


Maintenance costs of male dominance and sexually antagonistic selection in the wild

Zbyszek Boratyński^{1,2}  | Esa Koskela² | Tapio Mappes² | Suzanne C. Mills^{2,3,4} | Mikael Mokkonen^{2,5,6}

¹CIBIO/InBIO, Research Center in Biodiversity and Genetic Resources, University of Porto, Vairão, Vairão, Portugal; ²Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; ³PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, Papetoai, Moorea, French Polynesia; ⁴Laboratoire d'Excellence "CORAIL", Corail, France; ⁵Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada and ⁶Department of Biology, Kwantlen Polytechnic University, Surrey, British Columbia, Canada

Correspondence

Zbyszek Boratyński
Email: boratyns@cibio.up.pt

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Abstract

1. Variation in dominance status determines male mating and reproductive success, but natural selection for male dominance can be detrimental or antagonistic for female performance, and ultimately their fitness. Attaining and maintaining a high dominance status in a population of competing individuals is physiologically costly for males. But how male dominance status is mediated by maintenance energetics is currently not well understood, nor are the corresponding effects of male energetics on his sisters recognized.
2. We conducted laboratory and field experiments on rodent populations to test whether selective breeding for male dominance status (dominant vs. subordinate breeding lines) antagonistically affected basal metabolic rate (BMR) and fitness of females under wild conditions.
3. Our results showed elevated BMR in females, but not in males, from the dominant breeding line. However, phenotypically dominant males from the subordinate breeding line had the highest BMR.
4. Males from the dominant line with low BMR sired the most litters and offspring in the field. Similarly, females from the dominant selection line tended to have more offspring if they had lower BMR, while the opposite trend was found in females from the subordinate selection line. Females with high and low BMR reproduced most often, as indicated by a significant quadratic selection gradient.
5. The increased female BMR resulting from selection for male dominance suggests genetic incompatibility between sexes in metabolism inheritance. Elevated BMR in behaviourally dominant males, but not in males from the dominant breeding line, suggests physiological costs in males not genetically suited for dominance.
6. Fitness costs of elevated maintenance costs (measured as BMR) shown here support the energetic compensation hypothesis where high BMR is selected against as it would trade off energy required for other important life-history attributes.

KEYWORDS

antagonistic selection, basal metabolic rate, dominance behaviour, energetics, sexual conflict, testosterone

1 | INTRODUCTION

Intralocus sexual conflict can drive males and females from their sex-specific life-history optima, thereby compromising lifetime fitness (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Mokkonen, Koskela, Mappes, & Mills, 2016). Such conflict occurs when the same alleles have opposing fitness between males and females that, unless there is sex-limited gene expression, impedes adaptive evolution (Bonduriansky & Chenoweth, 2009; Mills, Koskela, & Mappes, 2012; Van Doorn & Fe, 2009). Intralocus conflict has the potential to generate sexually antagonistic selection affecting fitness through survival and the reproductive components of fitness, such as mating and reproductive success. However, male success in mating and reproduction is physiologically costly (Vehrencamp, Bradbury, & Gibson, 1989). Currently, the maintenance energetics mediating male fitness are not clear, nor is the presence of sexual antagonism for such maintenance costs.

Behavioural dominance often defines a male's access to mates (Qvarnström & Forsgren, 1998). Testosterone, which mediates the dominance hierarchy in males, can impose differential expression of many physiological pathways between males and females (Peterson et al., 2014). Testosterone can affect mating behaviour (Mills et al., 2012; Mokkonen, Koskela, Mappes, & Mills, 2012) and fitness: For example, red deer male calves born to first-time mothers were less likely to survive if they had high neonatal testosterone level (Pavitt, Walling, Mcneilly, Pemberton, & Kruuk, 2014). Male dominance is also directly influenced by the tactics of other males in the population, showing negative frequency-dependent selection in the wild, that is, being costly for males when common in the population (Mokkonen et al., 2011). Dominance status and testosterone level can both be heritable and respond to selection (Pavitt, Walling, Mcneilly, et al., 2014; Schroderus et al., 2010), but the evolution of sex-specific testosterone levels can be constrained by cross-sex genetic correlation (Pavitt, Walling, Pemberton, & Kruuk, 2014). The status of a highly dominant male, with a high testosterone level, can reveal physiological costs (Bryant & Newton, 1994; Røskaft, Järvi, Bakken, Bech, & Reinertsen, 1986). However, selection for testosterone level can differentially associate with son versus daughter reproductive success, causing a negative correlation in fitness between siblings (Mills et al., 2012; Mokkonen et al., 2012). Testosterone may differentially affect overall gene expression between males and females, affecting many metabolic and physiological traits (Peterson et al., 2014). Yet, currently it is unclear how selection for dominance in males affects maintenance costs in both sexes, females in particular, or whether frequency-dependent selection on dominance promotes or constrains adaptations in metabolic traits (Buchanan, Evans, Goldsmith, Bryant, & Rowe, 2001).

Many studies have been carried out to explain intra- and inter-specific variation observed in the lower limit of energy metabolism, the basal metabolic rate (Boratyński, Jefimow, & Wojciechowski, 2016; Keil et al., 2012; Polymeropoulos, Oelkrug, White, & Jastroch, 2017; Sadowska et al., 2015; Tieleman, Williams, & Bloomer, 2003). The level of basal metabolic rate relative to its body mass

(hereafter BMR) is invoked to reflect an individual's maintenance costs (Konarzewski & Książek, 2012). According to two main competing models, a high BMR reflects either energetic predisposition to support costly behaviours, such as reproduction (the "increased intake" hypothesis; Nilsson, 2002), or that a high BMR trades off with other important life functions (the "compensation" or "allocation" hypothesis; Gadgil & Bossert, 1970; Pettersen, Marshall, & White, 2018). It is already known that variation in BMR can influence fitness (Boratyński, Koskela, Mappes, & Schroderus, 2013; Careau et al., 2013; Møller, 2009; Nilsson & Nilsson, 2016; Pettersen et al., 2018) and that both of its genetic and fitness consequences can be sex specific (Boratyński, Ketola, Koskela, & Mappes, 2016; Boratyński, Koskela, Mappes, & Oksanen, 2010; Rønning et al., 2016). Nevertheless, the cross-sex genetic correlation can constrain independent evolution of BMR between males and females, thereby providing a potential opportunity for intralocus sexual conflict in maintenance energetics (Bonduriansky & Chenoweth, 2009; Rand, Clark, & Kann, 2001).

BMR and testosterone can be involved in the expression of life-history traits linked to fitness (Moore & Hopkins, 2009). For example, females with higher metabolism can transfer more testosterone to eggs (Tschirren et al., 2016), while the close physiological association between testosterone level and metabolic rate can result in testosterone-mediated honest sexual signalling in males (Buchanan et al., 2001). But it is still unclear how BMR affects the evolution of sexually antagonistically selected life-history traits and whether it links to frequency-dependent selection on male tactics (Mills et al., 2009, 2012; Mokkonen et al., 2011). Bateman's principle predicts that male fitness is primarily shaped by mating success, whereas female fitness is primarily shaped by longevity to optimize their lifetime reproductive effort (Roff, 2002). As mating and reproductive success can be affected by energetic physiology (Boratyński & Koteja, 2010), selection for increased male fitness would theoretically affect physiological performance of both sexes as well as their level of BMR (i.e., maintenance costs). In particular, according to the parental care concept of the evolution of endothermy, which provides an adaptive explanation for the evolution of a high level of BMR, selection for increased reproductive output should result in a correlative response in increase of the level of maintenance metabolism, at least in females (Bacigalupe, Moore, Nespolo, Rezende, & Bozinovic, 2017; Koteja, 2004). However, it is unclear whether the cross-sex genetic correlation of metabolism can constrain responses to antagonistic selection between males and females.

We would predict that (1) if the cross-sex genetic correlation for BMR is relatively low in our study species (Boratyński et al., 2013), males and females can theoretically approach their optimal levels of maintenance metabolism. Being dominant is energetically costly, and thus according to the "increased intake" hypothesis, we would predict that (2) metabolic performance, rather than size alone, along with the level of expressed testosterone, can constrain expression of male dominance (Buchanan et al., 2001). Alternatively, and according to the "allocation" hypothesis, low BMR might release

resources to invest in behavioural performance such as dominance. We would therefore predict that (3) energetic costs for individuals expressing high dominance status might be different between males whose fathers were dominant versus those whose fathers were subordinate. Males not genetically predisposed to high dominance might manifest higher energetic costs (sensu “increased intake” hypothesis) of expression of such status than those males which inherited genes of dominance (sensu “allocation” hypothesis). Theories predicting the evolution of a high level of BMR (Angilletta & Sears, 2003; Farmer, 2000) postulate that individuals with a higher metabolic capacity can sustain elevated energetic demands of reproduction (e.g., males maintaining larger territories, females providing their pups with more food). However, information is lacking on the fitness costs of high versus low maintenance physiology, and BMR, for males and females selected for high versus low reproductive output. Theoretically, we predict that (4) a high BMR could result from correlative selection for high reproductive output and physiological capacity. However, previous studies have shown that not only can the direction of selection on BMR differ between males and females, and among seasons (Boratyński & Koteja, 2009, 2010; Boratyński et al., 2010), but a low BMR can generally be beneficial for fitness (Boratyński et al., 2013).

We experimentally tested these hypotheses in a field study on bank voles subjected to artificial selection in the laboratory that resulted in the selection lines of behaviourally dominant males with sisters of low fecundity and subordinate males with sisters of high fecundity (Mokkonen et al., 2011). We tested whether selective breeding of male bank voles with high and low dominance status influenced their BMR and whether any associated sexually antagonistic effects can be observed in female metabolic performance. We tested whether BMR is inflated in males due to inherited correlative line-specific selection effects or whether they are related to behavioural (dominance) and physiological (testosterone level) phenotypic status. We also estimated whether male dominance status is primarily determined by testosterone level or whether it is constrained by BMR. Ultimately, we tested whether BMR influenced the main reproductive fitness components, mating and reproductive success, and whether frequency-dependent selection operated on male dominant vs. subordinate breeding lines in the field.

2 | MATERIALS AND METHODS

2.1 | Study species and artificial selection for male dominance

The bank vole is a Palearctic species with a polygynandrous mating system. Bank voles have been shown to experience sexually antagonistic selection for testosterone: Artificial selection for testosterone is associated differentially with son versus daughter reproductive success, causing a negative correlation in fitness between full-siblings (Mills et al., 2012; Mokkonen et al., 2012). To further investigate phenotypic traits related to sexually

antagonistic relationship between son and daughter fitness, we artificially selected bank voles in the laboratory based on male dominance, the details of which are described elsewhere (Mokkonen et al., 2011). Briefly, two selection lines were created for this experiment using artificial selection; high-dominance males, M, were mated with females of low fertility, f (Mf line), and low-dominance (subordinate) males, m, were mated with females of high fertility, F (mF line). Male dominance was tested in non-repeated male–male competition trials where a high-dominance line male and a low-dominance line male competed in an arena with each other to mate with a wild female in oestrus, until the successful males out-competed opponent males and mated with the female. We used a total of 168 males in the male–male competition trials reported in this study. Matings were conducted by pairing a chosen male with a female in a standard cage for a period of 2 weeks, after which the male was separated from the female, and gravidity of the female assessed. Approximately 3 weeks after initial pairing with a sire, pregnant females gave birth. Within 24 hr of birth, common litter characteristics were measured, including: body mass of each offspring and mother, sex of offspring (based on visual cues and anogenital distance; Koskela, Mappes, Niskanen, & Rutkowska, 2009) and litter size (number of offspring). Offspring were kept with mothers until they were weaned 21 days after birth. Study individuals were fourth and fifth generation descendants of wild individuals. Males and females in the laboratory were housed at 22°C in standard cages measuring 43 × 26 × 15 cm with wood shavings and hay for bedding, ad libitum water and food (Labfor 36; Lactamin AB, Stockholm, Sweden) and kept on a 16:8 L:D photoperiod.

2.2 | Physiological measurements

We measured plasma testosterone levels of 164 adult males (mean ± SD age of 306 ± 55 days) by sampling individuals prior to their release to field enclosures. A 75 µl intra-orbital blood sample was taken from each individual and then analysed using the radioimmunoassay technique (TESTO-CTK, DiaSorin, Byk-Sangtec Diagnostica GmbH & Co, Germany). Further details of the protocol are described elsewhere (Mills, Grapputo, Koskela, & Mappes, 2007; Mills et al., 2009). To measure maintenance costs, we estimated basal metabolic rate (BMR) on the resting, post-absorptive, non-reproductive and exposed-to-thermoneutral temperature (30.0 ± 0.5°C) individuals (Labocha, Sadowska, Baliga, Semer, & Koteja, 2004; White & Kearney, 2013). We used open positive flow respirometry system with multiple (7) animal and one control chambers (Sable Systems, Henderson, NV, U.S.A.) equipped with oxygen analyser (Fc-1B; Sable Systems). Seven and a half hours of trials, with this system, gave reliable O₂ data for estimating repeatable and heritable BMR in a study organism (Boratyński et al., 2011; Boratyński, Ketola, et al., 2016; Šichová, Koskela, Mappes, Lantová, & Boratyński, 2014). We estimated BMR for 40 males and 30 females from the dominant male (Mf) line and 34 males and 32 females from the subordinate male (mF) line.

2.3 | Field selection experiment

To measure strength and form of natural selection on the phenotype, we used a total of 91 females and 91 males in a field experiment. In total, 20 populations were created in two replicates (11 and 9 populations) using 11 field enclosures measuring 40 × 50 m each (Mokkonen et al., 2011). Each population consisted of an equal number of males to females and contained 1 male and 1 female from a given selection line with 4 (1st) or 3 (2nd replicate) males and females from the other selection group (e.g., population A: 1 Mf male + 1 Mf female + 4 mF males + 4 mF females; population B: 4 Mf males + 4 Mf females + 1 mF male + 1 mF female) to test for the frequency-dependent selection on breeding lines (Mokkonen et al., 2011). Individuals were randomly assigned to enclosures; however, sibling assignments to the same enclosure were avoided. Each enclosure contained 20 Ugglan live traps in a 4 × 5 grid pattern, and they were spaced 10 m apart. Sheet metal fencing (1.0 m above, 0.5 m below ground) surrounded each enclosure, preventing escape of study individuals while at the same time allowing possible predators to enter the enclosures. Study individuals relied on natural field conditions and resources to survive. Initially, females were released to enclosures. After 4 days, males were then released and all individuals were left to survive and breed in the field enclosures. Eighteen days after males were introduced, all study individuals were trapped out of the enclosures and brought to the laboratory for females to give birth. In the laboratory, pregnant females were monitored every 24 hr. After a birth, tissue samples were taken from each offspring individual and common litter characteristics were recorded. Each offspring was genotyped by extracting DNA using the Qiagen DNeasy Tissue kit and KingFisher magnetic particle processor, and then, Cervus 3.0 software was used to assign paternity (Kalinowski, Taper, & Marshall, 2007). The use of study animals and all above protocols adhered to ethical guidelines for animal research in Finland (Finnish National Animal Experiment Board, permission numbers: ESLH-2008-04660/Ym-23 and ESLH-2009-09663/Ym-23).

2.4 | Statistical analysis

2.4.1 | Correlative responses in BMR

We used a generalized mixed model (GLMM) procedure to test for female and male correlative responses (maternal and heritable effects) in BMR to artificial selection for male dominance status. Log-transformed BMR was included as the dependent variable (Gaussian family function), male selection line affiliation (dominant vs. subordinate line) and sex as fixed cofactors, and (log-transformed) age and body mass at metabolic trials as covariates. Due to a significant effect of sex on dependent variables, models were also run separately for males and females.

2.4.2 | Dominance phenotype and BMR

To tests if maintenance metabolism constrains a male's dominance phenotype (dominant vs. subordinate status), we ran a GLMM with male dominance status as the dependent variable (binomial family function), line affiliation as fixed cofactor, and (log-transformed) age, body mass at metabolic trials, BMR and testosterone level as covariates.

2.4.3 | BMR, dominance phenotype and genotype

To test for energetic costs between dominance phenotypes and genotypes of male bank voles we ran a GLMM including log-transformed BMR as the dependent variable (Gaussian family function), dominance status (dominant vs. subordinate status) and selection line affiliation (dominant vs. subordinate line) as fixed cofactors, and (log-transformed) testosterone level, age and body mass at metabolic trials as covariates.

All models included mother ID and respirometry chamber ID as random factors (to control for common early environment/relatedness among individuals and variation in respirometry machine) and tested factorial interactions (those insignificant were sequentially excluded). Effect sizes are presented as percentages of differences between back-transformed least-squares means predicted from above models. Statistical tests from models with residual BMR (from linear regression of BMR on age and body mass) as the dependent variable (or covariate) are presented in the main text for simplicity.

2.4.4 | Selection analyses

The strength and form of selection on phenotype in the wild was tested with generalized mixed modelling (GLMM) with separate models for dependent variables: (a) number of sired litters (Poisson family function) and (b) number of sired offspring (Poisson family function, zero inflated), for male fitness components, and (c) probability to reproduce (binomial family function) and (d) litter sizes (Poisson family function), for fitness components of females. The strength and form of natural selection was tested in GLMMs including independent variables of line type (dominant vs. subordinate line) and its frequency as fixed cofactors, and (log-transformed) BMR, body mass and age at the onset of experiment as covariates. We tested factorial interactions between all characters while controlling for maternal, common environmental and replication effects (random factors of mother ID, population ID and replication of experiment). Linear and quadratic effects and interactions between BMR, age and body mass were tested to account for directional, stabilizing/disruptive and correlational selections, respectively (due to limited power, interactions were first tested in separate models per interaction type, and finally, significant terms were included in one model; Artacho, Saravia, Ferrandière, Perret, & Le Galliard, 2015; Rønning et al., 2016). Age did not affect fitness components and it was excluded from final tests. To remove the correlation between

TABLE 1 Generalized mixed models (GLMMs) to quantify effects of selection procedure (line: dominant vs. subordinate) and sex on residual BMR values (accounted for variation in age and body mass; see Supporting Information Table S2 for similar results for absolute BMR values). Line-by-sex interaction was not significant ($z = -1.34$, $p = 0.18$)

	Est. (SE)	z	p
BMR			
Line	-0.04 (0.02)	-2.44	0.015
Sex	0.05 (0.02)	2.47	0.013
BMR_{Males}			
Line	-0.02 (0.03)	-0.83	0.40
BMR_{Females}			
Line	-0.07 (0.03)	-2.51	0.012
BMR_{Dominant line}			
Sex	0.07 (0.03)	2.61	0.009
BMR_{Subordinate line}			
Sex	0.03 (0.03)	0.95	0.34

Variance (SD) for random factors: mother ID = $2e-09$ ($5e-05$), BMR chamber = 0.002 (0.046), for males: mother ID = $2e-09$ ($5e-05$), BMR chamber = 0.003 (0.052); and for females: mother ID = $2e-09$ ($5e-05$), BMR chamber = 0.001 (0.030); for dominant line: mother ID = $2e-09$ ($5e-05$), BMR chamber = 0.002 (0.045); and for subordinate line: mother ID = $3e-09$ ($6e-05$), BMR chamber = 0.002 (0.042).

linear and quadratic terms, continuous predictors were standardized within datasets. Statistical modelling with GLMM was performed with “glmmADMB” (<http://glmmadmb.r-forge.r-project.org/>)

and “lme4” packages in R (www.r-project.org). For comparison of strength and form of selection with other studies standardized selection gradients were estimated (Artacho & Nespolo, 2009; Lande & Arnold, 1983; Pettersen, White, & Marshall, 2016; Schluter, 1988). Linear (β) and nonlinear (γ ; quadratic, correlational) selection gradients were estimated by means of coefficients from multiple regression analyses, separately for females and males, and within selection lines, with relative fitness as dependent variable and standardized quantitative traits (BMR and body mass) as predictors. Linear effects (β) were estimated in multiple regression models including only main effects, while nonlinear effects (γ) were estimated in models including also quadratic or correlational terms along the linear effects. Coefficients for quadratic terms were multiplied by two (Fairbairn & Reeve, 2001). The 95% confidence intervals of the coefficients were estimated with 1,000 bootstrapping.

3 | RESULTS

3.1 | Correlative responses in BMR

Residual values were calculated from a multiple linear regression with BMR as the dependent variable and body mass and age as independent variables to account for significant correlations of BMR with age ($t = 2.86$, $p = 0.005$) and body mass ($t = 8.60$, $p < 0.001$). We used BMR residuals to test for statistical differences between groups (results for absolute BMR values from models that included age and body mass were qualitatively similar; Table 1, Supporting Information Tables S1 and S2). Females (Figure 1a) and individuals

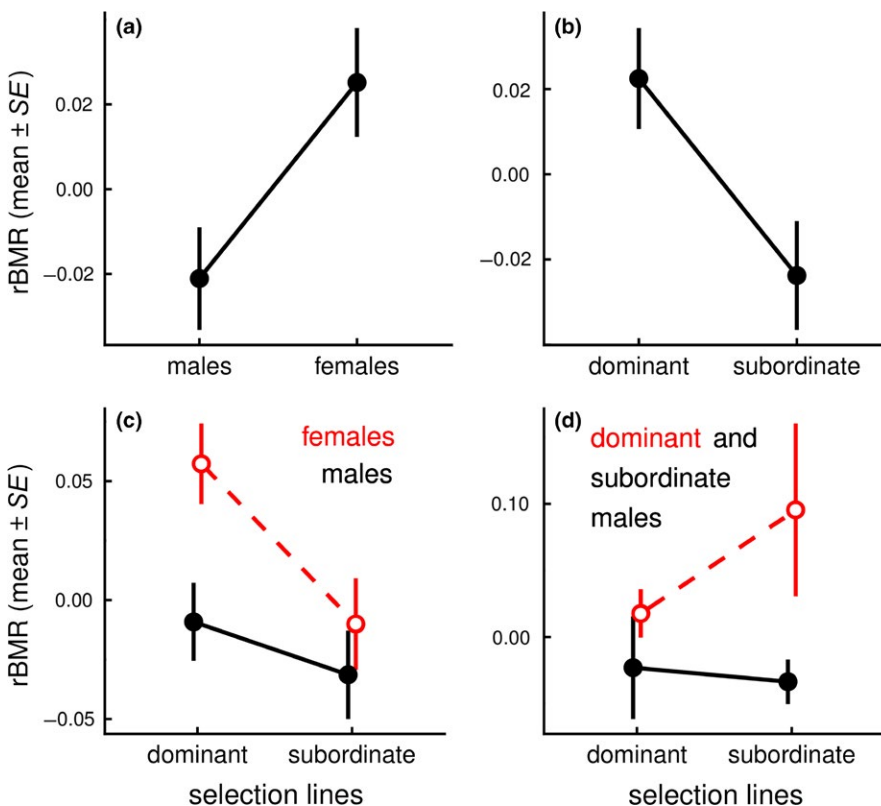


FIGURE 1 Differences in residual basal metabolic rate (rBMR) in bank voles: (a) between males and females, (b) between selection lines, (c) between males (black closed circles, solid lines) and females (red open circles, dashed lines) within and between selection lines, and (d) between males of either dominant (red open circles, dashed lines) or subordinate (black closed circles, solid lines) behaviours within their respective selection lines. Residual BMR values were calculated from mixed models accounting for variation in body mass and age, as covariates, and mother and respirometric chamber IDs, as random factors

TABLE 2 Generalized mixed models for males only to quantify effects of residual BMR (accounted for variation in age and body mass), selection procedure (line: dominant vs. subordinate) and (log-transformed) testosterone level (Testo) on behavioural dominance status (dominant vs. subordinate; see Supporting Information Table S3 for similar results for absolute BMR values)

	Est. (SE)	z	p
Line	-3.94 (0.87)	-4.52	<0.0001
rBMR	9.13 (3.62)	2.53	0.012
Testo	-0.43 (0.50)	-0.85	0.39

Variance (SD) for random factors: mother ID = 2e-06 (1e-03), BMR chamber = 5e-07 (7e-04).

TABLE 3 Generalized mixed model for males to quantify effects of selection procedure (line, dominant/subordinate), behavioural dominance status (dominant/subordinate) and testosterone level (Testo) on residual BMR (accounted for variation in age and body mass; Figure 2)

	Est. (SE)	z	p
Line	0.28 (0.11)	2.60	0.009
Dominance	0.35 (0.10)	3.36	0.0008
Testo	0.16 (0.06)	2.68	0.007
Dom × Testo	-0.15 (0.06)	-2.63	0.009
Line × Testo	-0.14 (0.06)	-2.27	0.023

Variance (SD) for random factors: mother ID = 2e-09 (5e-05), BMR chamber = 0.003 (0.050).

from lines selected for male dominance (Figure 1b) had on average 6.5% and 4.7% higher BMR than males and individuals from the male subordinate line, respectively (Table 1 and Supporting Information Table S2). The difference in BMR between lines (Figure 1b) was

generated by the significant differences in BMR between females (6.8%), not males (2.3% of difference; Figure 1c), with females from the male dominance line having the highest BMR (despite a non-significant sex-by-line interaction, $p > 0.1$; Table 1 and Supporting Information Table S2). In the male dominance line, BMR was higher in females than in males by 7.3% ($z = 2.61$, $p = 0.009$; Figure 1c), whereas the difference in BMR between the sexes did not meet significance in the male subordinate line (5.6%, $z = 0.95$, $p = 0.34$; Figure 1c).

3.2 | Dominance phenotype and BMR

In male–male competition trials, males were 81.4% more likely dominant in the line selected for dominance status. When analysed over both selection lines, phenotypically dominant males have 8.8% higher BMR than subordinate males (line-by-BMR interaction was insignificant, $z = 0.14$, $p = 0.89$; Table 2 and Supporting Information Table S3). However, phenotypically dominant males from the subordinate selection line have the highest BMR (Figure 1d). BMR was 11.6% higher than in phenotypically subordinate males from the same line ($z = 2.49$, $p = 0.013$) and 8.4% higher than in phenotypically dominant males from the dominant line (Figure 1d). There was no significant difference in BMR between phenotypically dominant and subordinate males from the dominant selection line (7.1%, $z = 0.58$, $p = 0.30$; Figure 1d).

3.3 | BMR, dominance phenotype and genotype

We found that variation in male BMR was explained by the interactions between selection line and testosterone level, and between dominance status and testosterone level (but line-by-testosterone-by-dominance status interaction was insignificant: $z = 0.71$, $p = 0.48$; Table 3 and Supporting Information Table S4).

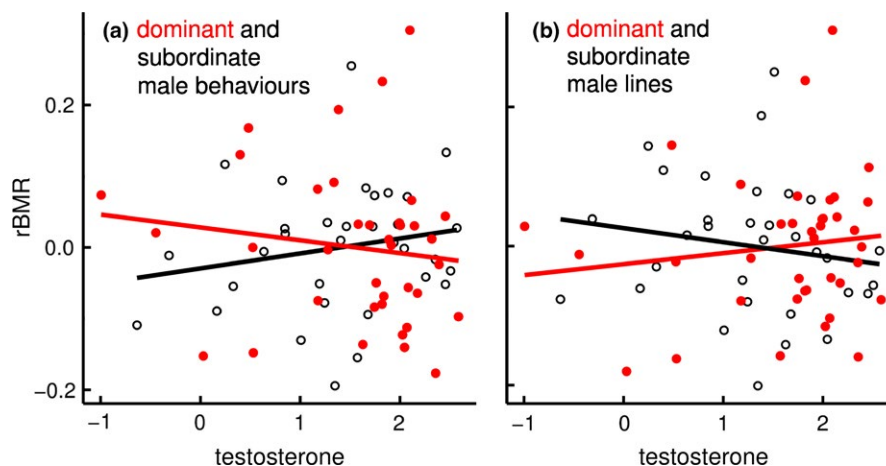


FIGURE 2 The relation between residual basal metabolic rate (rBMR) of male bank voles and testosterone level (log-transformed) between (a) behaviourally dominant (red closed circles, solid line) and subordinate (black open circles, dashed line) groups and (b) between dominant (red close circles, solid line) and subordinate (black open circles, dashed line) selection lines. Residual BMR values were calculated from mixed models (accounting for variation in body mass and age, as covariates, and mother and respirometric chamber IDs, as random factors) after excluding significant interactions between testosterone level and dominance, and line and testosterone (Table 3)

TABLE 4 Generalized mixed models for males to quantify effects of artificial selection procedure (line: dominant vs. subordinate), frequency of individuals from selection lines (frequency: low vs. high), and (log-transformed) body mass (BM), age (on the onset of field experiment) and BMR on male fitness components: number of sired litters and offspring

	Est. (SE)	z	p
Number of sired litters			
Line	-0.14 (0.34)	-0.40	0.69
Frequency	1.15 (0.88)	1.30	0.19
sBMR	-0.75 (0.33)	-2.29	0.022
sBM	-1.34 (0.79)	-1.70	0.090
sBMR ²	-0.54 (0.26)	-2.10	0.036
Freq × sBM	1.89 (0.80)	2.37	0.018
Number of sired litters _{Dominant line}			
sBMR	-0.76 (0.26)	-2.94	0.003
Number of sired litters _{Subordinate line}			
sBMR	0.11 (0.45)	0.26	0.80
Number sired offspring			
Line	0.61 (0.30)	2.00	0.046
Frequency	0.93 (0.67)	1.38	0.17
sBMR	-0.53 (0.22)	-2.45	0.014
sBM	-1.54 (0.61)	-2.55	0.011
Line × sBMR	0.92 (0.43)	2.13	0.033
Freq × sBM	1.44 (0.61)	2.36	0.018
Number of sired offspring _{Dominant line}			
Frequency	1.18 (0.75)	1.56	0.12
sBMR	-0.65 (0.23)	-2.86	0.004
sIBM	-2.04 (0.74)	-2.74	0.006
Freq × sBM	1.98 (0.74)	2.69	0.007
Number of sired offspring _{Subordinate line}			
sBMR	0.65 (0.44)	1.48	0.14

Variance (SD) for random factors for number of sired litters: mother ID = 4e-09 (6e-05), enclosure = 3e-08 (2e-04), replicate = 0.05 (0.22); in dominant line: mother ID = 0.10 (0.32), enclosure = 2e-09 (5e-05), replicate = 3e-08 (2e-04); in subordinate line: mother ID = 6e-07 (8e-04), enclosure = 1.41 (1.19), replicate = 1.03 (1.02); for number sired offspring: mother ID = 2e-09 (5e-05), enclosure = 0.03 (0.17), replicate = 0.12 (0.35); for dominant line: mother ID = 2e-09 (5e-05), enclosure = 0.07 (0.26), replicate = 0.30 (0.55); and for subordinate line: mother ID = 3e-09 (5e-05), enclosure = 3.99 (2.00), replicate = 3.51 (1.87).

The BMR of males that behaved phenotypically dominant tended to decrease with increasing testosterone levels, whereas the BMR of males that behaved phenotypically subordinate tended to increase with increasing testosterone levels (Figure 2a). On the other hand, the BMR of males from the male dominant line tended to increase with increasing testosterone, whereas the BMR of males from the male subordinate line tended to decrease with increasing testosterone (Table 3 and Supporting Information Table S4, Figure 2b).

3.4 | Fitness costs

3.4.1 | Sired litters and offspring

In our initial analysis, we found a significant interaction between frequency (rare or common) and line (dominant vs. subordinate line) on reproductive success, in accordance with reported negative frequency-dependent selection on male reproductive morphs in bank voles ($z = 2.35$, $p = 0.019$, line: $z = -1.11$, $p = 0.27$, frequency: $z = -3.84$, $p = 0.0001$; Morkkonen et al., 2011). Rare males from lines selected for high dominance sired the highest number of offspring ($z = -3.57$, $p = 0.0004$), but frequency did not have a significant effect on the siring success of subordinate line males ($z = 0.19$, $p = 0.85$).

After including phenotypic data (body mass and BMR), stabilizing selection on BMR and frequency-dependent selection on body mass were suggested in overall analyses of number of sired litters (Table 4), but not in separate tests within selection lines. Instead, dominant line males with the lowest BMR values sired on average 1.4 more litters than males with the highest BMR values (on average 1.5 vs. 0.1 litters; Figure 3a), but a non-significant opposite trend was found between males from the subordinate selection line (average difference in number of litters was 0.6; Table 4; see Supporting Information Table S5 for selection gradients). Furthermore, we found that the BMR-by-line interaction significantly explained variation in the number of sired offspring (Table 4). Males in the dominant line with the lowest BMR values sired on average 5.0 more offspring than males with the highest BMR values (on average 5.5 vs. 0.5 sired offspring; Figure 3a). But an opposite trend of BMR on number of sired offspring was not significant for males from the subordinate line (average difference in number of offspring was 2.7; Table 4).

Frequency-dependent selection on body mass was significant in our overall tests for the number of sired litters and offspring, and in the test within the dominant line for the number of sired offspring (Table 4). Males from the dominant line sired 3.6 more offspring if they were rare than if they were common in the population (5.8 vs. 2.2 offspring sired; Table 4).

3.4.2 | Female mating success and litter size

Females that reproduced were 13.0% heavier than females that did not reproduce, but the trend was not significant ($p = 0.059$; Table 5). Females from around the median of the BMR distribution tended to reproduce less often than both females with the lowest (16.7%) and highest (55.1%) BMR (Table 5). The number of pups raised by females from the subordinate line increased as their BMR values increased (2.8 more pups: 6.4 vs. 3.6 pups from females with the highest vs. lowest BMR; Figure 3b), whereas the number of pups raised by females from the dominant line decreased as their BMR values increased (1.9 fewer pups: 3.75 vs. 5.6 pups from females with the highest vs. lowest BMR). However, this contrasting effect of BMR between lines (BMR-by-line interaction on litter sizes: $p = 0.015$) did not meet significance in our within-line tests ($p \geq 0.13$; Table 5; see also results for selection gradients in Supporting Information Table S6).

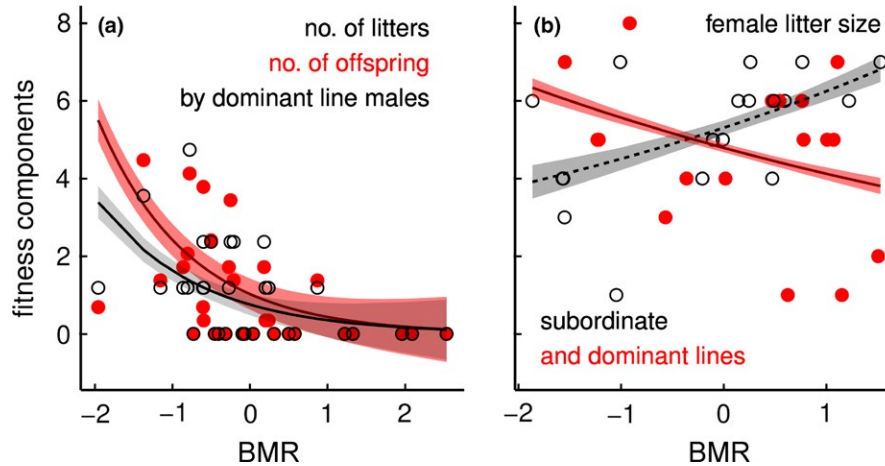


FIGURE 3 Relative fitness components (individual fitness/population mean fitness; from wild conditions experiment) and its 95% confidence intervals (shadings) for (a) males from the dominant selection line [number of litters sired (red closed circles and shading, solid line), number of sired offspring (black open circles and grey shading, dashed line)] and (b) litter size of females from the dominant selection line (red closed circles and shading, solid line) and from the subordinate line (black open circles and grey shading, dashed line) as explained by variation in basal metabolic rate (BMR). Predicted values for fitness components are derived from generalized mixed models (Tables 4 and 5)

4 | DISCUSSION

Selective breeding on male dominance status resulted in a significant elevation of maintenance costs for females, characterized by a higher basal metabolic rate (BMR; Figure 1a–c). Phenotypically dominant males from the subordinate selection line have the highest BMR (Figure 1d). However, the interactions between dominance (behavioural and that related to selection lines) and testosterone with respect to the response variable of BMR, point to an uncoupling of the genetic and the phenotypic components of dominance status (Figure 2a,b). Males from the dominant selection line with high BMR suffered decreased fitness (negative linear selection gradients) in the natural environment, as the males with low BMR sired the greatest number of litters and offspring (Figure 3a; Supporting Information Table S5). Similarly, the sisters of these males from the dominant line tended to suffer fitness disadvantages of high BMR, characterized by smaller litter sizes (Figure 3b; Supporting Information Table S6). However, a positive trend of BMR on fitness components did not meet significance for individuals from the subordinate selection line (Tables 4 and 5).

Increased maintenance costs, characterized by elevated BMR, in females compared to males in the line selected for male dominance (Figure 1), suggests linkage between male fitness and female energetics (Hayward & Gillooly, 2011; Watson, Arnqvist, & Stallmann, 1998), or more specifically, genetic mito-nuclear incompatibility between the sexes (Hill, 2018; Rand et al., 2001). As the inheritance of mitochondria, the “energetic factories” of the cells, in mammals is mostly via females, selection on a male’s energetic performance might be ineffective. However, such selection may promote nuclear genomic variation towards male (and not female) fitness optima due to counter-adaptation in males and an imperfect match between (male) nuclear and (female) mitochondrial co-expressed genes (Boratyński, Ketola, et al., 2016; Hill & Johnson, 2013). As low maintenance costs can be, in general, considered selectively beneficial (Boratyński et al., 2013),

the increased BMR in sisters of males selected for high dominance may suggest unresolved conflict and gender load mediated by mito-nuclear incompatibilities (Bonduriansky & Chenoweth, 2009; Mills et al., 2012; Petersen et al., 2013). Alternatively, the parental care (and related) models for the evolution of endothermy argued that females benefited from an increased metabolic rate and BMR (Lovegrove, 2017; Wone, Sears, Labocha, Donovan, & Hayes, 2009). Accordingly, our results suggest that selection for male fitness can also benefit females via its physiological performance. However, in our natural selection experiment in the field we had conflicting results. While there was an indication of disruptive selection on female BMR in terms of their probability to reproduce (Table 5), BMR had also opposing effects on a female’s litter size between male dominance selection lines (Figure 3b; Table 5 and Supporting Information Table S6). Females from the subordinate male line tended to have larger litters if they also have higher BMR level. Conversely in the dominant male line, characterized by elevated BMR in females, selection tended to favour females with a lower BMR (Figure 3b). These results suggest that selection for male fitness has rather negative outcomes on female reproductive performance.

In general, males with a high BMR level were more likely to express dominant behaviour (Table 2). But, elevated BMR in phenotypically, but not genetically, dominant males entails high physiological costs of behavioural dominance in males not genetically suited for dominance (Figure 1d). The proposed models explaining intraspecific variation in BMR distinguish between compensatory and predisposition functions of BMR in relation to other life-history traits (Petersen et al., 2018; Ricklefs & Wikelski, 2002; Šichová et al., 2014). The results for male behavioural dominance status (Table 2), and the variation in association between BMR and testosterone levels (Table 3), suggest that the two models may perform on different, phenotypic and genetic, levels (Figure 2). At the phenotypic level, we found that a high BMR, and high maintenance costs, may limit the expression of testosterone in phenotypically dominant males

TABLE 5 Generalized mixed models for females to quantify effects of artificial selection procedure (line: dominant vs. subordinate), frequency of individuals from selection lines (frequency: low vs. high), and (log-transformed) body mass (BM), age (on the onset of field experiment) and BMR on fitness components: probability of female reproduction and litter size

	Est. (SE)	z	p
Probability of reproduction			
Line	-0.15 (0.82)	-0.19	0.85
Frequency	0.74 (0.81)	0.91	0.36
sBMR	0.14 (0.44)	0.32	0.75
sBM	0.96 (0.51)	1.89	0.059
sBMR ²	1.00 (0.40)	2.49	0.013
Probability of reproduction _{Dominant line}			
sBMR	0.04 (0.39)	0.10	0.92
Probability of reproduction _{Subordinate line}			
sBMR	-0.43 (0.64)	-0.67	0.50
Litter size			
Line	0.01 (0.17)	0.08	0.93
Frequency	0.09 (0.21)	0.42	0.68
sBMR	-0.19 (0.12)	-1.58	0.11
sBM	0.16 (0.08)	1.85	0.064
Line × sBMR	0.40 (0.16)	2.43	0.015
Litter size _{Dominant line}			
sBMR	-0.15 (0.11)	-1.30	0.19
Litter size _{Subordinate line}			
sBMR	0.17 (0.11)	1.53	0.13

Variance (SD) for random factors for probability of reproduction: mother ID = 0.95 (0.97), enclosure = 2e-06 (1e-03), replicate = 3e-09 (5e-05); in dominant line: mother ID = 8e-01 (9e-01), enclosure = 1e-06 (1e-03), replicate = 8e-01 (9e-01); in subordinate line: mother ID = 1.91 (1.38), enclosure = 0.83 (0.91), replicate = 4e-08 (2e-04); for litter size: mother ID = 4e-08 (2e-04), enclosure = 5e-08 (2e-04), replicate = 5e-08 (2e-04); in dominant line: mother ID = 7e-07 (8e-04), enclosure = 2e-08 (1e-04), replicate = 9e-09 (9e-05); in subordinate line: mother ID = 1e-07 (4e-04), enclosure = 2e-08 (1e-04), replicate = 7e-08 (3e-04).

(Figure 2a), thus supporting the “compensation” (or “allocation”) hypothesis. However, at the genetic level, in the line selected for high dominance status in males, an elevated level of BMR may reflect a genetic predisposition to express testosterone (Figure 2b), thus supporting the “increased intake” hypothesis. However, the results from our field experiment support the energetic “compensation” hypothesis, where high BMR is selected against, as it may limit energy required for other important life functions (Figure 3a). In males from the dominant selection line, selection in the wild promoted low maintenance costs, as those males with lower BMR obtained the highest number of mates and offspring (Table 4, Figure 3a).

Is there evidence for intralocus sexual conflict mediated by maintenance metabolism? In a previous experiment it has been shown that negative frequency-dependent selection on bank vole male dominance maintains variation in sexually antagonistic alleles

(Mokkonen et al., 2011). Here we showed that the selection on maintenance metabolism in the wild can also constrain the fitness of both sexes. While artificial selection for male dominance resulted in increased male dominance, greater male reproductive success and higher female BMR, the field selection experiment pointed to selective disadvantages of high BMR in both sexes in the dominant line. However, while high BMR was selected against in males and female from the dominant line, at the same time females from the subordinate line tended (not statistically significant trend) to be selected for higher BMR (Figure 3). As those are the most reproductively successful individuals, this result suggests an opportunity for sexual antagonism over maintenance metabolism in bank voles. Thus, along with the findings of energetic costs of selection for dominance, our results suggest conflict between males and females in energy metabolism. It is possible that energetic capacity, rather than maintenance costs *per se*, more closely determines fitness, with BMR only being correlated with it. Thus, future work in this and other systems should investigate complete animal energetic budgets to assess the extent mito-nuclear conflicts shape fitness in the field.

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AUTHORS' CONTRIBUTIONS

E.K., T.M., M.M. and S.C.M. designed the research. M.M. led the collection of data with help from all co-authors. Z.B. carried out the energetic laboratory work and the statistical analyses, and drafted the manuscript together with MM and other co-authors.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vt4m939> (Boratyński, Koskela, Mappes, Mills, & Mokkonen, 2018).

ORCID

Zbyszek Boratyński  <http://orcid.org/0000-0003-4668-4922>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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