



Daily energy expenditure of males following alternative reproductive tactics: Solitary roamers spend more energy than group-living males

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

► To cite this version:

Rebecca Rimbach, Stéphane Blanc, Alexandre Zahariev, Neville Pillay, Carsten Schradin. Daily energy expenditure of males following alternative reproductive tactics: Solitary roamers spend more energy than group-living males. *Physiology & behavior*, 2019, 199, pp.359-365. 10.1016/j.physbeh.2018.12.003 . hal-02108741

HAL Id: hal-02108741

<https://hal.science/hal-02108741>

Submitted on 24 Jul 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Published as

5 Rimbach, R., Blanc, S., Zahariev, A., Pillay, N. & Schradin, C. 2019. Daily energy
6 expenditure of males following alternative reproductive tactics: Solitary roamers
7 spend more energy than group-living males. *Physiology & Behavior*, **199**, 359-365.

8

9

10

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, 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

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

2. Materials and methods

2.1. Study site and species

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

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

2.2. Determination of reproductive tactics

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

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

2.3. Daily energy expenditure (DEE)

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

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

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

Table 1. Overview of sample sizes for measurements of DEE, RMR, change in body mass and all-day focal observations. All four variables are treated as independent studies as it was not possible to obtain all four measures from all males, even though there is some overlap between 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

2.4. Resting metabolic rate (RMR)

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

respirometry system (Foxbox, Sable Systems, New Jersey, USA) in a respirometry laboratory
 next to the field site. We determined each individual's body mass (± 0.1 g) and transferred
 them into one of three metabolic chambers (1000cm³ each). After an initial 20 min, we initiated
 O₂ measurement and video recorded the mice in the metabolic chambers using a webcam
 (Microsoft HD webcam). The metabolic chambers were immersed in a propylene container
 and each chamber was equipped with a metal grid to separate mice from their urine and faeces.
 Temperature was controlled using a temperature controller (Pelt5, Sable Systems). We
 measured RMR at 30 °C \pm 1.0 °C, which lies within the striped mouse thermoneutral zone [44].
 Measurements were taken every 3 sec., and data were collected in three 45 min cycles, each
 cycle consisting of a 5 min baseline recording, followed by a 10-min recording per mouse
 chamber and ended with a 10 min baseline recording. This cycle was repeated four times,
 resulting in 40 min of measurements per mouse and a total data collection period of 3h. A flow
 regulator (FB8, Sable Systems) controlled the air flow through the chambers ($\sim 700 \pm 0.28$ ml
 min⁻¹) and measurements of oxygen consumption were taken using an oxygen analyser
 (Foxbox, Sable Systems). Weekly, we calibrated the oxygen analyser to an upper and lower
 value in dry air. We analysed metabolic records using a macro program in ExpeData software
 (Sable Systems). To establish RMR, we used the mean of the lowest 89 consecutive readings
 (equivalent to 4.45 min) of oxygen consumption (ml O₂h⁻¹) per individual [45]. In a first step,
 we corrected O₂, CO₂, and the flow rate for water vapour dilution and subsequently, we
 calculated oxygen consumption using the equation:

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

where FR is the flow rate, FiO₂ and FiCO₂ are input fractional concentrations of O₂ and CO₂
 to the chamber, respectively; FeO₂ and FeCO₂ are excurrent fractional concentration of O₂ and
 CO₂ from the chamber, respectively. Further, we visually checked all videos to confirm that

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

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

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

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

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

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

2.6. Statistical analyses

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

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

3. Results

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

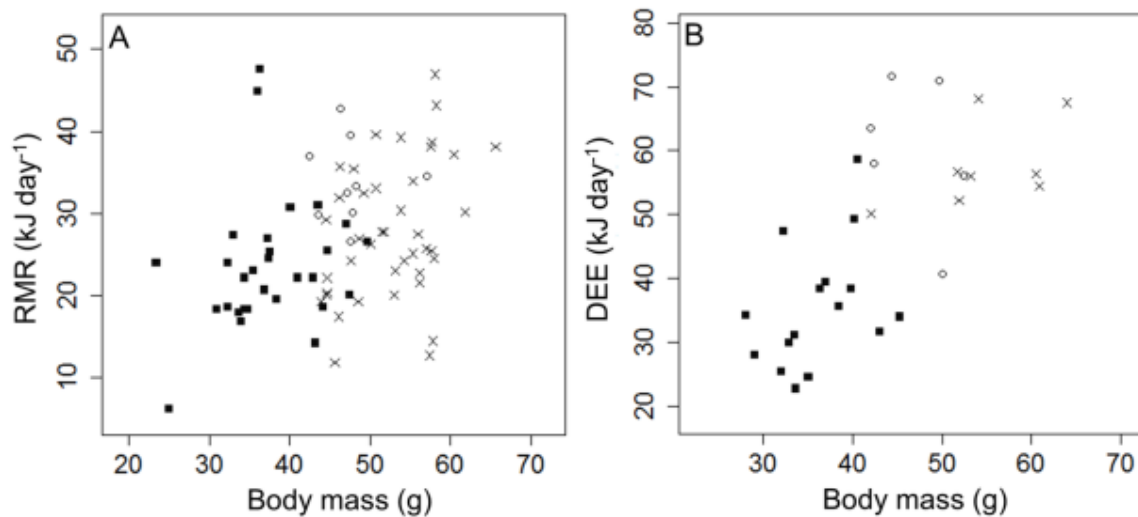


Figure 1. Relationship between body mass and (A) resting metabolic rate ($N = 79$ males) and (B) daily energy expenditure ($N = 30$ males) of philopatrics, roamers, and breeders (*filled squares, open circles and crosses, respectively*).

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

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

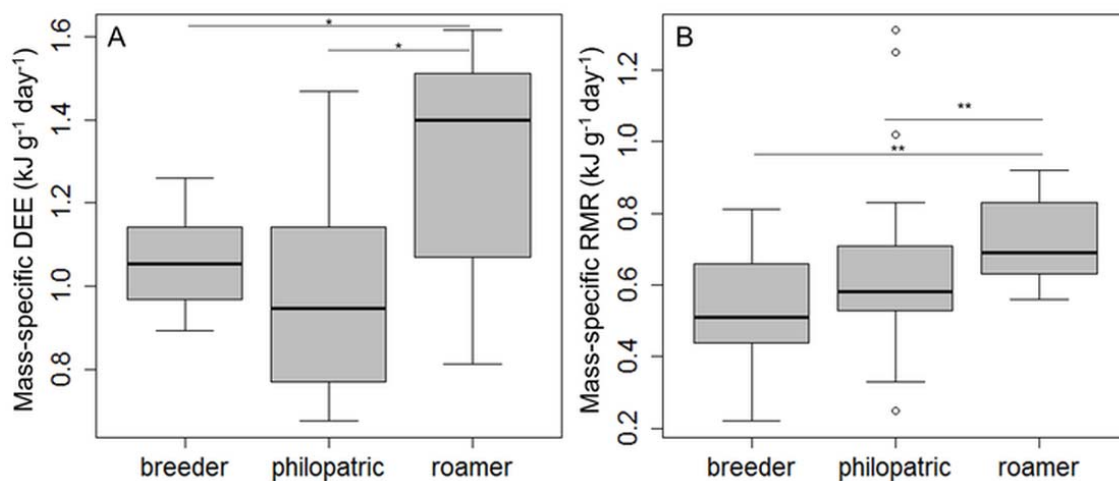


Figure 2. (A) Differences in mass-specific DEE between breeders ($N = 8$), philopatrics ($N = 16$) and roamers ($N = 6$). (B) Differences in mass-specific RMR between philopatrics ($N = 29$),

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

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

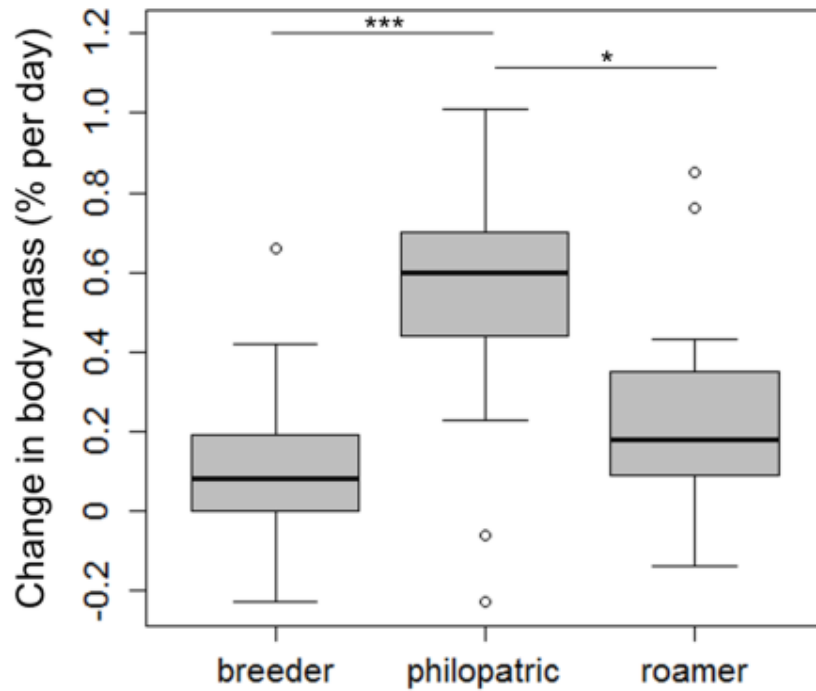


Figure 3. Differences in body mass change between breeders (N = 19), philopatrics (N = 17) and roamers (N = 15). Black lines indicate median values, boxes confidence intervals, whiskers minimum and maximum values of non-outlier data, and open circles show outliers. Significant differences are illustrated (*P < 0.05; **P < 0.01; *** P < 0.001).

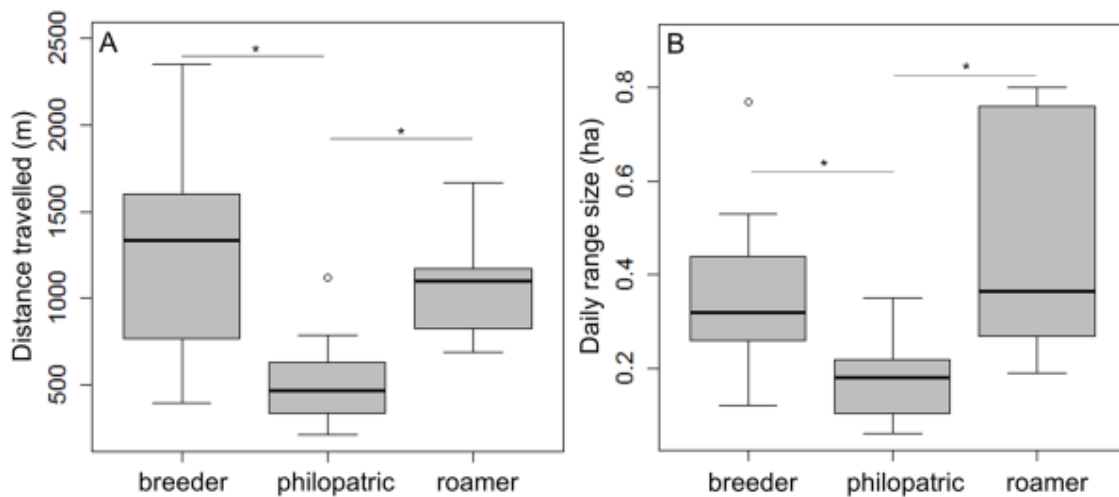


Figure 4. Differences in (A) travel distance and (B) daily range size between breeders (N = 14), philopatrics (N = 11) and roamers (N = 6). Black lines indicate median values, boxes

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

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

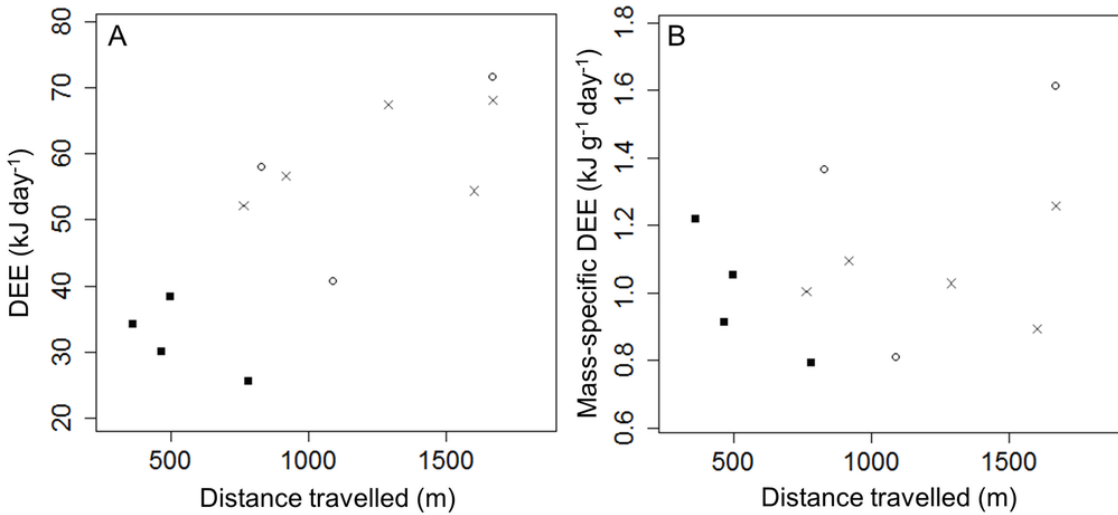


Figure 5. Relationship between travel distance and (A) daily energy expenditure (DEE) and (B) mass-specific DEE of philopatrics, roamers, and breeders (*filled squares, open circles and crosses*, respectively; $N = 4$ philopatrics, 3 roamers and 5 breeders).

4. Discussion

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

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

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

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

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

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

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

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

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

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

Acknowledgements

This study was made possible with the support of the Succulent Karoo Research Station (registered South African NPO 122-134), Goegap Nature Reserve and several field assistants. We thank two anonymous reviewers for their comments on an earlier version of the manuscript. Animals were captured and handled following protocols approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2012/37/2A extended until December 2019, AESC 2014/40/B). This work was supported by the University of Strasbourg Institute for Advanced Study (USIAS); the University of the Witwatersrand; the Claude Leon Foundation; the National Research Foundation [grant number 87769]; and the CNRS.

Competing Interest

444 No competing interests declared.

445

446 **References**

- 447 [1] M.R. Gross, Alternative reproductive strategies and tactics: diversity within sexes,
448 Trends Ecol. Evol. 11 (1996) 92–98.
- 449 [2] P. Stockley, J.B. Searle, D.W. MacDonald, C.S. Jones, Alternative reproductive tactics
450 in male common shrews: relationships between mate-searching behaviour, sperm
451 production, and reproductive success as revealed by DNA fingerprinting, Behav. Ecol.
452 Sociobiol. 34 (1994) 71–78.
- 453 [3] C. Schradin, M. Scantlebury, N. Pillay, B. König, Testosterone levels in dominant
454 sociable males are lower than in solitary roamers: physiological differences between
455 three male reproductive tactics in a sociably flexible mammal, Am. Nat. 173 (2009)
456 376–388. doi:10.1086/596535.
- 457 [4] J.L. Koprowski, Alternative reproductive tactics in male eastern gray squirrels:
458 “making the best of a bad job,” Behav. Ecol. 4 (1993) 165–171.
- 459 [5] M. Taborsky, R.F. Oliveira, H.J. Brockmann, The evolution of alternative reproductive
460 tactics: concepts and questions, in: H.J. Oliveira, R F, Taborsky, M, Brockmann (Ed.),
461 Altern. Reprod. Tactics, Cambridge University Press, Cambridge, 2008: pp. 1–21.
- 462 [6] R.F. Oliveira, A.V.M. Canário, A.F.H. Ros, Hormones and alternative reproductive
463 tactics in vertebrates, in: R.F. Oliveira, M. Taborsky, H.J. Brockmann (Eds.), Altern.
464 Reprod. Tactics, Cambridge University Press, Cambridge, 2008: pp. 132–173.
- 465 [7] M. Hadley, J. Levine, Endocrinology, Pearson, 2006.
- 466 [8] L. Gautron, J.K. Elmquist, Sixteen years and counting: an update on leptin in energy
467 balance, J. Clin. Invest. 121 (2011) 2087–2093. doi:10.1172/JCI45888.on.
- 468 [9] IUPS Thermal Commission, Glossary of terms for thermal physiology, J. Therm. Biol.

469 75 (2003) 75–106. doi:10.1016/S0306-4565(02)00055-4.

470 [10] D.S. Glazier, Is metabolic rate a universal ‘pacemaker’ for biological processes?, Biol.
 471 Rev. 90 (2015) 377–407. doi:10.1111/brv.12115.

472 [11] M. Scantlebury, J.M. Waterman, N.C. Bennett, Alternative reproductive tactics in male
 473 Cape ground squirrels *Xerus inauris*, Physiol. Behav. 94 (2008) 359–367.
 474 doi:10.1016/j.physbeh.2008.02.003.

475 [12] M. Scantlebury, J. Speakman, M. Oosthuizen, T. Roper, N. Bennett, Energetics reveals
 476 physiologically distinct castes in a eusocial mammal, Nature. 440 (2006) 795–797.

477 [13] R.E. Ricklefs, M. Konarzewski, S. Daan, The relationship between basal metabolic
 478 rate and daily energy expenditure in birds and mammals, Am. Nat. 147 (1996) 1047–
 479 1071.

480 [14] J.R. Speakman, The cost of living: field metabolic rates of small mammals, Adv. Ecol.
 481 Res. 30 (2000) 177–297. doi:10.1016/S0065-2504(08)60019-7.

482 [15] R. Drent, S. Daan, The prudent parent: energetic adjustments in avian breeding,
 483 Ardea. 68 (1980) 225–252.

484 [16] K.A. Nagy, I.A. Girard, T.K. Brown, Energetics of free-ranging mammals, reptiles,
 485 and birds, Annu. Rev. Nutr. 19 (1999) 247–277.

486 [17] H.. Brockmann, M. Taborsky, Alternative reproductive tactics and the evolution of
 487 alternative allocation phenotypes, in: R.F. Oliveira, M. Taborsky, H.J. Brockmann
 488 (Eds.), Altern. Reprod. Tactics, Cambridge University Press, Cambridge, 2008: pp.
 489 25–51.

490 [18] M. Scantlebury, N.C. Bennett, J.R. Speakman, N. Pillay, C. Schradin, Huddling in
 491 groups leads to daily energy savings in free-living African four-striped grass mice,
 492 *Rhabdomys pumilio*, Funct. Ecol. 20 (2006) 166–173. doi:10.1111/j.1365-
 493 2435.2006.01074.x.

- 494 [19] J. Kotze, N.C. Bennett, M. Scantlebury, The energetics of huddling in two species of
495 mole-rat (Rodentia: Bathyergidae), *Physiol. Behav.* 93 (2008) 215–221.
496 doi:10.1016/j.physbeh.2007.08.016.
- 497 [20] C. Schradin, A.K. Lindholm, Relative fitness of alternative male reproductive tactics in
498 a mammal varies between years, *J. Anim. Ecol.* 80 (2011) 908–917.
499 doi:10.1111/j.1365-2656.2011.01831.x.
- 500 [21] Z.-G. Song, D.-H. Wang, Basal metabolic rate and organ size in Brandt's voles
501 (*Lasiopodomys brandtii*): effects of photoperiod, temperature and diet quality, *Physiol.*
502 *Behav.* 89 (2006) 704–170. doi:10.1016/j.physbeh.2006.08.016.
- 503 [22] S. Daan, D. Masman, A. Groenewold, Avian basal metabolic rates: their association
504 with body composition and energy expenditure in nature, *Am. J. Physiol.* 259 (1990)
505 R333–R340.
- 506 [23] M. Konarzewski, J. Diamond, Evolution of basal metabolic rate and organ masses in
507 laboratory mice, *Evolution* (N. Y). 49 (1995) 1239–1248.
- 508 [24] C. Selman, S. Lumsden, L. Bünger, W.G. Hill, J.R. Speakman, Resting metabolic rate
509 and morphology in mice (*Mus musculus*) selected for high and low food intake, *J. Exp.*
510 *Biol.* 204 (2001) 777–784.
- 511 [25] A.F. Bennett, J.A. Ruben, Endothermy and activity in vertebrates, *Science* (80-.). 206
512 (1979) 649–654.
- 513 [26] P.A. Biro, J.A. Stamps, Do consistent individual differences in metabolic rate promote
514 consistent individual differences in behavior?, *Trends Ecol. Evol.* 25 (2010) 653–659.
515 doi:10.1016/j.tree.2010.08.003.
- 516 [27] M.A. Chappell, T.J. Garland, E.L. Rezende, F.R. Gomes, Voluntary running in deer
517 mice: speed, distance, energy costs and temperature effects, *J. Exp. Biol.* 207 (2004)
518 3839–3854. doi:10.1242/jeb.01213.

- 519 [28] M.W. Sears, J.P. Hayes, M.R. Banta, D. McCormick, Out in the cold: physiological
520 capacity influences behaviour in deer mice, *Funct. Ecol.* 23 (2009) 774–783.
521 doi:10.1111/j.1365-2435.2009.01559.x.
- 522 [29] C. Schradin, N. Pillay, Demography of the striped mouse (*Rhabdomys pumilio*) in the
523 succulent karoo, *Mamm. Biol. - Zeitschrift Für Säugetierkd.* 70 (2005) 84–92.
524 doi:10.1016/j.mambio.2004.06.004.
- 525 [30] C. Schradin, Territorial defense in a group-living solitary forager: who, where, against
526 who?, *Behav. Ecol. Sociobiol.* 55 (2004) 439–446. doi:10.1007/s00265-003-0733-x.
- 527 [31] C. Schradin, N. Pillay, The striped mouse (*Rhabdomys pumilio*) from the Succulent
528 Karoo, South Africa: a territorial group-living solitary forager with communal
529 breeding and helpers at the nest, *J. Comp. Psychol.* 118 (2004) 37–47.
530 doi:10.1037/0735-7036.118.1.37.
- 531 [32] C. Schradin, N. Pillay, Female striped mice (*Rhabdomys pumilio*) change their home
532 ranges in response to seasonal variation in food availability, *Behav. Ecol.* 17 (2006)
533 452–458. doi:10.1093/beheco/arj047.
- 534 [33] J. Raynaud, C. Schradin, Regulation of male prolactin levels in an opportunistically
535 breeding species, the African striped mouse, *J. Zool.* 290 (2013) 287–292.
536 doi:10.1111/jzo.12040.
- 537 [34] N. Pillay, Reproductive isolation in three populations of the striped mouse *Rhabdomys*
538 *pumilio* (Rodentia, Muridae): interpopulation breeding studies, *Mammalia.* 64 (2000)
539 461–470. doi:10.1515/mamm.2000.64.4.461.
- 540 [35] N. Solmsen, J. Johannesen, C. Schradin, Highly asymmetric fine-scale genetic
541 structure between sexes of African striped mice and indication for condition dependent
542 alternative male dispersal tactics, *Mol. Ecol.* 20 (2011) 1624–1634.
543 doi:10.1111/j.1365-294X.2011.05042.x.

- 544 [36] C. Schradin, C.-H. Yuen, Hormone levels of male African striped mice change as they
545 switch between alternative reproductive tactics, *Horm. Behav.* 60 (2011) 676–80.
546 doi:10.1016/j.yhbeh.2011.09.002.
- 547 [37] J.R. Speakman, Doubly-labelled water: theory and practice, Chapman and Hall,
548 London, 1997.
- 549 [38] A.A. Degen, B. Pinshow, P.U. Alkon, H. Arnon, Tritiated water for estimating total
550 body water and water turnover rate in birds, *J. Appl. Physiol.* 51 (1981) 1183–1188.
- 551 [39] S. Poppitt, J.R. Speakman, P.A. Racey, The energetics of reproduction in the common
552 shrew (*Sorex araneus*): a comparison of indirect calorimetry and the doubly labeled
553 water method, *Physiol. Biochem. Zool.* 66 (1993) 964–982.
- 554 [40] I. Chery, A. Zahariev, C. Simon, S. Blanc, Analytical aspects of measuring 2H/1H and
555 18O/16O ratios in urine from doubly labelled water studies by high-temperature
556 conversion elemental analyser-isotope-ratio mass spectrometry, *Rapid Commun. Mass*
557 *Spectrom.* 29 (2015) 562–572. doi:10.1002/rcm.7135.
- 558 [41] S.B. Racette, D.A. Schoeller, A.H. Luke, K. Shay, J. Hnilicka, R.F. Kushner, Relative
559 dilution spaces of 2H- and 18O-labeled water in humans, *Am. J. Physiol.* 30 (1994)
560 E585–E590.
- 561 [42] J.R. Speakman, C. Hambly, Using doubly-labelled water to measure free-living energy
562 expenditure: some old things to remember and some new things to consider, *Comp.*
563 *Biochem. Physiol. Part A.* 202 (2016) 3–9. doi:10.1016/j.cbpa.2016.03.017.
- 564 [43] J. Weir, New methods for calculating metabolic rate with special reference to protein
565 metabolism, *J. Physiol.* 109 (1949) 1–9.
- 566 [44] A. Haim, F. le R. Fourie, Heat production in nocturnal (*Praomys natalensis*) and
567 diurnal (*Rhabdomys pumilio*) South African murids, *South African J. Zool.* 15 (1980)
568 91–94. doi:10.1080/02541858.1980.11447692.

- 569 [45] J. Jäger, C. Schradin, N. Pillay, R. Rimbach, Active and explorative individuals are
570 often restless and excluded from studies measuring resting metabolic rate: do
571 alternative metabolic rate measures offer a solution?, *Physiol. Behav.* 174 (2017) 57–
572 66. doi:10.1016/j.physbeh.2017.02.037.
- 573 [46] R. Rimbach, S. Blanc, A. Zahariev, M. Gatta, N. Pillay, C. Schradin, Seasonal
574 variation in energy expenditure in a rodent inhabiting a winter-rainfall desert, *J. Comp.*
575 *Physiol. B.* (2018). doi:10.1007/s00360-018-1168-z.
- 576 [47] C. Schradin, C. Schneider, C.H. Yuen, Age at puberty in male African striped mice:
577 the impact of food, population density and the presence of the father, *Funct. Ecol.* 23
578 (2009) 1004–1013. doi:10.1111/j.1365-2435.2009.01569.x.
- 579 [48] C. Schradin, Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid
580 rodent, *J. Ethol.* 24 (2006) 37–43. doi:10.1007/s10164-005-0158-2.
- 581 [49] R. Rimbach, M. Wastavino, C.H. Yuen, N. Pillay, C. Schradin, Contrasting activity
582 budgets of alternative reproductive tactics in male striped mice, *J. Zool.* 301 (2017)
583 280–289. doi:10.1111/jzo.12414.
- 584 [50] R.E. Kenward, A.B. South, S.S. Walls, Ranges6: For the Analysis of Tracking and
585 Location Data, (2003).
- 586 [51] R Core Team, R: a language and environment for statistical computing. R Foundation
587 for Statistical Computing, Vienna, Austria, [Www.r-Project.Org/](http://www.R-project.org/). (2017).
- 588 [52] P. Meerlo, L. Bolle, G.H. Visser, D. Masman, S. Daan, Basal metabolic rate in relation
589 to body composition and daily energy expenditure in the field vole, *Microtus agrestis*,
590 *Physiol. Zool.* 70 (1997) 362–369.
- 591 [53] K.A. Nagy, Field metabolic rate and body size, *J. Exp. Biol.* 208 (2005) 1621–1625.
592 doi:10.1242/jeb.01553.
- 593 [54] J.R. Speakman, Measuring energy metabolism in the mouse – theoretical, practical,

and analytical considerations, *Front. Physiol.* 4 (2013) 1–23.
doi:10.3389/fphys.2013.00034.

[55] K.H. Elliott, J. Welcker, A.J. Gaston, S.A. Hatch, V. Palace, J.F. Hare, J.R. Speakman, W.G. Anderson, Thyroid hormones correlate with resting metabolic rate, not daily energy expenditure, in two charadriiform seabirds, *Biol. Open.* 2 (2013) 580–586.
doi:10.1242/bio.20134358.

[56] D. Bates, M. Maechler, *lme4: Linear mixed-effects models using Eigen and Eigenpack*, (2010).
<http://cran.r-project.org/package=lme4>.

[57] S. Holm, A simple sequentially rejective multiple test procedure, *Scand. J. Stat.* 6 (1979) 65–70.

[58] V. Careau, D. Thomas, M.M. Humphries, D. Réale, Energy metabolism and animal personality, *Oikos*. 117 (2008) 641–653. doi:10.1111/j.2008.0030-1299.16513.x.

[59] V. Careau, D. Réale, D. Garant, F. Pelletier, J.R. Speakman, M.M. Humphries, Context-dependent correlation between resting metabolic rate and daily energy expenditure in wild chipmunks, *J. Exp. Biol.* 216 (2013) 418–426.
doi:10.1242/jeb.076794.

[60] J.-A. Nilsson, Metabolic consequences of hard work, *Proc. R. Soc. B.* 269 (2002) 1735–1739. doi:10.1098/rspb.2002.2071.

[61] K.A. Hammond, J. Diamond, Maximal sustained energy budgets in humans and animals, *Nature*. 386 (1997) 457–462.

[62] P. Koteja, On the relation between basal and field metabolic rates in birds and mammals, *Funct. Ecol.* 5 (1991) 56–64.

[63] M. Fyhn, G.W. Gabrielsen, E.S. Nordøy, B. Moe, I. Langseth, C. Bech, S. Physiological, B. Zoology, N.M. June, Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period, *Physiol. Biochem. Zool.*

619 74 (2001) 343–355.

620 [64] J. Welcker, J.R. Speakman, K.H. Elliott, S.A. Hatch, A.S. Kitaysky, Resting and daily
621 energy expenditures during reproduction are adjusted in opposite directions in free-
622 living birds, *Funct. Ecol.* 29 (2015) 250–258. doi:10.1111/1365-2435.12321.

623 [65] B.I. Tieleman, T.H. Dijkstra, K.C. Klasing, G.H. Visser, J.B. Williams, Effects of
624 experimentally increased costs of activity during reproduction on parental investment
625 and self-maintenance in tropical house wrens, *Behav. Ecol.* 19 (2008) 949–959.
626 doi:10.1093/beheco/arn051.

627 [66] M.A. Hack, The energetics of male mating strategies in field crickets (Orthoptera:
628 Gryllinae: Gryllidae), *J. Insect Behav.* 11 (1998) 853–867.
629 doi:10.1023/A:1020864111073.

630 [67] G.J. Kenagy, S.M. Sharbaugh, K.A. Nagy, Annual cycle of energy and time
631 expenditure in a golden-mantled ground squirrel population, *Oecologia.* 78 (1989)
632 269–282.

633 [68] M. Taborsky, Sperm competition in fish: “bourgeois” males and parasitic spawning,
634 *Trends Ecol. Evol.* 13 (1998) 222–227. doi:10.1016/S0169-5347(97)01318-9.

635 [69] M.E. Cummings, R. Gelineau-Kattner, The energetic costs of alternative male
636 reproductive strategies in *Xiphophorus nigrensis*, *J. Comp. Physiol. A.* 195 (2009)
637 935–946. doi:10.1007/s00359-009-0469-9.

638