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RESEARCH ARTICLE

Spatial variation in the evolutionary potential and constraints of basal metabolic rate and body mass in a wild bird

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Abstract

An organism's energy budget is strongly related to resource consumption, performance, and fitness. Hence, understanding the evolution of key energetic traits, such as basal metabolic rate (BMR), in natural populations is central for understanding life-history evolution and ecological processes. Here we used quantitative genetic analyses to study evolutionary potential of BMR in two insular populations of the house sparrow (*Passer domesticus*). We obtained measurements of BMR and body mass (M_b) from 911 house sparrows on the islands of Leka and Vega along the coast of Norway. These two populations were the source populations for translocations to create an additional third, admixed 'common garden' population in 2012. With the use of a novel genetic group animal model concomitant with a genetically determined pedigree, we differentiate genetic and environmental sources of variation, thereby providing insight into the effects of spatial population structure on evolutionary potential. We found that the evolutionary potential of BMR was similar in the two source populations, whereas the Vega population had a somewhat higher evolutionary potential of M_b than the Leka population. BMR was genetically correlated with M_b in both populations, and the conditional evolutionary potential of BMR (independent of body mass) was 41% (Leka) and 53% (Vega) lower than unconditional estimates. Overall, our results show that there is potential for BMR to evolve independently of M_b, but that selection on BMR and/or M_b may have different evolutionary consequences in different populations of the same species.

KEYWORDS
artificial selection, basal metabolic rate, birds, constraints, evolutionary physiology, experimental evolution, quantitative genetics

Stefanie Muff and Henrik Jensen are shared senior authors.

1 | INTRODUCTION

Organisms need resources for growth, maintenance, reproduction, and survival. The allocation of energy to each of these processes will affect fitness and shape life history (Auer et al., 2018). Hence, energy budget-related traits, such as metabolic rate, underpin both ecological and evolutionary processes (Mckechnie & Swanson, 2010) and have a strong potential to influence the responses of natural populations to environmental (e.g. climate) change. Patterns of temperature and precipitation are changing at alarming rates worldwide (IPBES, 2019; IPCC, 2022). Therefore, for persistence of natural populations, the ability for energetic traits to undergo adaptive evolution is crucial (Bonebrake et al., 2020; Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014; Mitchell et al., 2018; Morgan et al., 2020; Stevenson & Bryant, 2000).

A central energetic trait for endotherms, the minimum resting metabolic rate measured in ambient temperatures within the thermoneutral zone and during post-absorptive rest, can be quantified as basal metabolic rate (BMR) or resting metabolic rate (RMR, when not post-absorptive) (Clarke, 2017; IUPS Thermal Commission, 2001). The relationship between BMR and ecological conditions remains complex and unresolved, and often context-dependent (Arnold et al., 2021; Burton et al., 2011; Mathot et al., 2019). Interspecific comparisons indicate that differences in BMR are closely linked to adaptations to different environments and variation in life history (Bryant & Furness, 1995; McNab, 1994; White et al., 2006; Wiersma et al., 2007). For example, species living in cool and wet areas have higher BMR than those living in warmer and drier areas (Liknes & Swanson, 1996; Swanson & Liknes, 2006; Tieleman et al., 2003; Wiersma et al., 2007). At the intraspecific level, there is evidence for genetic differentiation in BMR between bird populations inhabiting different environments (Broggi et al., 2005; Wikelski et al., 2003). Relationships between components of individual fitness and BMR have been documented in some populations (Nilsson & Nilsson, 2016; Rønning et al., 2016), whereas (Petit et al., 2017) found that thermogenic capacity rather than BMR determined winter survival. Several recent reviews have found patterns that fit with various hypotheses, such as (i) the 'increased intake' or 'performance' hypothesis (i.e. individuals with a higher BMR also have a higher capacity to acquire energy; Arnold et al., 2021), (ii) the 'compensation' or 'allocation' hypothesis (i.e. individuals with low BMR can afford to allocate more energy to other functions such as growth and reproduction; Swanson et al., 2017), and (iii) 'the context-dependent' hypothesis (the availability of certain resources shapes the relationship between metabolic rate and fitness; Arnold et al., 2021; Burton et al., 2011).

Despite being a central trait in comparative physiology, ecology and evolutionary biology (Hayssen & Lacy, 1985; Mckechnie & Swanson, 2010), information about the evolutionary potential of BMR in free-living populations in their natural environment, potentially critical for responses to climate change, is scarce. BMR is tightly connected to body mass (M_b), a frequently measured and fitness-related life-history trait (Pettersen et al., 2018; White et al., 2019; White & Seymour, 2005). The allometric relationship between BMR and M_b has been described as $\mathrm{BMR} = aM_b^{b_P}$, where a is a constant and b_P is a phenotypic scaling exponent (or slope, in log–log space, such that $b_P = \frac{\mathrm{cov}_P(\mathrm{BMR},M_b)}{V_P(M_b)}$) traditionally thought to be ⅔ or ¾, but the generality of this is debated (Careau & Glazier, 2022; Glazier, 2005; White et al., 2009). Both BMR and M_b are flexible and need not fluctuate in perfect synchrony (Broggi et al., 2019), thus also allowing for flexibility in phenotypic covariance, and thus in b_P. Moreover, to what degree evolutionary potential in BMR is dependent on M_b through allometric scaling and phenotypic and genetic integration remains an open question.

The evolutionary potential in a population, the standing level of additive genetic variance (V_A) within, and covariance (cov_A) between traits, can be described by the additive genetic covariance matrix **G**, with V_A along the diagonal and cov_A in the off-diagonal elements. The vector of responses (**R**) to selection in correlated traits can then be expressed as $\mathbf{R} = \mathbf{G\beta}$ (Lande, 1979; Lande & Arnold, 1983). Here **β** is the vector of selection gradients on each trait. For comparisons across traits, populations and species, V_A is commonly standardized as narrow-sense heritability ($h^2 = V_A/V_P$, i.e. the ratio of V_A to total phenotypic variance [V_P]), or as evolvability ($I_A = V_A/\mu^2$, i.e. V_A divided by the squared mean of the phenotype [μ^2]) (Falconer, 1996; Houle, 1992), whereas cov_A between traits are standardized as genetic correlations ($r_A = \frac{\mathrm{cov}_A(x,y)}{\sqrt{V_A(x)}\sqrt{V_A(y)}}$). Recently, estimating the additive genetic scaling exponent ($b_A = \frac{\mathrm{cov}_A(\mathrm{BMR},M_b)}{V_A(M_b)}$) has been suggested as a way to increase the understanding of the links between BMR and M_b (Careau & Glazier, 2022). Interestingly, b_A appears not to deviate from the traditional ⅔ or ¾ allometric scaling exponents, although studies on more taxa are needed to infer any generality (Careau & Glazier, 2022; Videlier et al., 2019). The exponent b_A reflects the line of least genetic resistance and thus indicates the most likely direction of evolution of BMR and M_b. The magnitude of b_A relative to other components of b_P, such as the residual scaling exponent ($b_R = \frac{\mathrm{cov}_R(\mathrm{BMR},M_b)}{V_R(M_b)}$), provides insight into the contribution of environmental or genetic influence on the allometric relationship (Careau & Glazier, 2022).

A predominance of studies of genetic variation in BMR in endotherms has been conducted on captive-bred populations (of mostly rodents and passerines), finding heritabilities ranging from almost zero up to over 0.60 with a median around 0.21 (Bacigalupe et al., 2004; Boratyński et al., 2013; Careau et al., 2011; Careau & Glazier, 2022; Konarzewski et al., 2005; Mathot et al., 2013; Nespolo et al., 2003; Pettersen et al., 2018; Rønning et al., 2007; Sadowska et al., 2005; Tieleman et al., 2009; White & Kearney, 2013; Wone et al., 2009). However, in laboratory populations environmental variation may be lower compared to natural populations (Auer et al., 2016; Hoffmann et al., 2017; Weigensberg & Roff, 1996). In free-living populations, estimated heritabilities in BMR or RMR range from non-significant in leaf-eared mouse (*Phyllotis darwini*) up to $h^2 = 0.61$ in weasels (*Mustela nivalis*) (Bacigalupe et al., 2004; Bushuev et al., 2011, 2012; Nespolo et al., 2003; Nilsson et al., 2009; Zub et al., 2012).

The potential for evolutionary change in a trait can be constrained by genetic correlation with other traits under selection such as M_b, and the effect depends on the strength of selection on each trait and their genetic correlation (Hansen & Houle, 2008; Lande & Arnold, 1983). As BMR and M_b are tightly connected, phenotypic and genetic correlations between BMR and M_b have the potential to influence selection on and evolution of metabolic rate, respectively (Lande & Arnold, 1983). In birds, heritability estimates of M_b vary from effectively zero in tree swallows (*Tachycineta bicolor*) to at least $h^2 = 0.73$ in stonechats (*Saxicola torquate maura*), with most estimates being roughly around $h^2 = 0.4$ (e.g. Bushuev et al., 2012; Gosler & Harper, 2000; Jensen et al., 2003; Nilsson et al., 2009; Rønning et al., 2007; Teplitsky et al., 2009; Tieleman et al., 2009; Wiggins, 1989). Genetic correlations between BMR and M_b in passerines range from $r_A = 0.08$ in free-living pied flycatchers (*Ficedula hypoleuca*) (Bushuev et al., 2012), to $r_A = 0.87–0.91$ in captive zebra finch (*Taeniopygia guttata*) (Mathot et al., 2013; Rønning et al., 2007) and effectively one in wild blue tits (*Cyanistes caeruleus*) (Nilsson et al., 2009). The genetic correlation between BMR and M_b was also found to vary between geographically separated stonechat populations (*Saxicola torquata* subspp.) (Tieleman et al., 2009), indicating potential differences among populations in responses to selection on these traits. Selection on metabolic rate may be expected to change with climate change (Broggi et al., 2007; Nilsson & Nilsson, 2016; White et al., 2006), whereas a range of selective forces – most of which are independent of weather and climate, can together result in a strong stabilizing selection on M_b (Blanckenhorn, 2000). For example, (Broggi et al., 2019) found BMR to be more sensitive than M_b to seasonal changes in ambient temperatures, contrary to the prior expectation of the importance of energetic fat reserves. A future altered directional selection on BMR due to climate change, combined with strong stabilizing selection on M_b, is therefore plausible. Hence, quantifying the magnitude, sign and stability of genetic correlations and the independent evolutionary potential of fitness-related traits, such as BMR and M_b, is of great importance for understanding the capacity for populations to adapt and persist under changing environments.

Selection regimes on BMR and M_b may vary because of climate change. The present study aims to quantify components of evolutionary potential, namely h^2, I_A, r_A, and b_A between BMR and M_b in two free-living populations of house sparrows, to investigate the potential for adaptive evolution under changing selection. The two populations inhabit two different islands (Leka and Vega) along the coast of mid-Norway and northern Norway. Individuals from each population were translocated to a third island (Lauvøya) in 2012 as a common garden experiment. Thus, the genetic structure of this population system makes application of the recently developed genetic groups animal model (GGAM) highly suitable. GGAM allow to investigate spatial differences in evolutionary potentials by controlling for potential biases caused by genetic structure in the pedigree and separating environmental from genetic sources of population differences in phenotypic (co)variance (de Villemereuil et al., 2016; Muff et al., 2019; Wolak & Reid, 2017). Phenotypic measurements (BMR and M_b) were conducted on birds both in their original environment and in the common garden in the years 2012–2015. This study contributes to increase understanding of the allometric and evolutionary relationships between BMR and M_b, and whether there may be spatial variation in these relationships across populations.

2 | METHODS

2.1 | Study populations, design, and data collection

We examined house sparrows in three insular house sparrow populations on the islands Leka, Vega, and Lauvøya, separated by 60–220 km along coastal mid-Norway and northern Norway (Figure S1.1 in Appendix S1). The house sparrow is a sedentary bird in Norway, breeding in buildings and nest boxes and in the study islands they live near dairy farms that provide shelter and food. Yet, evolution in house sparrows is still shaped largely by environmental variation (Geue et al., 2016). Adult sparrows feed on seeds, whereas nestlings rely on insects for food, whose abundance and availability varies locally with for example, vegetation and weather conditions (Anderson, 2006). Local population densities and age, structure may vary both temporally and spatially (Baalsrud et al., 2014; Holand et al., 2016). The house sparrows within the study area are exposed to predation with cats and sparrow hawks as the main predators. For a more comprehensive overview of the ecology of house sparrows, see (Anderson, 2006; Husby et al., 2006; Jensen et al., 2013; Pärn et al., 2009). The study populations were included in a long-term study (e.g. Jensen et al., 2013; Kvalnes et al., 2017; Le Pepke et al., 2021; Pepke et al., 2021; Ringsby et al., 1820; Rønning et al., 2016; Stubberud et al., 2017), where a large proportion of birds (>85%) were captured annually at Leka and Vega during winters 2002–2015 (Vega until 2014) and since 2012 at Lauvøya (Kvalnes et al., 2017). They have a known history of different selection regimes, as Leka and Vega were subjected to an artificial selection experiment (on tarsus length) during 2002–2005 (Kvalnes et al., 2017; Pepke et al., 2021; Ringsby et al., 1820). Kvalnes et al. (2017) showed that the traits returned to fluctuate around their original population means by 2012, thus demonstrating stabilizing selection around an optimum body size. In the present study, to disentangle environmental from genetic sources of phenotypic variation, the focal Leka and Vega populations were the sources for a translocation to create one admixed population on a third island Lauvøya, where native birds had been removed (further details below). Consequently, the pedigree is naturally structured into two distinct genetic groups from the two source populations. Natural dispersal between these populations has not been recorded and would thus be unexpected (Jensen et al., 2013; Pärn et al., 2012; Ranke et al., 2021; Tufto et al., 2005).

The three study islands have a coastal climate and weather, characterized by mild winters and moist, cool summers (monthly total precipitation and monthly mean temperature during 1990–2022: 20–300 mm and −4–+5°C during January, February and March; 20–210 mm and +8–+16°C for June, July, and August), largely

regulated by the oceanic water masses and the North Atlantic Gulf Stream (Ringsby et al., 2002; (MET), Norwegian Meteorological Institute, 2022). Leka tends to have more precipitation; otherwise, these islands largely experience similar climatic conditions (Table S1.1 in Appendix S1). Other environmental differences may exist between (and within) populations, such as social environment (sex ratio or relatedness clustering within or between farms), microclimate (due to differences in location, construction, and practices of farms), or population density (natural density fluctuations as well as density consequences of the selection experiment). Environmental differences between populations were pooled in the higher-order environmental effect of population. Most sparrows in each population (>90%) were captured using mist nets during late winter (February–March, to avoid interfering with the breeding season) 2012–2015 (Vega until 2014). At first capture, each bird was given a numbered metal ID-ring and a unique combination of three plastic colour rings. A small blood sample (25 μL) was collected by brachial venipuncture and stored on 96% ethanol for later genetic analyses. After the blood sample was taken, all birds were released into a sealed aviary (a former cowshed) on each island of approx. 150 m^2 and 2.5 m room height heated to 10–15°C, which is the normal temperature range in cowsheds in this part of Norway during winter. In the aviary, they were then provided water and food (a range of bird seeds and bread) *ad libitum*, and branches were put up to allow birds to perch and hide. As soon as possible (mostly within 0–1 day, range 0–7 days) the birds were recaptured, and their metabolic rates measured (see below).

To investigate spatial patterns in genetic and environmental sources of variation and any phenotypic differences between populations, we made use of a selection experiment conducted on BMR at Leka and Vega during 2012–2015 (Nafstad et al. in prep.). In that selection experiment, the populations at Leka and Vega were selected for low and high whole-body BMR, respectively. In the present study, we could take advantage of this selection experiment by translocating a subset of the birds that were removed from Leka and Vega to the common garden environment at Lauvøya. The individuals that were translocated to Lauvøya (in 2012) were the 35 with the lowest (within Vega, $mean_{Males}$ = 70.32 and $mean_{Females}$ = 72.28 mL O_2 h^{-1}) or highest (within Leka, $mean_{Males}$ = 90.33 and $mean_{Females}$ = 88.75 mL O_2 h^{-1}) whole-body BMR of each sex from each population (Table S2.1 in Appendix S1). No more individuals were artificially introduced to Lauvøya in later years. In February 2012, before release of the translocated Leka and Vega individuals, all native sparrows at Lauvøya and nearby populations had been captured and translocated to faraway locations (>65 km). This study design, where individuals originating from different populations were introduced and later phenotyped in a common garden environment, provides a unique demographic and genetic structure that is particularly well suited for application of the GGAM, to separate environmental from genetic sources of phenotypic differences in trait means and phenotypic (co)variances (de Villemereuil et al., 2016; Muff et al., 2019; Wolak & Reid, 2017). Given a genetic influence on BMR, individuals (and genetic groups) are expected to maintain their extreme BMR in the common garden environment, and because our common garden approach connects the pedigrees in the two source populations (genetic groups) in a shared common environment, we could estimate and account for any differences in genetic and environmental contributions to the means and variances in BMR and M_b.

2.1.1 | Phenotyping

BMR was either measured the same day a bird was captured in February–March, or usually within 1 (mean 0.54, range 0–7) day after capture. Each individual was measured once each year, and the following year any surviving and re-captured individuals were measured again. In total, 1143 measurements of BMR and M_b were obtained from 911 individuals in the Leka, Vega, and Lauvøya populations (Table 1). BMR measurements were conducted in two sessions per day, between 16:00–22:30 or 23:00–08:00 local time and measured following (Rønning et al., 2016) as oxygen consumption rate (mL O_2 h^{-1}) using an open flow system (see Supplementary Materials S2 in Appendix S1 for details). M_b was measured to the nearest 0.01 g using a digital balance at the beginning and the end of each metabolic rate measurement, and the mass at time of reaching BMR was estimated assuming constant mass loss between measurements. After metabolic measurements, all individuals were kept in the aviaries until artificial selection was conducted (see above). The study was carried out in accordance with permits from the Norwegian Food Safety Authority (permits 4011 and 5978) and the Bird Ringing Centre at Stavanger Museum, Norway.

2.2 | Determination of the genetic pedigree

SNP data were obtained from the blood samples following (Lundregan et al., 2018). A genetic pedigree was constructed using the sequoia R-package (Huisman, 2017) based on 603 SNPS that were shown to be highly informative for parentship in the study populations (Lundregan et al., 2018; Niskanen et al., 2020). Additionally, a microsatellite pedigree was available for ancestors in Leka and Vega providing additional relatedness information (Rønning et al., 2016). Of the 911 individuals phenotyped in our study, both parents were known for 53.4%, and one parent only was known for 22.0%. Mean number of ancestral generations across all populations was 3.83, whereas the highest number of ancestral generations for one individual was 12 (Figure S3.1 and Table S3.1 in Appendix S1).

2.3 | Statistical analyses

Analyses were performed by fitting GGAM with heterogeneous additive genetic variances (Aase et al., 2022; Muff et al., 2019). In our case, the base population was partitioned into three genetic groups (1) *Leka*; (2) *Vega* and (3) *unknown* (italics will be used for the genetic groups to distinguish them from the populations). The parents of the sparrows present in the Leka or Vega populations in 2012 were assigned

TABLE 1 Phenotypic mean and variance of whole-body BMR (mL O_2 h^{-1}) and M_b (g) in adult house sparrows in the three study populations each year.

	2012		2013		2014		2015	
	BMR	M_b	BMR	M_b	BMR	M_b	BMR	M_b
Leka								
Mean	80.91	29.82	80.09	29.05	75.64	28.64	76.63	29.01
Variance	86.49	2.60	103.55	2.17	73.10	3.14	88.15	2.90
n	177		116		154		122	
Vega								
Mean	79.90	29.52	80.44	29.62	81.48	29.76	–	–
Variance	98.74	3.29	56.78	3.55	119.88	3.62	–	–
n	165		68		100		–	
Lauvøya								
Mean	80.42	29.43	75.51	28.79	80.28	29.43	80.19	29.44
Variance	118.98	3.58	72.82	2.80	75.50	2.71	91.95	2.64
n	140		45		88		108	

Note: Note that Leka was selected for low BMR during 2012–2014 and Vega was selected for high BMR in 2012. The 140 individuals in Lauvøya 2012 are exclusively those translocated from Leka ($n = 70$) and Vega ($n = 70$) the same year, whereas in years 2013–2015, all individuals present in Lauvøya were measured.

to genetic groups *Leka* or *Vega*, respectively, whereas phantom parents of founder individuals that entered the study populations in later years (i.e. immigrants and any individuals with unknown resident parents) were assigned to the *unknown*. Consequently, *Leka* and *Vega* are defined by the respective populations in 2012, whereas *unknown* represents a genetically and demographically heterogeneous group that controls for bias in estimates of quantitative genetic parameters for the focal genetic groups *Leka* and *Vega* (Aase et al., 2022; Wolak & Reid, 2017). Proportional individual group affiliation was estimated from the genetic pedigree assuming Mendelian inheritance using the nadiv R package (Muff et al., 2019; Wolak, 2019). The group-specific relatedness matrices $\boldsymbol{A}_z$ (with $z = 1,2,3$ denoting the respective group) were computed using generalized Cholesky decomposition, following (Muff et al., 2019). To estimate the genetic correlation between BMR and M_b, we formulated a bivariate model with responses whole body BMR and M_b, to properly estimate (co)variances of the two traits. Supplementary Material S4 in Appendix S1 provides further details on the implementation of the full model and description of covariates. The GGAMs were fitted in a Bayesian framework using the packages MCMCglmm, nadiv, pedantics, tidyverse, and boot in R v4.1.0 (Canty & Ripley, 2017; Hadfield, 2010; Morrissey & Wilson, 2010; R Core Team, 2020; Wickham, 2017; Wolak, 2019).

The artificial selection experiment (see above) was performed on descendants of the base populations after measuring all individuals within each selection episode. The individuals removed during artificial selection thus contribute to the phenotypic data, which leaves the base populations *Leka* and *Vega* and their genetic parameters (the estimated V_A and cov_A) unaffected by the selection imposed during 2012–2015, thus making the quantitative genetic approach suitable even in populations under selection (Sorensen et al., 2001). To avoid potential model selection bias, no model selection was performed (Freedman & Freedman, 1983). BMR is expected to generally have a relatively large measurement error (ME) (Bouwhuis & Sheldon., 2011; Broggi et al., 2009; Rønning et al., 2005). Unpublished data from our own studies suggest that ME (instrumental and biological) may constitute up to 40% of V_P of BMR and 15% in M_b. Thus, to qualitatively explore if and how ME may influence estimation of parameters, we specified a point-prior for the ME variance (V_{ME}) using the mev-argument in MCMCglmm, assuming ME is normally distributed with mean 0 (Hadfield, 2010). In the absence of prior knowledge, but to illustrate potential effects of ME, models were fitted with V_{ME} corresponding to roughly 0, 20 and 40% of total variance of BMR and 0%, 8% and 15% of total variance in M_b (Bouwhuis & Sheldon, 2011; Broggi et al., 2009; Rønning et al., 2005).

The group-specific narrow sense heritability was estimated as $h^2_{(z)} = V_{A(z)}/V_{P(z)}$ (Falconer, 1996), and group-specific evolvability as $I_{A(z)} = V_{A(z)}/\mu^2_{(z)}$ (Houle, 1992). $V_{A(z)}$, $V_{P(z)}$ and $\mu^2_{(z)}$ are the group-specific additive genetic variance, phenotypic variance, and mean phenotype squared of each trait in group z in 2012, respectively. The base population in the respective genetic groups were used for calculation of $V_{P(z)}$, $\text{cov}_{P(z)}$ and $\mu^2_{(z)}$. Consequently, no admixed individuals contribute to $V_{P(z)}$, $\text{cov}_{P(z)}$ or $\mu^2_{(z)}$ for either trait. Note that due to inability to estimate ME the calculated V_P includes V_{ME}, thus downward bias h^2. The group-specific genetic correlation between BMR and M_b for each group z ($r_{A(z)}$) was calculated as

$$r_{A(z)} = \frac{\text{cov}_{A(z)}(\text{BMR}, M_b)}{\sqrt{V_{A(z),\text{BMR}}}\sqrt{V_{A(z),Mb,}}}. \quad (1)$$

Following (Hansen et al., 2003; Hansen & Houle, 2008), conditional genetic variance in one trait x independent of another trait y is given by

$$V_{C(z)}(x|y) = V_{Ax(z)}\left(1 - r^2_{A(z)}\right), \quad (2)$$

where $V_{C(z)}(x|y)$ is the group-specific additive genetic variance in trait x that is independent of trait y. The effect of conditioning $\left(1-r^2_{A(z)}\right)$ thus represents the proportion of V_A that is independent of the other trait within the genetic group. Conditional heritability and evolvability can then be calculated as above, substituting V_C for V_A. In addition, allometric scaling exponents were estimated by fitting the GGAM with $\log_e$-transformed BMR and M_b, yielding group-specific, among-individual, and residual (co)variances allowing to estimate group-specific additive genetic ($b_{A(z)}$), among-individual (b_{ID}) and residual (b_R) allometric scaling exponent, respectively (Careau & Glazier, 2022).

Below we report the results from the GGAM fitted with the highest prior level of V_{ME} (40% of BMR and 15% of M_b), presented as posterior means for fixed effects and modes for variance components, and 95% highest posterior density (HPD) credible interval in square brackets. Instead of relying on statistical significance testing with a set p-value threshold, we present our results in the gradual language of evidence, evaluated by the respective 95% HPD credible intervals (Muff et al., 2021). Results from models fitted with lower V_{ME} can be found in Supplementary Materials S5 in Appendix S1.

3 | RESULTS

3.1 | Phenotypic variation

There was little or no evidence for any phenotypic differences between Leka and Vega in BMR or M_b before the selection in 2012, either in mean (BMR: $T_{333} = 0.97$, $p = 0.33$, M_b: $T_{329} = 1.63$, $p = 0.10$) or variance (BMR: $F_{176,164} = 0.87$, $p = 0.39$, M_b: $F_{176,164} = 0.80$, $p = 0.14$). During the study, population- and year-specific phenotypic mean BMR ranged from 75.5 to 81.5 mL O_2 h^{-1} and variance from 56.8 to 119.9 (mL O_2 $h^{-1})^2$, and M_b from mean 28.6 to 29.8 g and variance from 2.17 to 3.62 g^2 (Table 1). During the selection experiment, there was very strong evidence for yearly reduction in both BMR ($\beta_{year} = -1.78$ mL O_2 h^{-1} $year^{-1}$ [SE = 0.50], $F_{1,565} = 26.3$, $p < 0.001$) and M_b ($\beta_{year} = -0.48$ g $year^{-1}$ [SE = 0.09], $F_{1,565} = 27.0$, $p < 0.001$) in Leka (across all adults), whereas there was no evidence for any change in Vega (BMR: $\beta_{year} = 0.76$ mL O_2 h^{-1} $year^{-1}$ [SE = 0.91], $F_{1,329} = 1.58$, $p = 0.21$, M_b: $\beta_{year} = 0.02$ g $year^{-1}$ [SE = 0.17], $F_{1,329} = 1.05$, $p = 0.31$) (Figure 1).

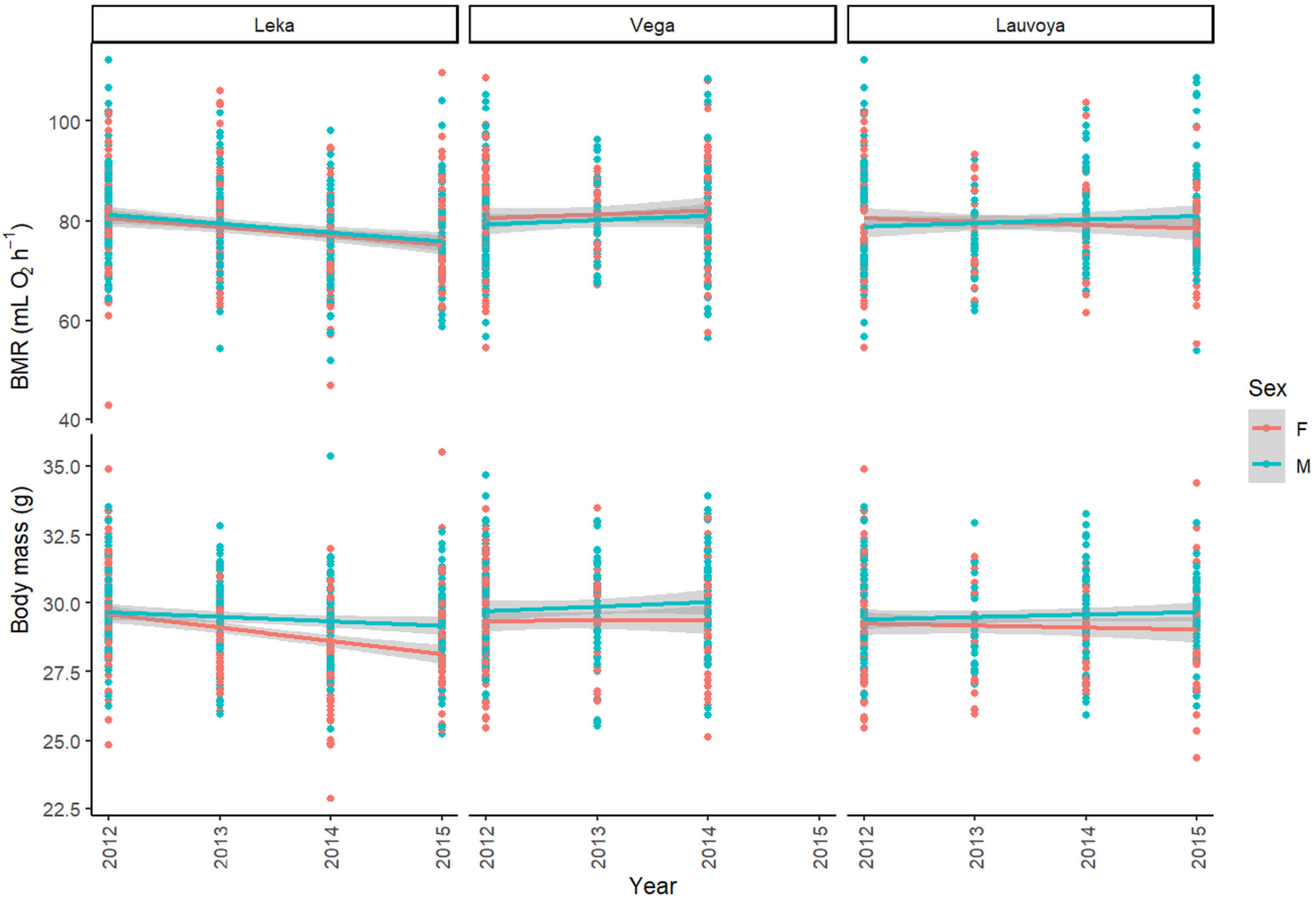

FIGURE 1 Phenotypic whole-body BMR measurements (top) and M_b (bottom) in female (F; red) and male (M; blue-green) adult house sparrows in three insular populations in years 2012–2015. Fitted linear model indicates general trends in the data. Artificial selection was performed in 2012–2014 at Leka and in 2012 at Vega, removing the ca 60% of individuals with the highest (Leka) or lowest (Vega) whole-body BMR. No artificial selection was performed at Lauvøya. The $n = 140$ individuals in Lauvøya in 2012 are exclusively those translocated from Leka ($n = 70$) and Vega ($n = 70$). No individuals were translocated between any of the islands in subsequent years. Thus, years 2013–2015 at Lauvøya show data for all individuals measured on the island during those years.

Sex-specific phenotypic Pearson's correlation across all years between BMR and M_b were intermediate in Leka (r_{male} = 0.49 [0.40, 0.57], r_{female} = 0.50 [0.41, 0.58]), stronger in Vega (r_{male} = 0.63 [0.54, 0.71], r_{female} = 0.68 [0.59, 0.76]), and in Lauvøya intermediate in males and weaker in females (r_{male} = 0.51 [0.38, 0.62], r_{female} = 0.36 [0.18, 0.52]) (Figure S5.1 in Appendix S1).

3.2 | Genetic group compositions

The proportion of the *unknown* group increased in all populations for each year (from 0% in 2012 to a maximum of 73% in Lauvøya in 2015), but the increase appeared to differ somewhat between populations and years (Figure 2). This variation was presumably due to demographic processes such as differences in immigration between populations and years. After 1 year (i.e. in 2013), the *unknown* group already constituted 48% at Lauvøya. After 2 years (i.e. in 2014) from the release to Lauvøya, the proportional genetic membership of Lauvøya individuals to *Vega* was more than twice as large as membership to *Leka* (21% vs 9% respectively). Hence, the low BMR individuals from Vega appear to have had higher rates of survival and reproduction or may have emigrated less after translocation than the high BMR individuals from Leka.

3.3 | Genetic group animal model results

3.3.1 | Mean breeding value

There was no evidence for a difference between the groups in mean breeding values in either trait. There was a very weak tendency that the mean breeding values of BMR in the base population of the *unknown* genetic group was somewhat higher than in the *Leka* and *Vega* genetic groups, with estimated differences of 1.24 [−1.27, 3.81] and 0.84 [−1.72, 3.43] mL O_2 h^{-1}, respectively, whereas the mean breeding values of M_b were 0.21 [−0.32, 0.76] g and 0.16 [−0.46, 0.76] g higher in *Leka* and *Vega*, respectively, than in *unknown*. The island effect (effect of local environment relative to the environment in the admixed population at Lauvøya) was also similar between Leka and Vega for both traits (Table S5.3 in Appendix S1).

3.3.2 | Evolutionary potential

There was strong evidence that both BMR and M_b have considerable additive genetic variation and thus the potential to evolve if under selection (Table 2). Among the two genetic groups, *Leka* tended to have the higher estimates of heritability and evolvability of BMR, although with little evidence, and this tendency was stronger in the conditioned ($h^2_{(BMR|Mb)}$ and $I_{A(BMR|Mb)}$) than unconditioned (h^2 and I_A) estimates (Table 2). In M_b, *Vega* tended to have the higher estimates, but only in the unconditioned estimates and with little evidence (Table 2). Furthermore, BMR was estimated to have lower heritability, but higher evolvability than M_b in both populations.

3.3.3 | Genetic correlations and additive genetic scaling exponent

There was a positive additive genetic covariance and genetic correlation between BMR and M_b in both genetic groups, suggesting that the two traits generally have partially the same genetic basis (Table 2). There was no evidence that cov_A(BMR, M_b) or r_A differed between the groups, although *Vega* tended to have higher estimates (Table 2). Conditional heritability and evolvability indicate that BMR and M_b can evolve independently of each other and suggest that genetic constraints on independent evolution were slightly stronger in *Vega* (Table 2). Conditioning the traits on each other following equation (2) reduced estimates of V_A, h^2 and I_A by 42% [13.5, 69.4] in Leka, and 57% [19.5, 82.2] in *Vega* (detailed results in Table S5.3–4 in Appendix S1). The additive genetic scaling exponents were similar

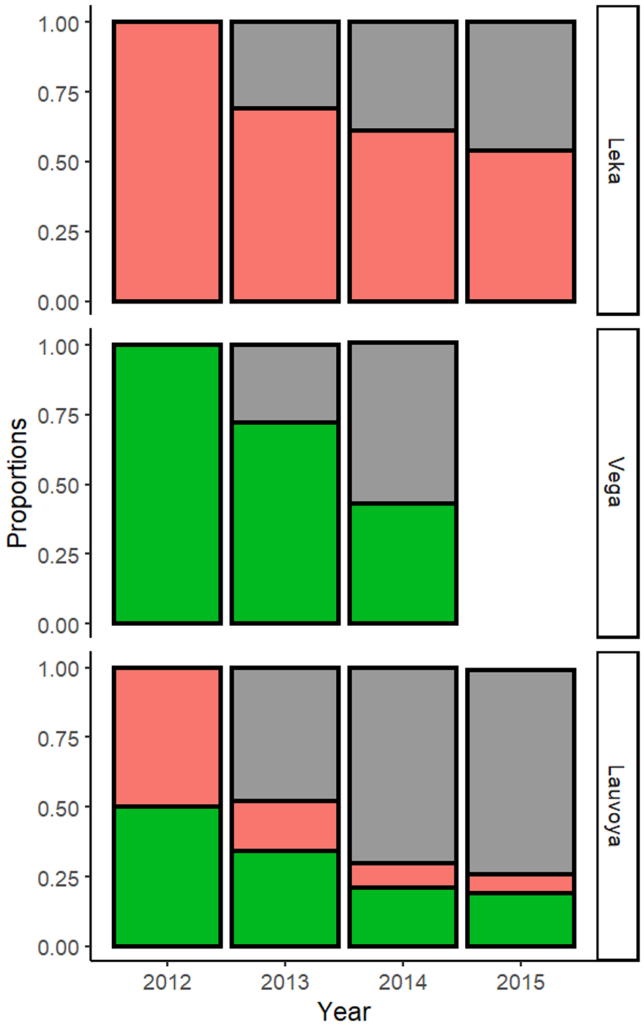

FIGURE 2 Genetic group structure in the three insular house sparrow populations (Lauvøya, Leka and Vega) measured as proportion of the total gene pool within the winter populations each year that belonged to each of the three genetic groups Leka (red), Vega (green) or unknown (grey). Individual genetic group affiliation was estimated from the pedigree assuming Mendelian inheritance. The population in Lauvøya in 2012 consisted exclusively of the released individuals from Leka and Vega.

TABLE 2 Group-specific estimates of evolutionary potential (additive genetic variance (V_A), heritability (h^2), conditioned heritability ($h^2_{(x|y)}$, 'heritability in trait × independent of trait y'), evolvability (I_A) and conditioned evolvability ($I_{A(x|y)}$)) and genetic constraints (additive genetic covariance (cov_A) and genetic correlation (r_A)) of BMR and M_b in the genetic groups Leka and Vega.

	BMR					M_b						
	V_A	h^2	$h^2_{(BMR\|Mb)}$	I_A	$I_{A(BMR\|Mb)}$	V_A	h^2	$h^2_{(Mb\|BMR)}$	I_A	$I_{A(Mb\|BMR)}$	cov_A(BMR, M_b)	r_A
Leka	27.3 [15.4, 43.5]	0.32 [0.18, 0.50]	0.18 [0.08, 0.32]	0.0042 [0.0023, 0.0066]	0.0023 [0.0011, 0.0042]	1.19 [0.75, 1.85]	0.46 [0.29, 0.71]	0.26 [0.13, 0.43]	0.0013 [0.0008, 0.0020]	0.0008 [0.0004, 0.0013]	3.84 [1.63, 6.27]	0.67 [0.39, 0.85]
Vega	24.3 [8.3, 46.5]	0.22 [0.07, 0.41]	0.11 [0.02, 0.21]	0.0038 [0.0013, 0.0072]	0.0019 [0.0004, 0.0037]	1.76 [0.96, 2.85]	0.53 [0.29, 0.86]	0.25 [0.10, 0.44]	0.0020 [0.0011, 0.0033]	0.0010 [0.0004, 0.0017]	4.82 [1.60, 8.74]	0.76 [0.46, 0.92]
ΔGG	2.72 [−19.4, 23.0]	0.10 [−0.12, 0.31]	0.09 [−0.06, 0.22]	0.0004 [−0.0031, 0.0035]	0.0007 [−0.0016, 0.0027]	−0.60 [−1.70, 0.40]	−0.09 [−0.43, 0.25]	0.02 [−0.21, 0.23]	−0.0007 [−0.0020, 0.0004]	−0.0001 [0.0010, 0.0005]	−1.24 [−5.34, 2.67]	−0.07 [−0.40, 0.26]

Note: Point estimates are posterior modes with 95% HPD intervals in square brackets, estimated by the GGAM with 40% and 15% prior V_{ME} of BMR and M_b, respectively. ΔGG shows the difference in the respective MCMC sample chains between the genetic groups Leka and Vega. Note that because the true ME and V_{ME} are unknown and therefore contained in V_P, estimates of h^2 are downward biased, whereas V_A, I_A, cov_A and r_A are presumably unbiased by ME.

between the two groups and there was no evidence for any difference from $b = ⅔$ or ¾ ($b_{A(Leka)} = 0.96$ [0.44, 1.47], $b_{A(Vega)} = 1.08$ [0.45, 1.55], posterior difference 0.13 [−0.63, 0.69]). In *Leka*, b_A was similar or higher than b_P ($b_{P(Leka)} = 0.86$ [0.55, 1.23]), whereas in *Vega*, b_P was higher ($b_{P(Vega)} = 1.39$ [1.15, 1.63]). Moreover, b_R was 1.45 [1.21, 1.71], thus higher than b_A in both genetic groups.

4 | DISCUSSION

We quantified the heritable genetic variation and covariation of BMR and M_b in two natural house sparrow populations (Leka and Vega) to improve our understanding of the evolutionary relationships between BMR and M_b and how these relationships may vary across populations. First, our analyses revealed both BMR and M_b had considerable amount of additive genetic variation in both populations (Table 2) and that there were only weak tendencies for differences in the evolutionary potential between the populations. Second, the positive phenotypic covariance between BMR and M_b had a strong genetic basis (r_A ca. 0.7) and this was similar in the two populations (Table 2). Third, despite strong phenotypic and additive genetic allometric relationships between BMR and M_b, estimates of conditional evolutionary potential suggested that BMR can evolve independently of M_b, even when M_b is under strong stabilizing selection. Finally, our analyses found no evidence for population differentiation in either phenotypic mean or mean breeding values before artificial selection, nor that the populations differed with respect to average environmental effects on either BMR or M_b.

A particular strength of our study was that we applied bivariate GGAMs jointly with a common garden experimental design (de Villemereuil et al., 2016; Muff et al., 2019). This allowed us to estimate additive genetic (co-)variance parameters separately in different genetic groups that were genetically connected within an admixed population, while controlling for potential biases in estimates caused by prior environmental differences and potential immigration from adjacent populations. ME did not appear to influence estimates of V_A or cov_A in the focal traits.

4.1 | Predictions for evolutionary responses

Both BMR and M_b are plastic traits in many taxa (Broggi et al., 2007; Konarzewski & Ksiazek, 2013; White et al., 2006). However, our study showed that these traits can harbour substantial heritable genetic variation thus allowing for adaptative evolution following changes in selection regimes due to for example changing climates. Our unconditioned heritability estimates of BMR ($h^2 = 0.22–0.32$) were in concordance with previous estimates in wild passerines, although in the lower range (Bushuev et al., 2011, 2012; Nilsson et al., 2009; Tieleman et al., 2009). Based on previously reported estimates of additive genetic variances and mean phenotypic values in wild passerine populations, evolvability of BMR range from $I_A = 0.0014$ to 0.0071 (Bushuev et al., 2011, 2012; Mathot et al., 2013; Nilsson et al., 2009; Rønning et al., 2007;

Tieleman et al., 2009). Thus, our estimates for BMR in free-living house sparrows (I_A = 0.0038–0.0042) agree with estimates from previous studies. Our estimates of unconditional heritability in M_b (h^2 = 0.46–0.53) were average to relatively high compared to previously reported values (h^2-range: 0–0.73), whereas our evolvability estimates in M_b (I_A = 0.0013–0.0020) were somewhat intermediate (range: 0.0003–0.014, see e.g. [Bushuev et al., 2012; Gosler & Harper, 2000; Jensen et al., 2003; Nilsson et al., 2009; Rønning et al., 2007; Teplitsky et al., 2009; Tieleman et al., 2009; Wiggins, 1989]). As our M_b measurements were taken at fixed timepoints, reducing the effects of diurnal fluctuations in M_b (Broggi et al., 2003; Cucco & Bowman, 2018; Haftorn, 1992; Lehikoinen, 1987), this methodological standardization reduced the biological ME and V_P, and, hence, reduced downward bias in h^2 (Ponzi et al., 2018).

The ability for evolution of BMR independent of M_b may be particularly important for population persistence under environmental change. Previous studies have suggested that the genetic correlation between BMR and M_b can be close to 0 or 1 in passerines (Bushuev et al., 2012; Nilsson et al., 2009). Consequently, the corresponding reductions in evolutionary potential when conditioning BMR and M_b were effectively 0% or close to 100% (Bushuev et al., 2012; Nilsson et al., 2009; Tieleman et al., 2009), whereas three studies have reported r_A ranging from 0.4–0.9, corresponding to 16–84% reduction due to conditioning (Mathot et al., 2013; Rønning et al., 2007; Tieleman et al., 2009). In the present study, we found 42% and 57% reduction in evolutionary potentials in *Leka* and *Vega*, respectively. Hence, after accounting for their common additive genetic basis, there was still additive genetic variance in both traits in both populations. That indicates that there is potential for their independent evolution, for example under directional selection on BMR and stabilizing selection on M_b or selection in opposing directions, although the rate of the independent evolution may be somewhat limited. Estimated b_A's were relatively high ($b_{A(Leka)}$ = 0.96 and $b_{A(Vega)}$ = 1.08), although highly uncertain. Thus, there was no evidence for any difference in b_A from the b = ⅔ or ¾ 'laws' that have been the common view (Careau & Glazier, 2022; Glazier, 2005). While (Careau & Glazier, 2022) found b_P and b_R to be lower than b_A, and ascribe the low estimates partly to ME, we found b_R to be higher than b_A in both groups, and $b_A > b_P$ in Leka whereas $b_A < b_P$ in Vega. This may suggest that some environmental conditions are important for the allometric relationship between BMR and M_b, and these conditions may differ between the two populations. But again, the uncertainty in estimates makes those conclusions highly speculative.

There was a tendency for differences between the populations in genetic covariance and correlation between the traits, but the uncertainties in estimates were too large for a clear assessment. Note that our estimated **G**-matrices are defined for the base population in 2012, thus unaffected by the selection experiment during 2012–2015 but potentially affected by the selection experiment on tarsus length during 2002–2005 (Boratyński et al., 2013). Any population differentiation in the **G**-matrix suggests evolutionary mechanisms (e.g. drift, gene flow or selection) have influenced its components differently across populations (Arnold et al., 2008; Guillaume & Whitlock, 2007; Phillips et al., 2001). The sizes of our study populations were both relatively small and variable prior to our study (annual census population sizes during 2002–2012: $N_{Leka} > 89$ and $N_{Vega} > 102$ [Kvalnes et al., 2017]), thus genetic drift may have influenced population **G**-matrices (Phillips et al., 2001). Furthermore, Vega had a higher increase of *unknown* individuals than Leka, which may indicate higher immigration from a somewhat genetically divergent gene pool, and also contribute to increased genetic diversity and changes in the **G**-matrix (Guillaume & Whitlock, 2007). However, both drift and gene flow should have similar effects across all loci; hence, the population differences in evolutionary potentials should be similar across traits. Our results indicate, however, that evolutionary potentials of BMR and M_b potentially may have been differently affected by evolutionary forces in these two populations. One obvious difference in evolutionary histories of the Leka and Vega populations is the artificial selection experiment on body size (for large size on Leka and small size on Vega) that was conducted over 4 years and ended 7 years prior to the start of the current study (Boratyński et al., 2013). Although we have previously shown that body size rapidly returned to pre-experimental means phenotypically, we know that body size and body mass are genetically correlated (Araya-Ajoy et al., 2019; Jensen et al., 2003) and can therefore hypothesize that the strong selection on body size in the recent past may have influenced **G**-matrices for BMR and M_b differently in the two populations. Direct and indirect selection target loci (and loci in linkage disequilibrium with those) that are causal to the trait under selection and is thus expected to reduce V_A, although selection alone will probably not substantially change genetic variation in traits that are determined by a large number of loci (Bulmer, 1971). Consequently, while we compared components of the group-specific **G**-matrices for BMR and M_b and found only weak tendencies for any differences (Table 2), several processes may have occurred in different strengths in these populations and caused the group-specific **G**-matrices to diverge, potentially resulting in different future evolutionary trajectories even under similar selection pressures.

4.2 | Measurement error considerations

We did not have statistical power to estimate ME directly, due to lack of within-session repeated measures, but prior specification of its contribution to the variance using the mev-argument in MCMCglmm show that our estimates of fixed effects as well as additive genetic (co)variances were little affected by ME variances up to 40% in BMR and 15% in M_b. Reassuringly, when increasing V_{ME}, the error largely appeared to be absorbed in the residual variance and affected the identifiability of the ID variance. Hence, the estimates of interest therefore remained little affected (Table S5.3 and Figure S5.2 in Appendix S1). This finding suggests that our estimates of V_A in both BMR and M_b as well as their cov_A and quantitative genetic parameters based on these estimates are robust and approximately unbiased by ME for both traits. Moreover, the discrepancy between conclusions regarding evolutionary potential based on heritability and evolvability (h^2 lower, whereas I_A higher, of BMR than of M_b)

highlights the importance of evaluating their specific suitability, for example by evaluating how the two measures may be biased by ME. Our inability to estimate the true ME means any potential contribution of ME to the phenotypic variance produces a downward bias in our h^2 estimates, whereas I_A is presumably unbiased by ME (Ponzi et al., 2018). Thus, I_A is likely to better reflect evolutionary potentials of our focal traits in the presence of ME.

5 | CONCLUDING REMARKS

Application of GGAM, concomitant with a common garden approach, allowed us to disentangle genetic from environmental effects on BMR and M_b in two natural populations of house sparrows. Differences in mean breeding values and local environmental effects between the two populations were negligible, whereas there were weak tendencies for differences in evolutionary potential of BMR and M_b. However, conditioning the traits on each other removed these differences. In general, our results indicate substantial evolutionary potential of BMR in natural populations, indicating that there is potential for responding to changing selection on BMR, induced by, for example, environmental change, but that the evolutionary responses may be population-specific. While studies on a larger number of populations and species are needed to assess generality, these findings suggest potential for intraspecific variation to influence species-level responses to climate change.

AUTHOR CONTRIBUTIONS

Ådne M. Nafstad: Conceptualization (supporting); data curation (equal); formal analysis (equal); investigation (equal); resources (equal); software (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Bernt Rønning:** Conceptualization (equal); data curation (equal); investigation (lead); methodology (equal); project administration (equal); resources (lead); supervision (equal); validation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Kenneth Aase:** Formal analysis (equal); methodology (equal); software (supporting); validation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Thor Harald Ringsby:** Conceptualization (equal); funding acquisition (supporting); investigation (supporting); project administration (supporting); resources (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Ingerid J. Hagen:** Investigation (supporting); resources (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Peter S. Ranke:** Investigation (supporting); methodology (supporting); resources (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Thomas Kvalnes:** Investigation (supporting); methodology (supporting); resources (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Clare Stawski:** Supervision (supporting); validation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Katja Räsänen:** Supervision (supporting); validation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Bernt-Erik Sæther:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); writing – original draft (supporting); writing – review and editing (supporting). **Stefanie Muff:** Conceptualization (equal); formal analysis (supporting); methodology (equal); project administration (equal); software (supporting); supervision (equal); validation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Henrik Jensen:** Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (supporting); software (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The pedigree and phenotype data used in this study are available in the Dryad repository: 10.5061/dryad.rv15dv49z

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