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Rebecca Rimbach, Stéphane Blanc, Alexandre Zahariev, Neville Pillay, Carsten Schradin

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1 **Daily energy expenditure of males following alternative reproductive tactics: solitary**
2 **roamers spend more energy than group-living males**

3

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11 Rebecca Rimbach^{*a}, Stéphane Blanc^b, Alexandre Zahariev^b, Neville Pillay^a, Carsten
12 Schradin^{a,b}

13

14 ^a School of Animal, Plant & Environmental Sciences, University of the Witwatersrand,
15 Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA

16 ^b IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, FRANCE

17 *Corresponding author: Rebecca.Rimbach@wits.ac.za, r_rimbach@gmail.com

18

19 **Abstract**

20 In many species, males follow alternative reproductive tactics (ARTs), where one tactic (called
21 bourgeois) has much higher reproductive success than alternative tactics followed by males
22 with lower competitive ability. The extent to which ARTs differ in energetic costs is unknown,
23 but it is important to understand the fitness payoffs of ARTs. We studied male African striped
24 mice (*Rhabdomys pumilio*) which follow one of three ARTs: heavy bourgeois males defend
25 harems of females and have 10 times higher reproductive success than smaller roamers, which
26 have ten times higher reproductive success than philopatric males, which remain in their natal
27 group and are the smallest males. Bourgeois and philopatric males live in social groups that
28 defend one territory, while roamers are solitary and roam over larger areas. We predicted that
29 roamers will face higher energetic costs compared to group-living males because they do not
30 gain thermoregulatory benefits of huddling in groups and might travel larger distances as they
31 have larger home ranges. We measured daily energy expenditure (DEE) of 30 males, resting
32 metabolic rate (RMR) of 79 males, travel distances and daily ranges of 31 males and changes
33 in body mass of 51 males. Roamers had higher DEE and higher RMR than both types of group-
34 living males. Philopatric males had shorter travel distances and smaller daily ranges than both
35 roamers and bourgeois males, which did not differ from each other. This indicates that the
36 higher DEE of roamers compared to bourgeois males cannot be explained by larger travel
37 distances. Philopatrics gained body mass faster than bourgeois males and roamers, thereby
38 increasing their competitive ability and thus the probability of later switching to a tactic of
39 higher reproductive success. Our results suggest that roamers suffer energetic costs that might
40 reduce their ability of gaining body mass and thus the likelihood of switching to the bourgeois
41 tactic, indicating evolutionary trade-offs between investing energy into roaming versus gaining
42 body mass.

43

44 **Key words:** alternative reproductive tactic, best-of-a-bad-job, energetics, field metabolic rate,
45 resting metabolic rate, trade-off

46 **1. Introduction**

47 Individuals can display discrete reproductive phenotypes, so-called alternative reproductive
48 tactics (ARTs), to maximize their fitness under intra-sexual reproductive competition [1].
49 Conditional ARTs are most common, in which the most competitive individuals (also called
50 bourgeois) follow a tactic which has a much higher reproductive success than alternative tactics
51 adopted by less competitive individuals [1]. Typically, bourgeois males defend a breeding
52 territory and multiple females, while males of lower competitive ability can be sneakers,
53 satellites or roamers. Males following these latter tactics make “the-best-of-a-bad-job” and
54 attempt to mate with females defended by bourgeois males until their competitive ability
55 increases and they are able to switch to the bourgeois tactic [2–4].

56 Much attention has been placed on the fitness consequences of ARTs [5] and the neuro-
57 endocrine mechanisms underlying different tactics [6]. Physiological mechanisms, such as the
58 activation of the hypothalamic–pituitary–adrenal axis and the release of sex steroids, do not
59 only influence behaviour [7], but also energy expenditure [8], and thus directly affect the
60 evolution of complex traits such as ARTs. Therefore, understanding the energetic
61 consequences of ARTs can help to integrate evolved physiological mechanisms with ultimate
62 consequences.

63 Maintenance metabolism, for example measured as resting metabolic rate (RMR), is the
64 cost of self-maintenance. RMR is the metabolic rate of an animal that is resting in a
65 thermoneutral environment but not necessarily in the post-absorptive state [9], and can
66 influence how much energy an individual can allocate to survival, growth, and reproduction
67 [10]. Individuals following different tactics can also differ in their RMR [3,11,12], where for
68 example, dispersing male Cape ground squirrels (*Xerus inauris*) have a higher RMR than natal
69 males [11]. While we have rudimentary knowledge that ARTs might differ in RMR, it is
70 unknown whether tactic-specific differences in RMR affect daily energy expenditure (DEE),

71 which is determined by a variety of factors, including RMR [13,14], which accounts for 30 -
72 40% of the daily energy demands [13–16].

73 Differences in DEE could influence growth, reproduction and health status, and thus
74 significantly affect evolutionary fitness. Growth influences the balance between development
75 time and size at maturity. In particular, small and young males of low competitive ability have
76 to trade-off energy between growth and reproductive behaviours. In conditional ARTs, somatic
77 growth and increases in body mass are important to improve a male's competitive ability and
78 to enable him to switch to the bourgeois tactic with high reproductive success [1,17]. Currently,
79 no information is available concerning differences in DEE between ARTs. Males following
80 ARTs can be expected to differ in DEE if they differ for example in the energetic costs of
81 tactic-specific behaviours such as travel distances and/or their RMR. Especially in small
82 mammals with ARTs, thermoregulatory costs can also influence DEE, which will be higher in
83 males sleeping solitarily than in males sleeping in huddling groups [18,19]. Thus, adopting
84 ARTs might significantly influence DEE, and the trade-off between investing energy into
85 reproduction or increasing competitive ability by gaining body mass, might differ between
86 different tactics.

87 In the diurnal African striped mouse (*Rhabdomys pumilio*) body mass determines ARTs
88 [3] and males pursue one of three tactics: (1) small philopatric male that remains in his natal
89 group, resulting in very low reproductive success; (2) medium-sized solitary roamer with a 10
90 times higher reproductive success than philopatric males; or (3) large bourgeois breeding male
91 which defends a territory with 2-4 breeding females and a reproductive success 10 times that
92 of roamers [20]. The aim of this study was to examine whether males following ARTs differ
93 in their DEE. To understand why DEE might differ, we also examined differences in RMR,
94 changes in body mass, travel distance and daily range size. We expected roamers to have higher
95 DEE, to travel greater distances and to have larger daily range sizes than breeders and

96 philopatrics. Individuals with a high RMR typically have a larger metabolic machinery [21–
97 24], allowing for greater energy uptake [25,26]. A high RMR may be required to support
98 energetically expensive processes, such as behaviour associated with reproduction and
99 thermoregulation, and high RMR can be associated with high levels of activity [27,28]. Thus,
100 we expected that roamers would have higher RMR than breeders and philopatrics, firstly
101 because roamers travel through the territories defended by several bourgeois males in search
102 of receptive females, and secondly because solitary roamers incur higher thermoregulatory
103 costs at night compared to group-living males. Compared to solitary males, philopatric males
104 may have to spend less energy for thermoregulation at night because they sleep in huddling
105 groups. Striped mice, including adult individuals, gain body mass during the breeding season
106 when food availability is highest [29]. Increasing body mass is important for males to gain a
107 high competitive status [3], as heavier males are more likely to win territorial encounters [30],
108 and to store energy reserves to cope with the coming summer dry season characterised by low
109 food abundance [29]. We predicted that differences in DEE will also be represented by
110 differences in body mass gain.

111

112 **2. Materials and methods**

113 *2.1. Study site and species*

114 We collected data in the Succulent Karoo semi-desert of South Africa. Here, striped mice live
115 in social groups, consisting of one breeding male (bourgeois tactic), two to four breeding
116 females and their adult philopatric offspring of both sexes [31]. Solitary roamers occur during
117 the breeding season [31]. Striped mice typically breed in the austral spring (August –
118 December) when food is abundant [31,32], but in some years there is a second breeding season
119 between January and March [33]. Females can give birth to 2–3 litters [34], at an average of 5
120 pups per litter [29]. Striped mice can reach sexual maturity at around 6 weeks of age, but

121 typically do not start reproducing in the breeding season when they are born [31]. Male striped
122 mice are more likely to disperse than females, while females show a higher level of natal
123 philopatry [35]. Approximately 70% of striped mice die before reaching the end of their first
124 year [29], while in some years survival rate is much lower at only 1%. Around 30% of young
125 males present at the start of the dry season survive until the next breeding season and can
126 become breeders (then approx. 1 year old), but very few (less than 1%) survive for a second
127 year (then being approx. 2 years old).

128

129 *2.2. Determination of reproductive tactics*

130 Using a combination of trapping, behavioural observations and radio-tracking, we determined
131 male tactics [3]. Long-term monitoring of the field site and all its striped mouse groups,
132 together with ear-tagging of all individuals at first capture, enabled us to track the tactic
133 followed by each individual at all times. Males can switch from being philopatric to roaming
134 to breeding male, or from philopatric directly to breeding male [3,36]. Sometimes males switch
135 from breeding male back to roaming male, but they cannot return to their natal group as
136 philopatrics. Roamers were either males that were born in the study site, and tagged when
137 living as a philopatric male in their natal group, or immigrated into the study site.

138 We defined roamers as males that did not share a nest with other individuals, and
139 territorial breeders as males that lived in groups other than their natal group [3]. Young adults
140 that remained in their natal group (i.e. the group where they were previously trapped as
141 juveniles) were defined as philopatrics. On average, philopatric males are significantly lighter
142 than both breeders and roamers, and roamers are lighter than breeders [3].

143

144 *2.3. Daily energy expenditure (DEE)*

145 Using the two-point ‘doubly-labelled water’ (DLW) method [37], we determined DEE of 30
146 males (Table 1) in the 2014 (N = 19) and 2015 (N = 11) breeding seasons. We weighed
147 individuals (± 0.1 g), anesthetized them with di-ethyl ether and took a first blood sample (~ 100
148 μl) from the sub-lingual vein into glass capillaries, which we then flame-sealed. After
149 disinfecting a part of the abdomen for an injection site, we injected DLW (1.0 g of 97 % ^{18}O
150 and 0.35 g of 99.9 % ^2H) intraperitoneally at a dose of 3.38 g/kg body mass ($0.2\% \pm 0.008\%$
151 of an individual’s body mass). We weighed syringes immediately before and after
152 administration (± 0.0001 g, Mettler-Toledo balance). In small vertebrates, an isotopic
153 equilibration in body water is typically reached within 1 hour [38,39]. Thus, after 1 hour, we
154 took a second blood sample (~ 100 μl) to determine the maximum isotope enrichment.
155 Subsequently, to compensate for the loss of feeding opportunities, each individual received
156 food which comprised 7% of its body mass and consisted of 40% sunflower seeds and 60%
157 apple. After another 30-45 min, individuals were released at their nests. We recaptured 27
158 individuals 24 h, one individual 48 h and two individuals 72 h after DLW injection and
159 collected a third blood sample (~ 100 μl) to estimate the isotope elimination rate. We kept sealed
160 capillaries in a fridge at 4°C until transport to the IPHC-DEPE laboratory in Strasbourg, France
161 for isotope analysis.

162 At the IPHC-DEPE laboratory, blood samples were vacuum distilled for 5 min and 0.1
163 μl distillate was injected into an elemental analyser with thermal conversion (TC/EA, Thermo,
164 Bremen, Germany) which was connected to a continuous flow isotope ratio mass spectrometer
165 (IRMS-DELTA V PLUS, Thermo, Bremen, Germany), as previously described [40]. In the
166 TC/EA, distillates were pyrolyzed at 1400°C into H_2 and CO gas in a glassy carbon tube under
167 pure He flow at 90 ml min^{-1} . H_2 and CO were further separated at 110°C on a molecular sieve
168 GC column before sequential analysis in the isotope ratio mass spectrometer. Results were first
169 drift corrected and optionally a memory effect correction was applied. Results were normalized

170 versus the VSMOW2/SLAP2 international scale. All analyses were performed in
 171 quadruplicate. As it is routinely done in all mass spectrometry laboratories, we re-measured
 172 samples if more than 3 out of 4 replicates of a given sample exceeded the standard deviation
 173 of the 4 replicates; limits were 2‰ for ^2H and 0.2 ‰ for ^{18}O . TBW was calculated from the
 174 ^{18}O dilution space divided by 1.007 to correct for *in vivo* isotopic exchange [41]. The average
 175 isotope dilution space ratio was 1.037 ± 0.011 (mean \pm SD). Production rate of CO_2 was
 176 calculated from the single pool model as recommended for the body size of striped mice
 177 [37,42]. CO_2 production was calculated following Speakman [37] and converted to DEE using
 178 Wier's equation [43] assuming a food quotient of 0.925 based on estimated proportions of
 179 macronutrients in the folivorous and granivorous diet of striped mice [32].

180

181 **Table 1.** Overview of sample sizes for measurements of DEE, RMR, change in body mass and
 182 all-day focal observations. All four variables are treated as independent studies as it was not
 183 possible to obtain all four measures from all males, even though there is some overlap between
 184 samples (for example, data for all four measures are available for 11 males).

	DEE	RMR	Body mass change	All-day observation
Breeder	8	41	19	14
Roamer	6	9	15	6
Philopatric	16	29	17	11
TOTAL	30	79	51	31

185

186 2.4. Resting metabolic rate (RMR)

187 We determined RMR of 79 males (Table 1) in the breeding seasons of 2015 (15 breeder, 3
 188 roamer, 2 philopatric), 2016 (13 breeder, 3 roamer, 19 philopatric) and 2017 (13 breeder, 3
 189 roamer, 8 philopatric). We trapped males in the morning at their nest using Sherman-style live-
 190 traps ($26 \times 9 \times 9$ cm) and measured oxygen consumption ($\text{ml O}_2\text{h}^{-1}$) using an open circuit

191 respirometry system (Foxbox, Sable Systems, New Jersey, USA) in a respirometry laboratory
192 next to the field site. We determined each individual's body mass (± 0.1 g) and transferred
193 them into one of three metabolic chambers (1000cm^3 each). After an initial 20 min, we initiated
194 O_2 measurement and video recorded the mice in the metabolic chambers using a webcam
195 (Microsoft HD webcam). The metabolic chambers were immersed in a propylene container
196 and each chamber was equipped with a metal grid to separate mice from their urine and faeces.
197 Temperature was controlled using a temperature controller (Pelt5, Sable Systems). We
198 measured RMR at $30\text{ }^\circ\text{C} \pm 1.0\text{ }^\circ\text{C}$, which lies within the striped mouse thermoneutral zone [44].
199 Measurements were taken every 3 sec., and data were collected in three 45 min cycles, each
200 cycle consisting of a 5 min baseline recording, followed by a 10-min recording per mouse
201 chamber and ended with a 10 min baseline recording. This cycle was repeated four times,
202 resulting in 40 min of measurements per mouse and a total data collection period of 3h. A flow
203 regulator (FB8, Sable Systems) controlled the air flow through the chambers ($\sim 700 \pm 0.28$ ml
204 min^{-1}) and measurements of oxygen consumption were taken using an oxygen analyser
205 (Foxbox, Sable Systems). Weekly, we calibrated the oxygen analyser to an upper and lower
206 value in dry air. We analysed metabolic records using a macro program in ExpeData software
207 (Sable Systems). To establish RMR, we used the mean of the lowest 89 consecutive readings
208 (equivalent to 4.45 min) of oxygen consumption ($\text{ml O}_2\text{h}^{-1}$) per individual [45]. In a first step,
209 we corrected O_2 , CO_2 , and the flow rate for water vapour dilution and subsequently, we
210 calculated oxygen consumption using the equation:

$$211 \quad VO_2 = \frac{FR * ((FiO_2 - FeO_2) - FeO_2 * (FeCO_2 - FiCO_2))}{(1 - FeO_2)},$$

212 where FR is the flow rate, FiO_2 and $FiCO_2$ are input fractional concentrations of O_2 and CO_2
213 to the chamber, respectively; FeO_2 and $FeCO_2$ are excurrent fractional concentration of O_2 and
214 CO_2 from the chamber, respectively. Further, we visually checked all videos to confirm that

215 individuals were resting (i.e. motionless and not showing piloerection) during the selected 4.45
216 min period used to establish RMR.

217 Measuring RMR in striped mice during the active phase instead of during the night could
218 have led to measuring elevated metabolic rates. However, RMR values reported in this study
219 are lower [3] or comparable [44] to values reported in previous studies on striped mice, and
220 our RMR measures are not significantly different from striped mouse sleeping metabolic rate
221 (SMR) measured in our field respiratory laboratory [46]. To examine repeatability of RMR,
222 we used a second respirometry trial for 17 males (9 breeder, 2 roamer, 6 philopatric).
223 Respirometry trials were conducted within 25.2 days of each other on average (\pm 14.6 days).

224

225 *2.5. Body mass change, age determination and all-day focal observations*

226 We recorded body mass of 51 males (Table 1) in 2014 (N = 19), 2015 (N = 17) and 2016 (N =
227 15) at the beginning of the breeding season in September or October, or for roamers when they
228 first appeared in the breeding season, and again 4 weeks later. We calculated the change in
229 body mass as the percentage of body mass change per day. For 37 males (12 breeders, 9
230 roamers and 16 philopatrics) we were able to establish their age at the time of the body mass
231 measurement, because they were previously trapped as juveniles, enabling us to estimate their
232 birth date (using the growth curve from [47]). We were unable to determine the age of 7
233 breeders, 6 roamers and 1 philopatric because they were too old (too heavy) at first capture.

234 We conducted one all-day behavioural observation on 31 males (Table 1) in 2014 (N =
235 20) and 2015 (N = 11), as done in a previous study [48]. We observed individuals from the
236 time they emerged from their nest in the morning until they returned in the evening. During
237 observations, observers carried a GPS (Garmin etrex, Garmin International, Olathe, KS, USA),
238 automatically recording a track, which provided a proxy of the distance travelled by the focal

239 mouse [49]. Using Ranges 6 [50], we calculated daily range size (area covered during an all-
240 day observation) as 99% kernel.

241

242 2.6. Statistical analyses

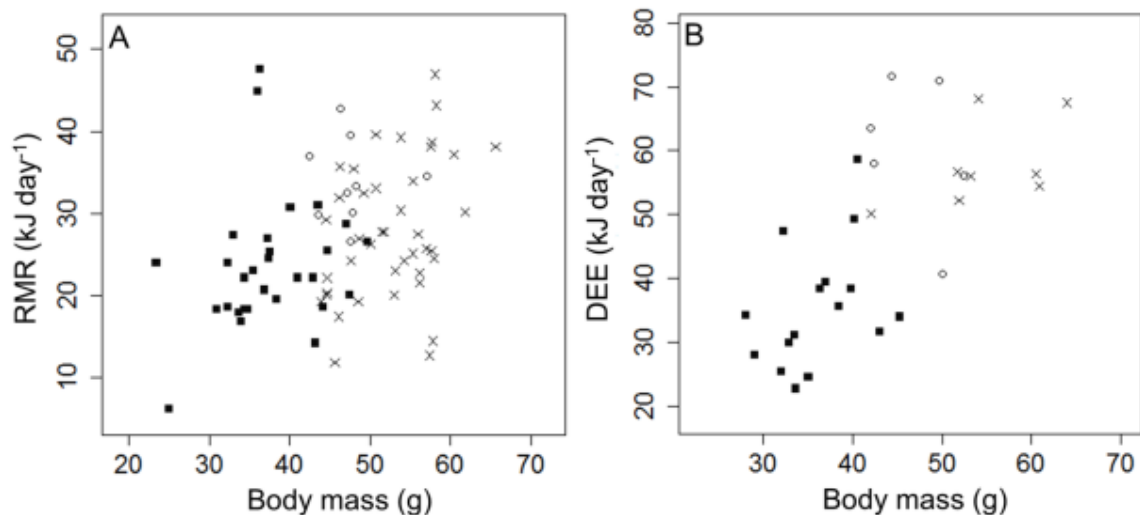
243 All analyses were conducted in R3.3.3 [51]. Raw data are presented as mean \pm SD. There is a
244 well-known positive relationship between body mass and both RMR and DEE [52,53].
245 Therefore, we used residual DEE and residual RMR, calculated as residuals of the regression
246 of DEE or RMR on body mass [14,54,55]. As we did not find a significant interaction between
247 body mass and tactic on RMR (ANCOVA: $F = 0.47$, $df = 2$, $P = 0.62$; Fig. 1A), nor between
248 body mass and tactic on DEE (ANCOVA: $F = 1.26$, $df = 2$, $P = 0.30$; Fig. 1B), we assumed
249 that the relationship between RMR and body mass and between DEE and body mass was
250 similar for all tactics. To examine differences between ARTs, we used five linear mixed models
251 (LMMs) with Gaussian error structure and identity link using the package ‘lme4’ [56]. As
252 response variables we used (a) residual DEE, (b) residual RMR, (c) change in body mass, (d)
253 travel distance or (e) daily range size. We log-transformed the daily range size data to reach
254 normality of residuals. We used tactic as a fixed predictor and group ID and year as random
255 factors. To account for potential influences of a group’s territory, we used group ID as a random
256 factor because more than one individual was measured per group. We assigned a unique group
257 ID to each roamer because they roam over the territories of several groups [3]. For model
258 validation, we visually inspected Q-Q plots and scatterplots of residuals plotted against fitted
259 values, and we checked for the assumptions of homogeneous and normally distributed
260 residuals. To analyse tactic-specific differences in age and body mass, we used one ANCOVA
261 per response variable and pairwise comparisons *post hoc* using t tests, with P-values which
262 were corrected for multiple testing using the Holm method [57]. For the subset of 12 males,
263 for which we concomitantly collected DEE, travel distance and RMR (measured on the same

264 day as DLW injection), we examined the influence of RMR and travel distance on DEE using
265 one ANOVA. We used DEE as the response variable and body mass, RMR and travel distance
266 as predictor variables. We used one ANCOVA to examine tactic-specific differences in the
267 relationship between travel distance and DEE *post hoc*. We used a paired t test and Kendall's
268 rank correlation to examine whether RMR measurements were repeatable within individuals.

269

270 3. Results

271 Age differed between tactics (ANCOVA: $F = 18.58$, $df = 2$, $P < 0.0001$), with breeders ($14.1 \pm$
272 4.3 months) being significantly older than roamers ($P = 0.025$; 10.6 ± 1.8 months) and
273 philopatrics ($P < 0.0001$; 6.3 ± 3.3 months). Roamers were significantly older than philopatrics
274 ($P = 0.008$). There were significant differences in body mass between males following different
275 tactics (ANCOVA: $F = 49.27$, $df = 2$, $P < 0.0001$), with breeders being heavier than roamers
276 ($P = 0.0004$; 56.3 ± 5.4 g vs. 48.8 ± 4.2 g) and philopatrics ($P < 0.0001$; 38.2 ± 6.0 g), and
277 roamers being heavier than philopatrics ($P < 0.0001$).



278

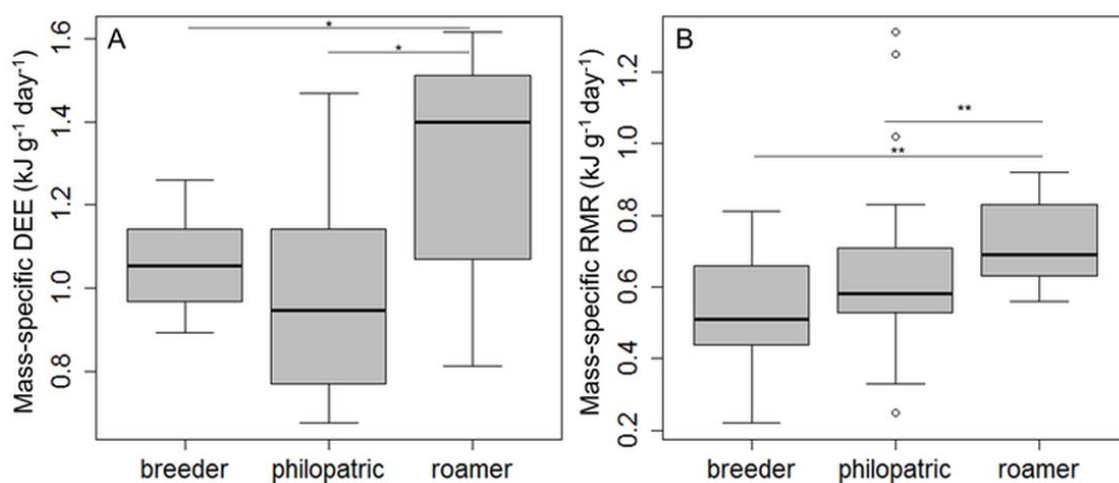
279 **Figure 1.** Relationship between body mass and (A) resting metabolic rate ($N = 79$ males) and
280 (B) daily energy expenditure ($N = 30$ males) of philopatrics, roamers, and breeders (*filled*
281 *squares, open circles and crosses, respectively*).

282

283 Mean absolute values of DEE were 35.5 ± 9.6 kJ day⁻¹ for philopatrics, 60.2 ± 11.5 kJ
284 day⁻¹ for roamers, and 57.6 ± 6.6 kJ day⁻¹ for breeders. Roamers had 1.2 higher mass-specific
285 DEE than breeders (LMM: Estimate \pm SE: 9.99 ± 4.74 , $t = 2.10$, $P = 0.04$) and 1.3 higher mass-
286 specific DEE than philopatrics (Estimate \pm SE: 11.79 ± 4.23 , $t = 2.78$, $P = 0.01$; Fig. 2A). There
287 was no difference between breeders and philopatrics (Estimate \pm SE: 1.79 ± 3.79 , $t = 0.47$, $P =$
288 0.64 ; Fig. 2A).

289 Mean absolute values of RMR were 23.5 ± 8.1 kJ day⁻¹ for philopatrics, 34.0 ± 5.1 kJ
290 day⁻¹ for roamers and 27.8 ± 8.3 kJ day⁻¹ for breeders. Roamers had 1.3 higher mass-specific
291 RMR than breeders (Estimate \pm SE: 15.65 ± 5.25 , $t = 2.97$, $P = 0.004$) and 1.1 higher mass-
292 specific RMR than philopatrics (Estimate \pm SE: 17.28 ± 5.56 , $t = 3.10$, $P = 0.003$; Fig. 2B).
293 There was no difference between breeders and philopatrics (Estimate \pm SE: -1.63 ± 3.68 , $t = -$
294 0.44 , $P = 0.65$; Fig. 2B). Paired RMR measurements of 17 males correlated with each other
295 (Kendall's rank correlation: $z = 2.60$, $P = 0.009$, $\tau = 0.46$) and were not significantly different
296 from each other (paired t test: $t = 0.21$, $df = 31.97$, $P = 0.83$).

297



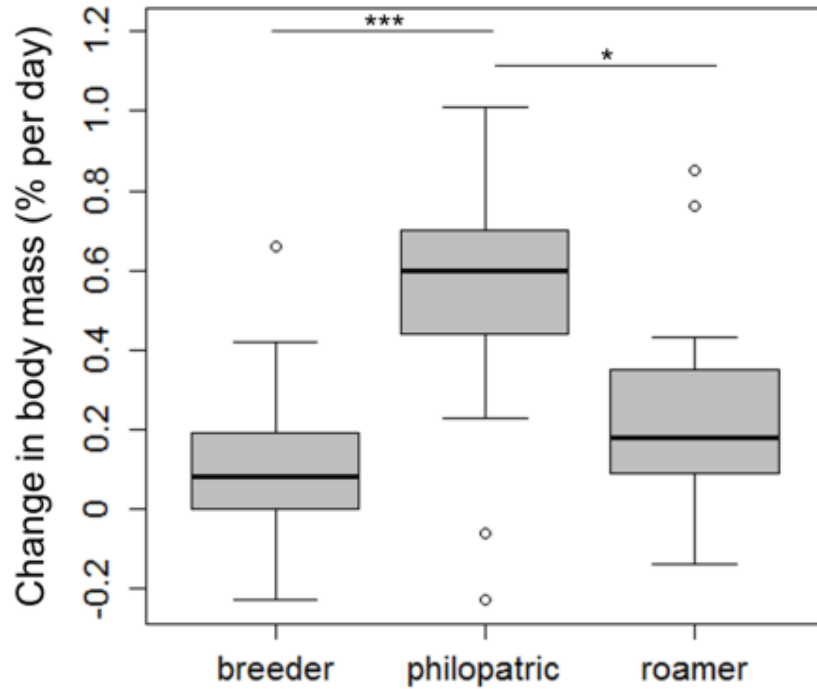
298

299 **Figure 2.** (A) Differences in mass-specific DEE between breeders (N = 8), philopatrics (N =
300 16) and roamers (N = 6). (B) Differences in mass-specific RMR between philopatrics (N = 29),

301 breeders (N = 41) and roamers (N = 9). Black lines indicate median values, boxes confidence
302 intervals, whiskers minimum and maximum values of non-outlier data, and open circles show
303 outliers. Significant differences are illustrated (*P < 0.05; **P < 0.01).

304

305 Philopatrics gained body mass faster than breeders and roamers (philopatric vs. breeder:
306 Estimate ± SE: 0.43 ± 0.09, t = 4.84, P < 0.0001; philopatric vs. roamer: Estimate ± SE: 0.28
307 ± 0.09, t = 2.94, P = 0.006; Fig. 3), while roamers and breeders did not differ with regard to
308 body mass changes (Estimate ± SE: 0.16 ± 0.09, t = 1.69, P = 0.09; Fig. 3). Philopatrics
309 travelled shorter distances than breeders and roamers (philopatric vs. breeder: Estimate ± SE:
310 695.47 ± 166.93, t = 4.17, P = 0.011; philopatric vs. roamer: Estimate ± SE: 599.19 ± 207.26,
311 t = 2.89, P = 0.012; Fig. 4A), but distance travelled did not differ between roamers and breeders
312 (Estimate ± SE: 96.28 ± 200.94, t = 0.47, P = 0.65; Fig. 4A). Philopatrics had smaller daily
313 range sizes than breeders and roamers (philopatric vs. breeder: Estimate ± SE: 0.61 ± 0.19, t =
314 3.12, P = 0.032; philopatric vs. roamers: Estimate ± SE: 0.93 ± 0.23, t = 3.91, P = 0.015; Fig.
315 4B), while roamers did not differ from breeders (Estimate ± SE: 0.33 ± 0.23, t = 1.40, P = 0.30;
316 Fig. 4B).



317

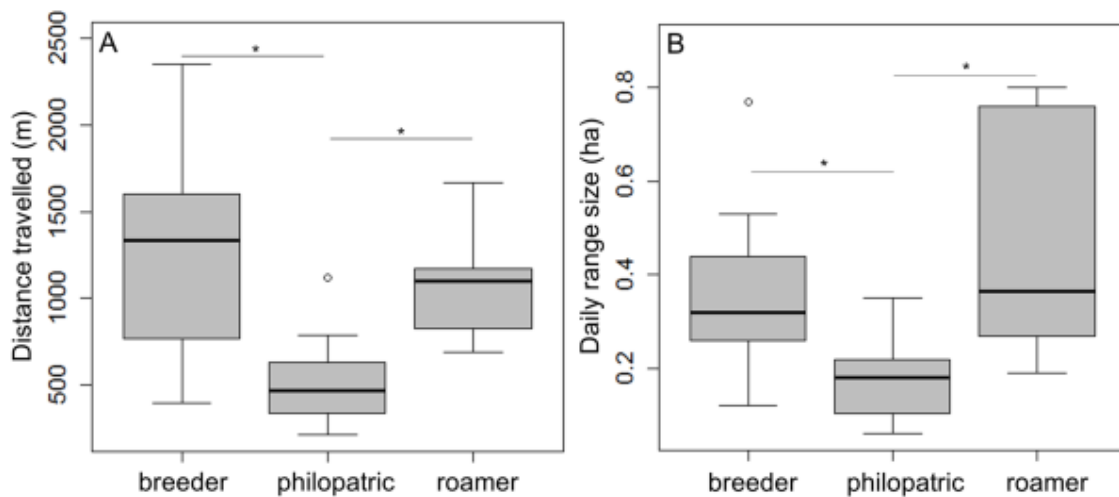
318 **Figure 3.** Differences in body mass change between breeders (N = 19), philopatrics (N = 17)

319 and roamers (N = 15). Black lines indicate median values, boxes confidence intervals, whiskers

320 minimum and maximum values of non-outlier data, and open circles show outliers. Significant

321 differences are illustrated (*P < 0.05; **P < 0.01; *** P < 0.001).

322



323

324 **Figure 4.** Differences in (A) travel distance and (B) daily range size between breeders (N =

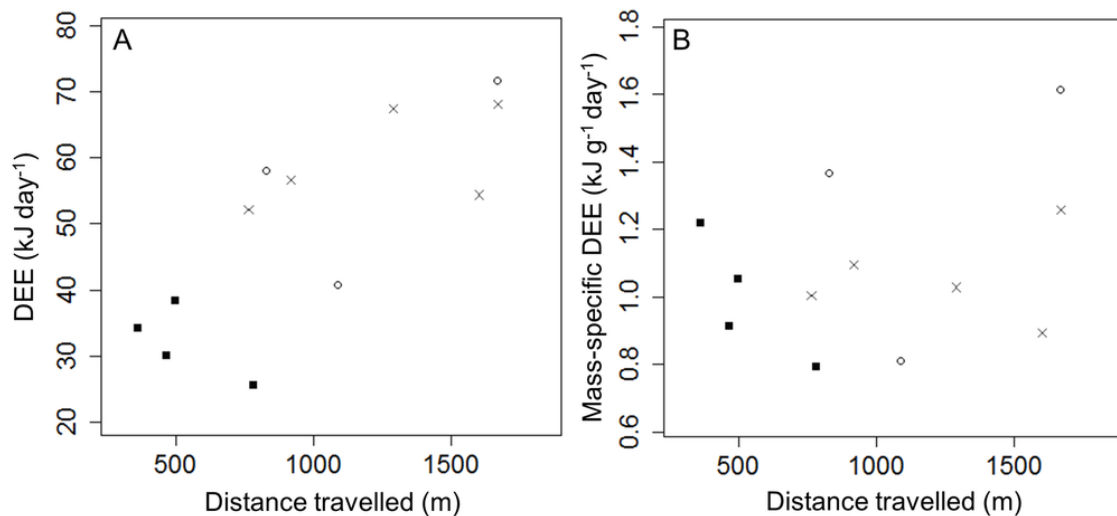
325 14), philopatrics (N = 11) and roamers (N = 6). Black lines indicate median values, boxes

326 confidence intervals, whiskers minimum and maximum values of non-outlier data, and open
327 circles show outliers. Significant differences are illustrated (* $P < 0.05$).

328

329 Body mass (ANOVA: $F = 17.08$, $df = 1$, $P = 0.003$, $N = 12$ males) and distance travelled
330 ($F = 5.68$, $df = 1$, $P = 0.04$) influenced DEE (Fig. 5A+B), while RMR ($F = 0.95$, $df = 1$, $P =$
331 0.35) did not. There was no significant interaction between travel distance and tactic on DEE
332 (ANCOVA: $F = 0.92$, $df = 2$, $P = 0.44$).

333



334

335 **Figure 5.** Relationship between travel distance and (A) daily energy expenditure (DEE) and
336 (B) mass-specific DEE of philopatrics, roamers, and breeders (*filled squares, open circles and*
337 *crosses*, respectively; $N = 4$ philopatrics, 3 roamers and 5 breeders).

338

339 4. Discussion

340 Acquisition and expenditure of energy are key factors influencing individual fitness. We found
341 that males following the solitary ‘roamer’ tactic spent more energy, in terms of RMR and DEE,
342 than group-living males. At the same time, roamers gained body mass at a slower rate than
343 philopatrics, indicating possible energy trade-offs between roaming and body mass gains.

344 In contrast to our results, a previous study on striped mice reported that roamers had a
345 lower RMR than breeders and philopatrics, which was argued to be due to roamers being
346 constrained by high thermoregulatory costs, which potentially forced them to save energy in
347 their total energy budget, via decreasing their RMR [3]. The contrasting findings of these two
348 studies may be the result of differences in the study design. An observer was present during
349 RMR measurements in the previous study [3], whereas we video recorded animals inside
350 metabolic chambers in the current study to minimize disturbance of the animals. Animals may
351 perceive the presence of an observer as stressful, which can influence metabolic rate [58].
352 Overall, 60% higher RMR values in the previous study compared to the current study support
353 this interpretation. Because we used a more controlled setting and had a higher sample size (79
354 males versus 27 males), we consider our current results as more representative with regard to
355 tactic-specific differences in RMR.

356 Roamers had a higher RMR than breeders and philopatrics and these differences in
357 RMR mirror the tactic-specific differences in DEE. It has been purported that RMR and DEE
358 are intrinsically linked [13,59–61], and thus, differences in RMR could explain why roamers
359 had a higher DEE than breeders. However, when concurrently measuring RMR and DEE in
360 the same individual, RMR did not significantly influence DEE, but our sample size was
361 restricted to 12 males for this part of the analysis. Inter-specific studies reported positive
362 relationships between DEE and RMR (or BMR) in mammals and birds [13–15,62], while at
363 the intra-specific level no such relationship was found [52,55,63,64]; with the exception of one
364 study [65]. Thus, the nature of the relationship between DEE and RMR (or BMR) remains
365 unclear.

366 As expected, roamers had a higher DEE than males of the two group-living tactics.
367 Males following ARTs often differ with regard to energetically costly behaviour. For example,
368 dispersed male Cape ground squirrels (*X. inauris*) spend less of their time feeding than natal

369 males [11] and in field crickets (*Gryllus integer*) courtship songs are more energetically costly
370 than the mobile activity associated with the silent satellite strategy [66]. Differences in the
371 expression of energetically costly behaviour between tactics of male striped mice could explain
372 differences in DEE, as we showed previously for striped mice [46]. Our study showed that
373 DEE increased with increasing travel distances and that this relationship was similar for males
374 of all tactics. While roamers have larger home ranges than both group-living males (measured
375 over 7 days; [3]), in the current study we found that roamers and breeders travelled similar
376 distances during the day and had similar daily ranges. Importantly, these results indicate that
377 the higher DEE found in roamers cannot be explained by higher locomotor activity. One
378 behavioural aspect that differs between group-living males and solitary roamers is huddling
379 with conspecifics at night. Striped mice nest above ground inside shrubs, and ambient night
380 temperatures (ranging between -2 and 19°C during the study) are always considerably below
381 their thermoneutral zone (30 ± 1.0 °C; [44]). Group-living males (breeders and philopatrics)
382 huddle with other group members and thereby save energy [18]. In contrast, solitary roamers
383 likely incur higher thermoregulatory costs at night, which can be up to 50% higher compared
384 to group-living males [18]. Thus, the higher energetic costs of the roaming tactic might be due
385 to the higher thermoregulatory costs of solitary living.

386 Why do males invest energy into the roaming tactic instead of surviving in the safety
387 of their natal group until their competitive abilities improve to become bourgeois males? This
388 could be due to their older age when compared to philopatrics combined with a high mortality
389 rate and the fact that males typically experience only one reproductive cycle in their lifetime.
390 Striped mice breed in spring and, although individuals can reach adulthood at the end of the
391 breeding season in which they were born [31], they have to survive the hot dry season in
392 summer before they can reproduce in the next spring. However, only around 30% of young
393 males present at the start of the dry season survive until the next breeding season and can

394 become breeders (then approx. 1 year old), but very few (< 1%) survive for a second year (then
395 being approx. 2 years old) [29]. If roamers were to remain philopatric and continue gaining
396 body mass, they might only be able to switch to the bourgeois tactic when the only breeding
397 season they experience has already passed. Thus, roamers might rather invest into gaining
398 some, although comparatively diminished, reproductive success [20], since the alternative of
399 remaining philopatric might not lead to any direct fitness benefits in the short breeding window
400 available for them.

401 Philopatrics were the youngest and lightest individuals, as also reported in a previous
402 study [3], and, as expected, travelled shorter distances and gained body mass at a faster rate
403 than breeders and roamers. Similarly, yearling male golden-mantled ground squirrels
404 (*Spermophilus saturatus*) allocate more energy into body mass gain than older males, thereby
405 improving their condition [67]. In the European ocellated wrasse (*Symphodus ocellatus*) non-
406 reproductive males also gain body mass while reproductive males show considerable weight
407 loss [68]. In contrast, male dispersed and natal Cape ground squirrels (*X. inauris*) have a similar
408 body mass and body condition [11]. Philopatric male striped mice had lower DEE and lower
409 RMR than roamers, suggesting that they followed an energy minimization strategy. Likewise,
410 natal male Cape ground squirrels (*X. inauris*) have a lower RMR than dispersed males [11],
411 and unadorned small male swordtails (*Xiphophorus nigrensis*) keep a stable metabolic rate in
412 the presence of females while males with a large sword increase their metabolic rate [69]. In
413 striped mice, faster body mass gain might be the main benefit of remaining philopatric versus
414 adopting a solitary roaming tactic. If philopatrics were to switch tactic before reaching an
415 appropriate body mass, they might gain only very little or no reproductive success. Small males
416 face a trade-off between following a roaming tactic with comparatively low reproductive
417 success versus remaining in the safety of their natal group to increase their competitive abilities,
418 allowing them to subsequently switch to a tactic with a much higher reproductive success.

419 Because they are significantly younger than roamers, they have a much higher probability to
420 survive until the next breeding season. Thus, small males might benefit the most if they invest
421 in gaining body mass to improve their competitive abilities.

422 In conclusion, our study indicates that male ARTs of striped mice differ in DEE and
423 RMR. Compared to group-living males, roamers had higher RMR and higher DEE. Roamers
424 invest energy into roaming to gain some reproductive success, but gain body mass at a slow
425 rate, which predicts a lowered likelihood of switching to the bourgeois tactic followed by the
426 heaviest males of the population. Small philopatric males primarily invest in gaining body
427 mass. Our study showed that ARTs are associated with changing investment and allocation
428 between metabolic processes and body mass, and that future tactics might depend on the energy
429 investment in prevailing tactics. In sum, considering energy-trade-offs in behavioural and life
430 history traits provides important insights into the evolution of ARTs.

431

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442

443 **Competing Interest**

444 No competing interests declared.

445

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