113   likely are facing different trade-offs between reproduction and other energy consuming tasks

114   like foraging, thermoregulation and predator avoidance. Hence, within the field of

115   evolutionary physiology there is great need for empirical studies on fitness consequences of

116   individual variation in BMR in free-living populations. In the present study we therefore

117   examined the relationship between BMR and important components of fitness in free-living

118   populations of a passerine bird. We measured BMR in adult house sparrows in late winter

119   prior to the breeding season. As a measure of fitness, we used number of recruits recorded the

120   subsequent year and adult survival to the next winter. First, we investigated whether natural

121   selection acted on BMR with respect to recruit production, by testing whether the relationship

122   was directional (as predicted by the 'compensation' and 'increased intake' hypothesis),

123   versus nonlinear (indicating stabilizing or disruptive selection). We then investigated whether

124   natural selection acted on BMR with respect to adult survival from one season to the next.

125   Whole body BMR, i.e. not controlled for the effect of body mass, is used in an ecological

126   context as a predictor of the cost of living (e.g. Tieleman *et al.* 2009), and is consequently a

127   potential target of selection. However, because body mass may influence both BMR and

128   fitness, we also fitted models which included body mass, in order to examine the residual

129   effect of BMR on fitness.

130

131   **Materials and methods**

132

133   STUDY SPECIES AND STUDY AREA

134

135   The study was conducted in 2007 and 2008 using two house sparrow (*Passer domesticus*,

136   Linnaeus, 1758, Fig. 1) populations living on the islands Leka (65.1 ºN 11.6 ºE) and Vega

137 (65.7 ºN 11.9 ºE) off the coast of northern Norway. These populations are included in a long

138 term study and nearly all birds (>90%) present on the two islands have been captured and

139 banded annually during winters 2002-2014. The house sparrows on these islands live in close

140 proximity to human settlements, and usually nest and seek shelter inside barns and cowsheds.

141 Birds were captured by mist-netting inside or close to farm buildings. Each bird was banded

142 with a metal ring, and a unique combination of coloured plastic rings to allow identification

143 with telescopes. To allow easier estimation of the overall proportion of birds captured during

144 the study, birds were continuously transferred to an empty barn (from now on referred to as

145 aviary) where they were provided water and food (bread, grain, grain feed and sunflower

146 seeds) *ad libitum*. After the experiment period, birds were released at the same location as

147 they were captured.

148

149 MORPHOLOGICAL AND PHYSIOLOGICAL MEASUREMENTS

150

151 Body mass was measured with a Pesola spring balance (to the nearest 0.1 g.). A small blood

152 sample (~25 µL) was collected from the brachial vein and stored on 96% ethanol for later

153 DNA genotyping. In 2007 measurements of BMR were obtained for 105 individuals on Leka

154 during the period 13-27.02 and for 89 individuals on Vega during the period 2-15.03.

155   Basal metabolic rate was measured as oxygen consumption rates using an open flow

156 system. Dried outside air was pumped (500 mL min^{-1}) through four metabolic chambers (1.1

157 L) located inside a climate cabinet at ca. 30.5 ºC, i.e. within the thermoneutral zone for the

158 house sparrow (Hudson & Kimzey 1966). Air flow into the chambers was adjusted using

159 calibrated Bronkhorst High-Tech mass flow meters (Ruurlo, The Netherlands), and a

160 Servomex type 4100 two-channel oxygen analyser (Crowborough, England) measured the

161 oxygen concentration in dried effluent air. An automatic valve-system switched between two

and two chambers (every 30 min), and the voltage output from the oxygen analyser, the flow

meters and thermocouples inside the metabolic chambers were stored every 30 s. on a Grant

Squirrel, type 1200 data logger (Cambridge, England). The baseline gas level (without birds

in the chambers) was recorded for one hour before and after each trial to enable correction for

linear analyser drift during the measurement period. The rate of oxygen consumption (VO_2)

was calculated following Withers (2001), using a respiratory quotient of 0.71. The lowest 10

min running average VO_2 value was used to represent BMR.

To reduce time spent in aviaries, birds were measured in two sessions per day, either in

the evening between 16:00 and 22:30 local time, or during the night from 23:00 to 08:00.

Note that in northern Norway day length is short in February and March. The average daily

light cycle during the measurement period was 10L:14D (light: 07:30 - 17:30 local time).

Consequently, the birds were measured during their normal resting phase, irrespectively of

whether they were measured late in the evening or during the night.

Birds were captured at different locations around the islands between 10:00 and 15:00,

and from these birds we selected eight individuals to be measured the same day, while the

rest of the birds were transferred to the aviary to be recaptured and measured another day.

Thus, some birds were measured before they were put in the aviary, while other birds were

measured after spending some days inside the aviary (mean 6 days; range 1-14 days).The

birds went through the same experimental protocol irrespective of whether they were

processed the same day as they were captured or if they were recaptured (around 15:00)

inside the aviary. Four birds were placed directly in the metabolic chambers for metabolic

measurements, whereas the remaining four birds were placed in individual cages until the

start of their measurements at 23:00. To ensure that the birds held in cages did not starve, but

at the same time reached a post absorptive state during measurement, they were supplied with

a small piece of moist bread while in the cage. Immediately after the birds were taken out of

187   the metabolic chamber they were released into the aviary in a section separated from birds

188   not yet measured.

189   Both measurement duration and circadian rhythm may affect physiological variables

190   (Page, Cooper & Withers 2011). However, neither number of days inside the aviary before

191   measurement nor measurement period (evening or night) affected oxygen consumption

192   significantly (Table S1 in Supporting Information). Thus, the metabolic measurements are

193   referred to as BMR regardless of being obtained in the evening or during the night.

194   Descriptive statistics of BMR and body mass are given in Table 1.

195

196   ESTIMATION OF FITNESS COMPONENTS

197

198   None of the birds measured for BMR in 2007 and assumed to be dead in 2008 were observed

199   in a subsequent year (until 2014). Thus, we are confident that a bird not observed during field

200   work in 2008 could be considered dead and we did not account for recapture rate in the

201   analyses (Lebreton *et al.* 1992). Furthermore, due to the high recapture rate in the study

202   system, we assumed that any unmarked bird captured in the winter was born the previous

203   year. These individuals were considered as being recruits to the breeding population and were

204   included as recruiting offspring in the calculations of reproductive success of putative parents

205   (i.e. previously marked birds). No data was collected during the breeding season. Thus, data

206   on e.g. number of eggs and fledglings is not available. A detailed description of the genetic

207   analysis and determination of parentage is provided in Appendix S1 in Supporting

208   Information. In short, birds were genotyped using 14 highly polymorphic microsatellite

209   markers. Microsatellite markers were amplified using polymerase chain reaction (PCR) and

210   their alleles separated by electrophoresis in an automated 16 capillary ABI Prism 3130xl

211   Genetic Analyser (Applied Biosystems, USA). Individual alleles at each microsatellite locus

212   were scored using the software GENEMAPPER 4.0 (Applied Biosystems, USA). The

213   parentage analysis software CERVUS version 3.0 (Kalinowski, Taper & Marshall 2007) was

214   used to determine the genetic parentage. All adult birds present on the islands in

215   February/March 2007 were classified as potential parents of any unmarked birds captured

216   during the 2008 field season assumed to be recruits from the previous breeding season. On

217   Leka, we identified the genetic father for 66.7% and the genetic mother for 69.2% of the

218   recruits. On Vega 62.3% and 81.2% of the recruits was assigned a genetic father and mother,

219   respectively.

220

221   STATISTICS

222

223   Variation in BMR was analysed in a generalized linear model (GLM) including body mass,

224   age, number of days in aviary, island (population), sex and measurement period (evening or

225   night) as explanatory variables. To test for differences between sexes and populations in the

226   effect of the other predictor variables, two- and three-way interactions between sex, island

227   and the other variables were included. The effect of BMR on fitness was examined in two

228   stages. First we tested for differences in selection between the populations and sexes by

229   investigating the effect of BMR on fitness (number of recruits and survival) in the pooled

230   data by including the linear and quadratic effects of BMR and the two- and three-way

231   interactions between sex, island and BMR. Secondly, linear and quadratic effects of BMR on

232   fitness were analysed separately for each sex in the two populations. Furthermore, as

233   variation in BMR was explained by body mass and age, we also examined the partial effect

234   of BMR on fitness by including body mass (measured shortly after the birds were captured)

235   and age in the models. To remove the correlation between linear and quadratic terms, values

236   of BMR and body mass were mean-centred within all birds in the pooled data analysis and

237   within the sexes in each population in the separate analysis. The models investigating the

238   effect on recruit production for the pooled data and for the males from both Leka and Vega

239   showed evidence of over-dispersion ('dispersiontest', R package AER, Kleiber & Zeileis

240   2008). Consequently, we applied negative binomial generalized linear models with a log link

241   using the function 'glm.nb' (including a parameter to model over-dispersion) in the R

242   package MASS (Venables & Ripley 2002). In females, number of recruits were analysed

243   using GLMs with a Poisson error distribution and a log link. The association between BMR

244   and survival was tested in a logistic regression, using a binomial GLM with a logit link

245   function. Survival was coded as a binary variable; alive the subsequent year (1) or not (0).

246   Note that standardized selection differentials and gradients, calculated following Lande &

247   Arnold (1983), are given in Supporting Information to allow for comparison of strength of

248   selection with other studies (Table S4). All statistical analyses were performed in R ver.

249   2.15.3 for Windows (R Development Core Team 2013).

250

251   **Results**

252

253   RECRUIT PRODUCTION

254

255   In the analysis including all individuals, BMR tended to be negatively associated with recruit

256   production (β = -0.022, χ^2_1 = 3.777, P = 0 .052, Table S2 in Supporting Information).

257   However, when analysing the data separately for each sex on each island, the relationship

258   between BMR and recruit production was only apparent in females. For females in the Vega

259   population, we found that lower BMR was associated with higher recruit production (Fig. 2).

260   Furthermore, the negative effect of BMR on number of recruits produced by the females on

261   Vega was significant also when controlling for body mass (Table 2). In the Leka population,

262 there was no significant linear relationship between BMR and recruit production, but females

263 with an intermediate BMR tended to produce more recruits as indicated by the quadratic term

264 (Fig. 2). The second-order effect was reduced when body mass was included in the model,

265 indicating that the apparent selection on BMR was partly mediated through indirect selection

266 on body mass (Table 2). In males, BMR did not influence number of recruits in any of the

267 two populations studied (Fig. 2, Table 2). Although the effect of BMR on recruit production

268 differed slightly between the sexes and populations (Fig. 2), the slopes did not differ

269 significantly (Table S2). Furthermore, neither body mass nor age affected recruit production

270 significantly in any sex in the populations studied (Table 2)

271

272 SURVIVAL

273

274 The linear and quadratic effect of BMR on survival differed between the sexes, as well as

275 between the populations (Table S2). We found no evidence for an effect of BMR on survival

276 on Vega, in neither sex. This was true both without (Fig. 2) and with body mass in the models

277 (Table 2). In the Leka population, there was no significant linear relationship between

278 survival and BMR. Instead, for the females we found a negative quadratic effect of BMR on

279 survival (Fig. 2). Furthermore, after controlling for body mass, the quadratic effect of BMR

280 on survival in the females was still highly significant (Table 2). For the males on Leka

281 survival tended to be higher in individuals with high and low BMR (Fig. 2). When

282 controlling for body mass, the positive quadratic relationship between survival and BMR was

283 significant (Table 2), indicating disruptive selection on BMR which was independent of body

284 mass.

285   In contrast to recruit production, survival was related to body mass. In the Vega

286 population, there was a linear effect of body mass on survival, but the direction of selection

287 differed between the sexes. In females the probability of survival decreased with increasing

288 body mass, whereas in males survival probability increased with body mass (Table2). In

289 males on Vega survival also increased with age (Table 2). For females in the Leka

290 population, survival probability increased with increasing body mass, whereas for males we

291 found evidence for stabilizing selection on body mass based on survival from 2007 to 2008

292 (Table 2).

293

294 **Discussion**

295

296 This study has demonstrated different patterns in the influence of BMR on both survival and

297 fecundity in two populations of house sparrows. In the population on Vega, BMR was

298 negatively related to recruit production in the females, and this relationship was present also

299 after controlling for body mass. Hence, the effect of BMR on recruit production was not

300 driven by indirect phenotypic influence of body mass. This implies that females with low

301 maintenance cost independent of body mass invested more energy into reproduction,

302 compared to high BMR females. This finding is in contrast with a previous study of house

303 sparrows further south (46.1 ºN) where individuals with high BMR prior to breeding season

304 produced more offspring, mainly as a consequence of starting breeding earlier in the season

305 and having more clutches (Chastel, Lacroix & Kersten 2003). Unfortunately, we cannot

306 determine whether individual differences in the number of recruits produced are due to

307 variation in the number of fledglings produced, differences in survival from fledging to

308 recruitment, or a combination of these factors. However, number of fledglings has previously

309 been shown to be a good predictor for number of recruits in passerine birds (e.g. Grant &

310 Grant 2000), making differences in number of fledglings produced the most plausible

311 explanation. In the Leka population there was no directional association between BMR and

312   production of recruits. Instead, females with an average BMR tended to produce more

313   recruits. Stabilizing selection on mass-corrected BMR based on number of hatchlings

314   produced has previously been found in free-living passerines (Bouwhuis *et al*. 2014).

315   However, when controlling for body mass in the present study the tendency of a stabilizing

316   selection on BMR was weakened, which may suggest that the influence of BMR was partly

317   driven by the correlation with body mass.

318   Basal metabolic rate is known to be a flexible trait, and to test the 'compensation' and

319   'increased intake' hypothesis metabolic measurements should ideally been obtained during

320   the energetically challenging breeding period. However, we measured BMR in February and

321   March, approximately 1.5-2 months before the start of the breeding season in these

322   populations (Kvalnes *et al.* 2013). Basal metabolic rate is generally found to be a repeatable

323   trait (Nespolo & Franco 2007). Thus, when discussing our results on the association between

324   BMR and recruit production, we assume that differences in BMR found among individuals

325   prior to the breeding season partly reflects differences in maintenance cost during breeding

326   (but see Bouwhuis, Sheldon & Verhulst 2011). The directional negative relationship between

327   BMR and reproduction found in the present study indicates that individuals with low

328   maintenance cost were able to devote more energy to reproduction, which supports the

329   'compensation' hypothesis (Gadgil & Bossert 1970; Nilsson 2002). However, although BMR

330   tended to have a negative effect on recruit production in the house sparrows, we have to

331   emphasize that this was only significant in females in one of the study populations. In

332   agreement with a previous study conducted in four Norwegian house sparrow populations

333   showing no effect of body mass on total recruit production measured as lifetime reproductive

334   success (Jensen *et al*. 2004), body mass was not found to be a significant predictor for recruit

335   production in any of the sexes in neither population in the present study (see also Jensen et al.

336   2008). Furthermore, although reproductive performance in birds is known to improve with

337 age (e.g. Forslund & Pärt 1995), we found no effect of age on recruit production in our study

338 populations.

339   We found no evidence for a directional association between BMR and survival. This

340 agrees with another study on a free-living passerine species, showing no effect of BMR on

341 survival of great tits (Bouwhuis *et al*. 2014). Contrary to the study on great tits, we found

342 evidence for a nonlinear relationship between BMR and survival in the house sparrows. In

343 the Leka population, the selection on BMR was stabilizing in the females, but disruptive in

344 the males. The fact that females with an average BMR were more likely to survive indicates

345 that there could be trade-offs between costs (e.g. compromised immunocompetence: Książek

346 *et al*. 2007) and benefits (e.g. increased cold tolerance: Liknes & Swanson 1996) of having a

347 high BMR. Based on the data in hand, we are unable to determine the underlying reasons for

348 why such trade-offs do not seem to apply for females on Leka and neither sex on Vega.

349 Nevertheless, because the house sparrows in our study populations spend much time inside

350 barns during the winter, they may not face trade-offs to the same degree as wintering forest

351 species which typically experience low temperatures as well as low food predictability

352 (Broggi *et al.* 2004).

353   The main predictor of survival in the house sparrow populations studied was body

354 mass. In the house sparrow population on Vega selection on body mass operated in opposite

355 directions in the sexes, being positive in the males and negative in the females. A difference

356 between the sexes was also found in the Leka population where an increase in survival with

357 increasing body mass was observed for females, whereas a stabilizing selection on body mass

358 was observed for males. Sexual differences in selection on body mass was not found in a

359 previous study of house sparrows living on the coast of northern Norway, which found body

360 mass to be positively related to survival in both sexes (Jensen *et al.* 2008). The effect of body

361 mass on fitness was not the main objective of the present study. Nonetheless, our results

362 indicate that costs and benefits of high body mass probably differed between the sexes, and

363 that this resulted in different relationships with survival. Furthermore, an interesting

364 observation in the Leka population was that the effects of body mass and BMR on male

365 survival differed indicating that these traits may evolve in different directions. This is

366 however depending on both traits being heritable and exhibiting independent additive genetic

367 variance (e.g. Lynch & Walsh 1998).

368   In the present study we found evidence for a link between BMR and fitness, but this

369 was more pronounced in female house sparrows. Although, studies investigating the link

370 between BMR and fitness in free-living population are scarce, sexual differences in the

371 association between BMR and fitness related components have been shown earlier in avian

372 studies (Blackmer *et al.* 2005; Bouwhuis *et al.* 2014). Furthermore, selection on BMR has

373 been found to differ both between sexes and seasons in free-living rodents (Boratyński &

374 Koteja 2009, 2010). Hence, several studies (including the present) investigating the

375 association between BMR and life history parameters important for individual fitness have

376 failed to find a general pattern. Based on this observation one could argue that a single

377 optimal BMR probably does not exist. However, it has to be mentioned that most studies

378 investigating the link between BMR and fitness are correlative studies measuring the effect of

379 BMR on short-term fitness. Fitness relationships may also be revealed by manipulating

380 genetic architecture (Ketola, Boratyński & Kotiaho 2014; see also Abbott 2014). Evidence

381 from studies using this approach is still limited, but suggests that the predominant direction of

382 past selection on BMR in e.g. bank voles has been negative (Ketola, Boratyński & Kotiaho

383 2014; Boratyński *et al.* 2013). Thus, at present we cannot exclude the possibility that there

384 might be a general trend of limiting maintenance cost which correlative studies measuring

385 short-term fitness effects fail to reveal. Nevertheless, it has been proposed that the association

386 between BMR and fitness probably varies temporarily and spatially depending on

387 environmental factors such as e.g. food availability, predator abundance and temperature

388 (Mathot *et al*. 2009; Boratyński & Koteja 2010; Larivée *et al.* 2010; Burton *et al*. 2011).

389 Looking at morphological traits, changes in direction of selection are frequently observed in

390 nature (e.g. Siepielski, DiBattista & Carlson 2009). More studies are needed to determine if

391 this also apply to physiological traits like e.g. BMR. However, the persistence of large

392 variation in BMR between and among species indicates that it is unlikely to be a single

393 metabolic phenotype which is favourable under all environmental conditions. Thus, the effect

394 of different stochastic environmental factors on the association between metabolic traits and

395 fitness warrants further investigation.

396

Acknowledgments

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409

Data Accessibility

411   All data are included in the manuscript and supporting information.

412

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605

Supporting Information

607   Additional supporting information may be found in the online version of this article.

608   **Appendix S1:** Description of the genetic analysis and determination of parenthood

609   **Appendix S2:** Data used in the study

610   **Table S1**: Sources of variation in BMR

611   **Table S2:** Relationship between BMR and fitness (pooled data)

612   **Table S3:** Relationship between BMR and fitness (separately for island and sex)

613   **Table S4:** Standardized selection differentials and gradients for BMR and body mass.

614

615

616　Table 1. Descriptive statistics of basal metabolic rate (BMR) and body mass in house

617　sparrows from Vega and Leka, Norway.

Population	Trait	Females				Males			
		N	Mean	S.D.	Range	N	Mean	S.D.	Range
Vega	BMR (mL O_2 h^{-1})	39	77.54	9.04	53.46 - 98.61	50	79.53	9.50	58.24 - 96.95
	Body mass (g)	39	30.76	1.73	27.50 - 33.90	50	31.67	2.12	26.60 - 37.70
Leka	BMR (mL O_2 h^{-1})	52	82.73	6.77	67.08 - 96.18	53	81.51	7.32	62.85 - 97.82
	Body mass (g)	52	31.81	2.04	27.50 - 36.90	53	32.01	1.45	28.80 - 35.00

618

619 Table 2. The association between basal metabolic rate (BMR, mL O_2 h^{-1}), body mass (g), age

620 (years) and components of fitness in two populations of house sparrows in northern Norway.

Population		Recruit production[*]			Survival[†]		
VEGA	Predictor variables	Estimate	χ_1^2	P	Estimate	χ_1^2	P
Females	Intercept	**0.755**	**7.553**	**0.006**	0.985	0.617	0.432
(N = 39)	BMR	**-0.034**	**6.281**	**0.012**	0.011	0.066	0.797
	BMR^2	-1e-4	0.160	0.690	1e-4	0.002	0.967
	Body mass	-0.011	0.026	0.873	**-0.528**	**5.498**	**0.019**
	Body mass^2	-0.033	1.095	0.295	0.018	0.023	0.878
	Age	0.137	0.967	0.325	-0.528	1.165	0.280
Males	Intercept	-0.332	0.570	0.450	**-1.807**	**4.289**	**0.038**
(N = 50)	BMR	-0.015	0.271	0.603	-0.067	1.854	0.173
	BMR^2	0.002	0.692	0.406	0.005	1.525	0.217
	Body mass	0.114	0.658	0.417	**0.839**	**11.162**	**<0.001**
	Body mass^2	0.015	0.194	0.660	-0.039	0.187	0.666
	Age	0.203	1.411	0.235	**0.986**	**4.870**	**0.027**
LEKA							
Females	Intercept	-0.762	2.538	0.111	0.561	0.465	0.495
(N = 52)	BMR	-0.017	0.163	0.687	0.047	0.343	0.558
	BMR^2	-0.009	3.152	0.076	**-0.030**	**10.920**	**<0.001**
	Body mass	-0.116	1.176	0.278	**0.425**	**4.798**	**0.029**
	Body mass^2	0.019	0.309	0.578	-0.010	0.022	0.882
	Age	0.093	0.213	0.645	-0.157	0.207	0.649
Males	Intercept	-0.246	0.195	0.659	-0.465	0.347	0.556
(N = 53)	BMR	-0.050	1.134	0.287	-0.044	0.639	0.424
	BMR^2	-0.003	0.549	0.459	**0.011**	**5.163**	**0.023**
	Body mass	-0.087	0.131	0.718	0.094	0.077	0.782
	Body mass^2	-0.212	2.767	0.096	**-0.427**	**6.264**	**0.012**

| Age | -0.013 | 0.002 | 0.968 | -0.194 | 0.206 | 0.650 |

621

622 *Recruit production = number of recruits recorded the subsequent year.

623 †Survival = adults surviving from late winter 2007 to late winter 2008 (1) or not (0).
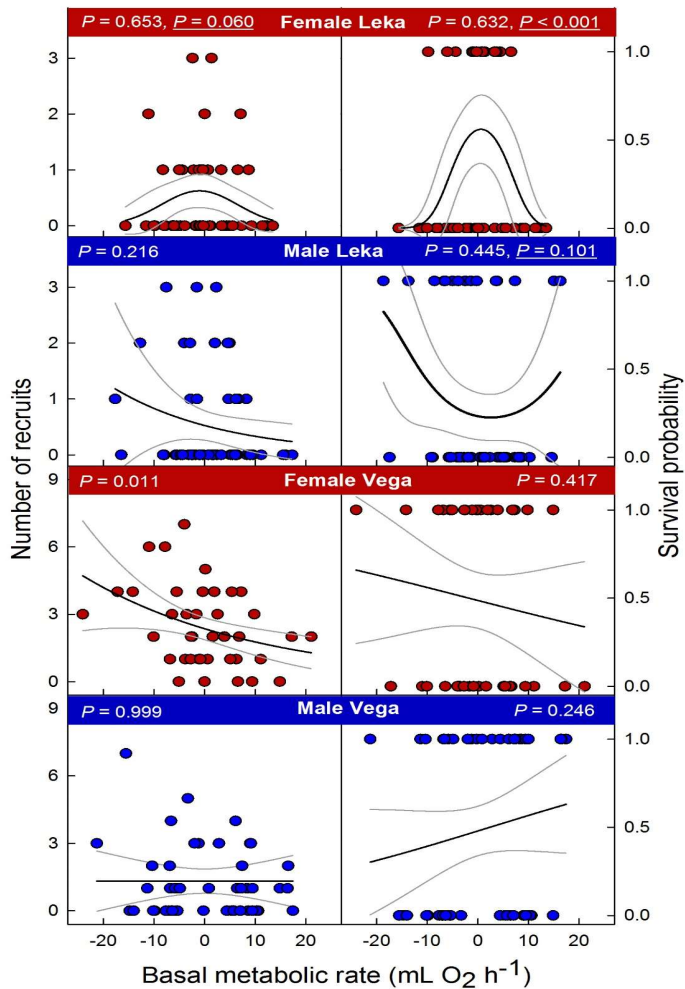
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626   FIGURES

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629

630   Fig. 1. Male house sparrow (*Passer domesticus* Linnaeus, 1758). The bird is banded with a

631   unique combination of coloured plastic rings which enables identification with telescope.

632   Photo: Bernt Rønning.

633

634

635

636   Fig. 2. Relationship between basal metabolic rate measured in late winter 2007, number of

637   recruits recorded the subsequent year (left panel) and the probability of survival to the

638   subsequent year (right panel) in house sparrows from Vega and Leka, Norway. Fitted lines

639   represent predicted values for the linear effect (solid lines) or a combination of the linear and

640   quadratic effect (if $P \leq 0.1$; short dashed lines) of BMR. Dotted lines represent the 95%

641   confidence intervals. P-values for the linear and quadratic (underlined) effect of BMR are

642   given. Statistics from models used to calculate the predicted values are shown in Table S3 in

643   Supporting Information.

644

Supporting Information Table S1. Sources of variation in basal metabolic rate (BMR) in free-living house sparrows (N = 194) from Leka and Vega, Norway. The model was simplified by backward stepwise removal of least significant terms, where significance was based on likelihood ratio tests. Statistics for excluded terms (P > 0.05 and not included in a significant interaction) correspond to the step when they were removed from the model.

650

Fixed effects	Estimate	χ^2_1	P
Intercept	57.005	995.62	<0.001
Island*	-64.156	12.842	<0.001
Sex[†]	3.361	2.703	0.100
Period[‡]	-0.384	0.133	0.716
DIA	0.157	1.197	0.274
Body mass	0.815	3.857	0.050
Age	-0.236	0.100	0.752
Sex : island	1.938	0.798	0.372
Sex : period	1.546	0.543	0.461
Sex : DIA	0.068	0.054	0.816
Sex : body mass	1.014	3.039	0.081
Sex : age	-2.807	9.036	0.003
Island : period	-2.742	1.702	0.192
Island : DIA	-0.169	0.305	0.581
Island : body mass	1.795	10.138	0.001
Island : age	3.305	6.731	0.009
Sex : island : period	-6.054	2.059	0.151
Sex : island : DIA	-0.494	0.667	0.414
Sex : island : body mass	-0.466	0.144	0.705
Sex : island : age	0.762	0.100	0.752

651

*Reference is Leka.

[†]Reference is female.

[‡]Reference is night measurement.

DIA = days inside aviary before BMR was measured.

Period= BMR measured in the evening or during the night.

657

658 **Supporting Information Table S2.** The association between basal metabolic rate (BMR, mL
659 O_2 h^{-1}), sex, island and components of fitness in house sparrows (N = 194) from Leka and
660 Vega, Norway. The models were simplified by backward stepwise removal of least
661 significant terms (BMR was retained in the models at all time), where significance was based
662 on likelihood ratio tests. Statistics for excluded terms (P > 0.05 and not included in a
663 significant interaction) correspond to the step when they were removed from the model.

664

	Recruit production[*]			Survival[†]		
Fixed effects	Estimate	χ^2_1	P	Estimate	χ^2_1	P
Intercept	-0.682	18.382	<0.001	0.020	0.002	0.960
Sex[‡]	-0.320	2.838	0.092	-1.174	4.721	0.030
Island[§]	1.216	37.285	<0.001	-0.101	0.034	0.854
BMR	-0.022	3.777	0.052	0.160	3.910	0.048
BMR^2	-1E-4	0.013	0.909	-0.029	11.233	<0.001
Sex : island	-0.663	2.789	0.095	1.104	2.034	0.154
Sex : BMR	0.012	0.272	0.602	-0.204	5.040	0.025
Island : BMR	0.023	0.601	0.438	-0.197	4.654	0.031
Sex : BMR^2	0.002	0.978	0.323	0.035	13.816	<0.001
Island : BMR^2	0.004	2.591	0.107	0.028	8.713	0.003
Sex : island : BMR	0.095	2.326	0.127	0.279	7.127	0.008
Sex : island : BMR^2	-0.004	0.302	0.583	-0.033	9.081	0.003

665

666 [*]Recruit production = number of recruits recorded the subsequent year.
667 [†]Survival = adults surviving from late winter 2007 to late winter 2008 (1) or not (0).
668 [‡]Reference is female.
669 [§]Reference is Leka.

670

671 **Supporting Information Table S3.** The effect of basal metabolic rate (BMR) on recruit
672 production and survival in free-living house sparrows from Vega and Leka, Norway.

673

Population		Recruit production[*]			Survival[†]		
VEGA	Predictor	Estimate	χ^2_1	P	Estimate	χ^2_1	P
Female	Intercept	0.857	49.37	<0.001	-0.052	0.026	0.872
(N = 39)	BMR	-0.029	6.462	0.011	-0.030	0.660	0.417
	BMR^2	-3E-4	0.158	0.691	-0.001	0.130	0.719
Male	Intercept	0.278	1.758	0.185	-0.082	0.082	0.774
(N = 50)	BMR	2E-5	<0.001	0.999	0.035	1.344	0.246
	BMR^2	0.001	0.496	0.481	0.001	0.146	0.702
LEKA							
Female	Intercept	-0.480	4.288	0.038	0.234	0.346	0.556
(N = 39)	BMR	-0.018	0.202	0.653	0.035	0.230	0.632
	BMR^2	-0.009	3.530	0.060	-0.029	11.23	<0.001
Male	Intercept	-0.687	21.389	<0.001	-1.192	11.308	<0.001
(N = 50)	BMR	-0.046	1.531	0.216	-0.032	0.599	0.445
	BMR^2	-0.004	0.992	0.319	0.006	2.687	0.101

674

675 [*]Recruit production = number of recruits recorded the subsequent year.
676 [†]Survival = adults surviving from late winter 2007 to late winter 2008 (1) or not (0).

34

Supporting Information Table S4. Standardized selection differentials and gradients for
basal metabolic rate (BMR) and body mass in relation to recruit production and survival in
house sparrows from Vega and Leka, Norway. Parameter estimates for linear effects were
obtained from models only including linear terms, while quadratic parameter estimates were
obtained from models including both linear and quadratic terms. 95 % confidence intervals
(CI) are based on 1000 bootstrap replicates. Note that parameter estimates for quadratic terms
were doubled before the nonparametric bootstrapping procedure was performed.

Recruit production		Selection differentials		Selection gradients	
	Trait	Estimates	95 % CI	Estimates	95 % CI
Vega					
Females	BMR	-0.266	-0.507, -0.102	-0.260	-0.521, -0.097
(N = 39)	BMR^2	0.017	-0.335, 0.319	0.029	-0.430, 0.519
	Body mass	-0.107	-0.346, 0.160	-0.015	-0.293, 0.253
	Body mass^2	-0.346	-0.604, 0.347	-0.174	-0.628, 0.471
Males	BMR	2e-4	-0.491, 0.463	-0.202	-0.746, 0.156
(N = 50)	BMR^2	0.316	-0.585, 1.525	0.341	-0.616, 1.489
	Body mass	0.175	-0.308, 0.940	0.307	-0.189, 1.514
	Body mass^2	0.292	-0.404, 2.156	0.230	-0.521, 1.817
Leka					
Females	BMR	-0.089	-0.529, 0.293	-0.069	-0.448, 0.337
(N = 52)	BMR^2	-0.556	-1.216, 0.248	-0.507	-1.208, 0.243
	Body mass	-0.186	-0.738, 0.344	-0.178	-0.746, 0.327
	Body mass^2	0.340	-0.502, 1.330	0.216	-0.491, 1.382
Males	BMR	-0.300	-0.733, 0.035	-0.271	-0.734, 0.159
(N = 53)	BMR^2	-0.173	-0.771, 0.396	-0.110	-0.795, 0.398
	Body mass	-0.179	-0.683, 0.187	-0.082	-0.513, 0.357
	Body mass^2	-0.556	-1.083, -0.049	-0.496	-1.033, 0.111
Survival					
Vega					
Females	BMR	-0.134	-0.419, 0.240	0.003	-0.338, 0.306
(N = 39)	BMR^2	-0.073	-0.584, 0.533	0.013	-0.573, 0.629
	Body mass	-0.388	-0.654, -0.062	-0.389	-0.694, 0.004
	Body mass^2	0.027	-0.532, 0.631	0.026	-0.610, 0.641
Males	BMR	0.172	-0.143, 0.460	-0.167	-0.521, 0.283
(N = 50)	BMR^2	0.111	-0.622, 0.623	0.242	-0.413, 0.755
	Body mass	0.406	0.160, 0.562	0.515	0.153, 0.806
	Body mass^2	-0.019	-0.335, 0.259	-0.075	-0.433, 0.224
Leka					
Females	BMR	0.029	-0.316, 0.408	-0.023	-0.363, 0.284
(N = 52)	BMR^2	-0.863	-1.414, -0.441	-0.842	-1.346, -0.370
	Body mass	0.447	0.047, 0.733	0.450	0.057, 0.735
	Body mass^2	0.184	-0.402, 0.555	-0.011	-0.531, 0.513
Males	BMR	-0.207	-0,679, 0.314	-0.207	-0.693, 0.277
(N = 53)	BMR^2	0.488	-0.343, 1.120	0.577	-0.113, 1.364
	Body mass	-0.075	-0.451, 0.321	-0.001	-0.411, 0.342
	Body mass^2	-0.581	-1.095, -0.016	-0.654	-1.259, -0.210