

# Contrasting activity budgets of alternative reproductive tactics in male striped mice

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## Keywords

alternative reproductive tactics; social behaviour; energy trade-off; allocation; movement ecology; biotelemetry; activity budgets; *Rhabdomys pumilio*.

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## Abstract

To maximize their fitness, individuals of one sex can display discrete reproductive phenotypes, called alternative reproductive tactics (ARTs). Individuals following ARTs show behavioural variation, which might result in differences in energy intake and expenditure. However, few studies have compared activity budgets and non-sexual behaviour of individuals following ARTs in nature. We studied male African striped mice *Rhabdomys pumilio*, which can follow three ARTs: (1) breeding male of a group of females; (2) philopatrics remaining in their natal group; or (3) solitary living roamers. We predicted that each tactic is characterized by its specific activity budget, representing alternative energy trade-offs. We conducted focal animal observations on 70 males following ARTs. Roamers had higher travelling rates than philopatrics, and breeders had larger daily range sizes compared to philopatrics but not roamers. Philopatrics had higher foraging rates than breeders and showed more socio-positive behaviour than roamers. Breeders and philopatrics were in their nest more often than roamers, potentially engaging in social interactions with other group members. Roamers were chased off more often than breeders, but the three tactics did not differ concerning rates of socio-negative behaviour. Overall, philopatrics allocated their time towards behaviours that would increase body mass and survival probability, which could improve the probability to switch to a tactic of higher reproductive success. In contrast, breeders and roamers allocated their time towards behaviours that would increase their chances to mate. In conclusion, following ARTs results in contrasting activity budgets that reflect the differences in reproductive behaviours observed between tactics.

## Introduction

In many animal species, individuals display discrete reproductive phenotypes, so-called alternative reproductive tactics (ARTs), to maximize their fitness under intra-sexual reproductive competition (Gross, 1996). Behavioural phenotypes of ARTs arise from genetically-based decision rules, which either differ between strategies (alternative strategies; Gross, 1996), or are the same (single strategy; Schradin & Lindholm, 2011). In species with a single strategy one decision-rule produces several phenotypes, and single strategies can either be mixed or conditional (Gross, 1996; Schradin & Lindholm, 2011; Hill, Pillay & Schradin, 2015). Most common are conditional ARTs, where the most competitive individuals follow a so-called bourgeois tactic with much higher fitness than alternative tactics (Young, Spong & Clutton-Brock, 2007; Schradin & Lindholm, 2011). Bourgeois males typically defend a breeding territory and its female(s), whereas the other phenotype(s) act as sneaker, satellite or roamer males, attempting to mate with

females defended by bourgeois males. To date, studies on male ARTs have focused on differences in mating behaviour and reproductive success, but differences in non-sexual behaviour have been neglected even though these might also significantly influence current and future reproductive success.

Males following ARTs can be expected to differ in the allocation of time towards social behaviour. For example, solitary roamers or satellite males can be expected to engage in fewer social interactions than bourgeois males due to their solitary lifestyle. Males following the bourgeois tactic are often more aggressive than males following other tactics (Koprowski, 1993; Kutsukake & Clutton-Brock, 2008). Group-living philopatrics or subordinates often provide allo-parental care (Brotherton *et al.*, 2001; Raynaud & Schradin, 2014) and participate in territory defence (Schradin, 2004; Mares, Young & Clutton-Brock, 2012), while roaming or satellite males do not defend territories. Furthermore, the allocation of time towards non-social behaviour should also differ between ARTs. Dominant males often invest in courting or guarding receptive

females and thus devote less time to foraging than males following other tactics (Corlatti *et al.*, 2013; Girard-Buttoz *et al.*, 2014). Such behavioural differences might lead to substantial variation in energy requirements (Kenagy, Sharbaugh & Nagy, 1989; Scantlebury *et al.*, 2006b; Cummings & Gelineau-Kattner, 2009). Thus, differences in time budgets could be related to alternative energy trade-offs associated with ARTs. To date, however, little is known about how behavioural differences between males following ARTs affect their activity budgets.

The diurnal African striped mouse *Rhabdomys pumilio* is a suitable species to investigate whether behavioural differences between males following ARTs result in contrasting activity budgets. During the breeding season, male striped mice display the following ARTs under conditions of high population density: (1) breeding males defend a territory with a group of females; (2) philopatric males remain in their natal group, resulting in very low reproductive success; or (3) solitary roamers with low reproductive success. Striped mice follow a conditional strategy, where relative body mass determines a male's tactic, with philopatrics being lighter than breeders and roamers, and roamers being lighter than breeders (Schradin *et al.*, 2009). In striped mice, body mass correlates with age, accordingly males following ARTs also differ in age, with philopatrics being younger than both breeders and roamers (Schradin *et al.*, 2009). Breeders mainly invest in defending their territory, which contains several communally breeding females (Schradin, 2004). Breeding males show paternal care (Schradin & Pillay, 2003, 2004) and amicable behaviour towards females and pups (Schradin & Anzenberger, 1999; Schradin & Pillay, 2004). Philopatrics act as helpers at the nest, providing allo-parental care (Raynaud & Schradin, 2014), and show socio-positive behaviour towards other group members (Schradin & Pillay, 2004). Moreover, philopatrics defend their natal territory against intruders (Schradin, 2004; Schradin & Pillay, 2004). Males following the roaming tactic only exist during the breeding season, when they travel long distances and occupy larger home ranges than males of the other tactics (Schradin *et al.*, 2009), investing mainly in obtaining access to females in multiple territories (Schradin & Lindholm, 2011). Differences in activity levels and in thermoregulatory benefits (i.e. huddling at night; Scantlebury *et al.*, 2006a) gained from group-living for breeders and philopatrics may require substantial differences in energy acquisition between individuals following different ARTs. These behavioural differences should result in distinct time allocation patterns between tactics.

The aim of our study was to test the hypothesis that males following ARTs show contrasting activity budgets to add to our understanding of the movement ecology of small mammals. We made specific predictions for each male ART. (1) We predicted breeders to patrol and aggressively defend their territories against intruders (Schradin, 2004). We expected breeders to return to their nest during the day and to show more socio-positive behaviour than solitary roamers. Since breeders are heavier than philopatrics and roamers, they consequently may need to forage less due to relatively lower energy requirements (per g body mass). (2) We predicted no investment into territory patrolling or long-distance travel by

philopatrics, but high levels of foraging to rapidly gain body mass. We expected philopatrics to spend more time in their nest and to show more socio-positive behaviour than solitary roamers. We expected aggression in philopatrics to be similar to breeders, and that philopatrics show more aggressive behaviour than roamers, which do not defend a territory. (3) Striped mice are solitary foragers (Schradin & Pillay, 2004; Schradin, 2006), which meet other individuals during foraging. Roamers often visit nesting sites of breeding females and they can show socio-positive behaviour when encountering females. However, most social interactions take part between group members at their nesting site before and after foraging. Thus, we predicted roamers to travel long distances through several territories, and consequently to receive more aggressive behaviour than group-living males. We predicted roamers to forage more than breeders to increase their body mass to switch to the breeder tactic. Moreover, we expected roamers, which cannot gain thermoregulatory benefits from group-living (i.e. through huddling) to bask more than breeders.

## Materials and methods

### Study site and study animals

We collected data during the breeding season in 2003, 2008, 2009, 2010, 2011, 2013 in Goegap Nature Reserve, Northern Cape Province, South Africa (S 41.56, E 1.60, elevation 950 m). The vegetation type is semi-arid Succulent Karoo. The area experiences winter rainfall (annual average of 190 mm at the field site), and striped mice breed in the following spring. The breeding season typically lasts 3–4 months (August–November). In the study area, striped mice are facultative group-living and groups typically consist of one breeding male, two to four breeding females and their philopatric offspring of both sexes (Schradin & Pillay, 2004). Most individuals born during the breeding season stay as non-breeders in their natal group (i.e. philopatric) until the next breeding season. Typically, males will then disperse and attempt to immigrate into groups of communally breeding females, remain philopatric or become solitary living roamers and attempt to mate with females from other groups (Schradin *et al.*, 2009).

### Trapping, marking and radio-tracking

We baited Sherman-style live-traps (26 × 9 × 9 cm) with bran flakes, raisins, salt and sunflower oil to capture striped mice. We placed traps at shrubs containing the nest of a group or a roamer in the morning and the late afternoon, and checked them again after 30–45 min. We weighed ( $\pm 0.1$  g) captured individuals using an electronic balance, and recorded whether males were scrotal (testes descended) or not (testes in the abdominal cavity). We marked mice permanently with ear-tags (National Band and Tag Co., Newport, KY, USA) and temporarily with hair dye (Rapido, Pinetown, South Africa) for individual recognition during behavioural observations. To locate individuals during observations we equipped them with radio-collars (Holohil, Carp, ON, Canada). Radio-collars weighed 2.5–3.5 g, which represented less than 10% of an

individuals' body mass. At the end of the breeding season all collars were removed.

### Determination of ARTs

We determined male tactics using a combination of trapping, behavioural observations and radio-tracking. We defined philopatrics as young adults that stayed in their natal group (i.e. the group where they were previously trapped as juveniles). All philopatrics were born in the year in which focal observations were conducted; they were at least 2 months old at the time of the focal observation and thus adults (Schradin & Pillay, 2004). We defined roaming males as scrotal males that did not share a nest with other individuals, and territorial breeders as scrotal males that lived in groups other than their natal group (Schradin *et al.*, 2009).

### Behavioural observations

At our field site striped mice are well-habituated to the presence of observers, due to the continuous monitoring of the population. To establish activity budgets of males following ARTs, we conducted behavioural observations on individuals equipped with radio-collars during peak activity periods, which meant early morning or late afternoon (Schradin, 2006). We observed focal individuals continuously for 3 h once in the morning (between 6:00–9:00 h) and once in the afternoon (15:00–18:00 h). We followed individuals at a distance of 5–10 m, and recorded their behaviour directly or by using binoculars (Schradin, 2006). We used radio-tracking to follow focal individuals and to determine their position when they were not visible. In such a case, we located individuals every 3 min to confirm their position. Every minute, we recorded all behaviours and states (Table 1) of a focal mouse during the previous minute. Because of the complexity of the situation (following a mouse in its natural environment, carrying radio-tracking equipment), we used 1/0 sampling (recording presence/absence of behaviours shown within a 1 min interval), such that more than one behaviour could be recorded per minute. We conducted a total of 140 focal observations on 70 different individuals belonging to 25 different groups (groups only apply to breeders and philopatrics; Table 2). Focal observations were equally divided between morning and afternoon observations (2 observations per individual). Both focal observations on one individual were usually conducted within 24 h (median 1.0 day, 1st–3rd quartile: 0–2 days). To examine activity budgets, we combined morning and afternoon 3 h focal observations per focal animal, and hence our data collection resulted in a total of 70 6 h focal observations (Table 2). To monitor body mass changes of males following ARTs we recorded the body mass of individuals around the day of the follow ( $SD \pm 4.3$  days) and again 4 weeks later (Table 2). For each individual, we calculated the percentage of body mass change per day between both body mass measurements to account for the variation in measurement interval.

For data analyses, we converted all behaviours and states into rates (number of events divided by 360 min of focal observation). Striped mice spend large parts of the day inside shrubs where their behaviour cannot always be observed. Thus,

**Table 1** Behaviours (b) and states (s) recorded during behavioural observations

Behaviour/state	Description
Basking	Focal mouse sits in the sun adopting a basking posture, often accompanied by piloerection
Resting (b)	Focal mouse sits in the shade
Travel (b)	Focal mouse moves from shrub to shrub, or within a shrub
Foraging (b)	Focal mouse locates and ingests a food item
Autogroom (b)	Focal mouse cleans its own fur
In nest (s)	Focal mouse is in the nest of its group
In shrub (s)	Focal mouse is in a shrub which is not the nest
<i>Socio-positive behaviours</i>	
Proximity (s)	Focal mouse is in same shrub as another mouse
Close proximity (s)	Focal mouse is less than one mouse length away from another mouse
Sniffing (b)	Focal mouse touches another mouse with its nose
Body contact (b)	Focal mouse sits next to and touches another mouse
Groom (b)	Focal mouse goes through the fur of another mouse
Groomed (b)	Focal mouse is groomed by another mouse
<i>Socio-negative behaviours</i>	
Chasing (b)	Focal mouse runs after another mouse
Chased (b)	Focal mouse is chased by another mouse
Fight (b)	Two mice standing on their hind legs and touching each other with their forelegs (i.e. boxing)
Bite (b)	Focal mouse touches another mouse with its teeth

we also recorded when mice were inside shrubs or their group's nest (i.e. states in Table 1) because these periods constituted substantial parts of their activity budgets (Schradin, 2006). Moreover, striped mice are solitary foragers, which only occasionally encounter other individuals during the day. Thus, to avoid underrepresentation of social behaviour, we recorded when focal mice were in the same shrub with another individual (i.e. in proximity).

We pooled resting, nest and shrub into a fourth category 'total inactive' to ascertain whether males following ARTs differed in the overall time spent inactive. We divided social behaviour/states, which occurred infrequently, into two categories, socio-positive (proximity, close proximity, sniffing, body contact, grooming) and socio-negative (chasing, being chased, fight, bite) behaviour (Table 1). We analysed the behaviours chasing, fighting and bite together as socio-negative and separately from being chased.

### Travel distance

During 46 6 h behavioural observations (out of 70 in total; Table 2), a GPS (Garmin etrex, Garmin International, Olathe, KS, USA) was mounted on the belt of the observer,

**Table 2** Number of focal observations, body mass measurements and travel distances recorded for male striped mice following alternative reproductive tactics, and their average age  $\pm$  SD at the time of the focal observation

	Focal observations	Body mass measurements	Travel distance	Age in months (M)	Year of focal observation (N)
Breeder	36	29	21	13.9 $\pm$ 4.2 (9)	2003 (10), 2008 (3), 2009 (10), 2010 (1), 2011 (2), 2013 (10)
Philopatric	13	11	11	2.2 $\pm$ 0.7 (11)	2003 (2), 2009 (10), 2010 (1)
Roamer	21	16 <sup>a</sup>	14	10.0 $\pm$ 5.2 (11)	2008 (2), 2009 (10), 2011 (9)
Total	70	56	46	(36)	

<sup>a</sup>Four roamers switched tactic and followed the breeder tactic at the time the second body mass measurement was taken.

automatically recording a track using the track function. The track function was turned on simultaneously with the start of the focal observation and turned off when it was terminated. As the observer followed the focal individual, this track provided a proxy of the distance travelled by the focal mouse. Using these tracks we calculated daily range size (area covered during a 6 h focal observation) as 95% and 99% kernel contours (Worton, 1989) using the program Ranges 6 (Kenward, South & Walls, 2003).

### Statistical analyses

All response variables differed significantly from normality (Shapiro–Wilk tests, all  $P < 0.001$ ). Thus, we used Kruskal–Wallis tests to analyse behavioural differences, differences in travel distance, daily range sizes, age, initial body mass and subsequent changes in body mass of males following ARTs. Subsequently, we used pairwise Wilcoxon rank sum tests to determine pairwise differences between the three ARTs *post hoc*. Both measurements of body mass differed from normality (Shapiro–Wilk tests,  $P < 0.05$ ) and could not be transformed to reach normality. Thus, to examine whether individuals gained or lost body mass in the 4 weeks between both measurements we used Mann–Whitney  $U$  tests *post hoc*. To avoid type 1 errors due to multiple testing, we corrected  $P$ -values using the Holm method (Holm, 1979). All analyses were conducted in R2.15.1 (R Development Core Team, 2012). All statistical tests were two tailed, and the statistical threshold was set at  $P \leq 0.05$ .

### Results

Male ARTs differed concerning rates of foraging, travelling, autogrooming, in their nest, in socio-positive behaviours, being chased by another mouse and travel distance (Table 3). They also differed with respect to daily range size (99% kernel), body mass changes and age (Table 3). They did not differ regarding rates of resting, in a shrub, total inactive, basking, in socio-negative behaviours or 95% kernel size (Table 3).

Breeders and philopatrics were in the nest more often than roamers, whereas breeders and philopatrics did not differ (Table 4; Fig. 1a). Philopatrics had higher foraging rates than breeders, but there were no differences between the other tactics (Table 4; Fig. 1c). Roamers had higher travelling rates than philopatrics, whereas the other tactics did not differ

**Table 3** Results of Kruskal–Wallis tests for the different behaviours, body mass changes, daily range sizes and age between males following alternative reproductive tactics (d.f. = 2 for all analyses)

	$\chi^2$	$P$ value
Nest	21.76	<b>&lt;0.001</b>
Shrub	2.22	0.299
Rest	0.40	0.816
Total inactive	2.89	0.245
Foraging	6.22	<b>0.044</b>
Basking	2.26	0.322
Travel	7.12	<b>0.028</b>
Being chased	9.97	<b>0.006</b>
Socio-positive	12.38	<b>0.002</b>
Socio-negative	4.63	0.098
Autogroom	15.06	<b>&lt;0.001</b>
Distance travelled	7.09	<b>0.028</b>
95% kernel size	5.79	0.055
99% kernel size	6.77	<b>0.033</b>
Initial body mass	28.96	<b>&lt;0.001</b>
Body mass change	7.72	<b>0.021</b>
Age	24.24	<b>&lt;0.001</b>

Significant differences are shown in bold.

(Table 4; Fig. 1d). Philopatrics had higher rates of autogrooming than breeders and roamers, but breeders and roamers did not differ (Table 4; Fig. 1f). Philopatrics showed higher rates of socio-positive behaviour than roamers, but there were no differences between the other tactics (Table 4; Fig. 2a). Roamers were chased more often than breeders, whereas the other tactics did not differ (Table 4; Fig. 2c).

Breeders travelled longer distances and had larger 99% kernel contour sizes than philopatrics, but the other tactics did not differ (Tables 4 and 5; Figs 3 and 4). Breeders were heavier than roamers and philopatrics, and roamers were heavier than philopatrics (Tables 2 and 4). Neither breeders nor roamers changed their body mass (median, 1st–3rd quartile; breeders: 0% per day,  $-0.09\%$  to  $0.26\%$ ,  $U = 143.5$ ,  $P = 0.27$ ; roamers:  $0.08\%$  per day,  $-0.09\%$  to  $0.32\%$ ,  $U = 29$ ,  $P = 0.083$ ) within the 4 weeks after initial recordings. Philopatrics increased their body mass by  $0.39\%$  per day ( $0$ – $0.73\%$ ,  $U = 1$ ,  $P = 0.012$ ; Table 5), and significantly increased more than breeders, whereas there was no difference between the other tactics (Tables 4 and 5; Fig. 5). Philopatrics were younger than breeders and roamers, and roamers were younger than breeders (Tables 2 and 4).



**Table 4** Results of pairwise Wilcoxon rank sum tests for the different behaviours, initial body mass and subsequent changes, daily range sizes and age between males following alternative reproductive tactics (*P* value corrections were made using the Holm method)

Category	Breeder versus roamer		Breeder versus philopatric		Philopatric versus roamer	
	<i>P</i> value	<i>W</i>	<i>P</i> value	<i>W</i>	<i>P</i> value	<i>W</i>
Nest	<b>&lt;0.001</b>	634.5	0.634	212.5	<b>&lt;0.001</b>	241.5
Foraging	0.601	346	<b>0.041</b>	125	0.135	188.5
Travel	0.398	326.5	0.129	316	<b>0.011</b>	54.5
Being chased	<b>0.017</b>	356	0.746	242	0.064	88
Socio-positive	0.058	492	0.058	138.5	<b>0.001</b>	232
Autogroom	0.169	298	<b>&lt;0.001</b>	74.5	<b>0.012</b>	213.5
Distance travelled	0.289	191	<b>0.022</b>	182	0.344	59
99% kernel size	0.55	116	<b>0.03</b>	123	0.07	25
Initial body mass	<b>0.03</b>	323.5	<b>&lt;0.001</b>	319	<b>&lt;0.001</b>	1
Body mass change	0.44	199	<b>0.006</b>	69	0.057	127
Age	<b>0.002</b>	88	<b>&lt;0.001</b>	99	<b>&lt;0.001</b>	0

Significant differences are shown in bold.

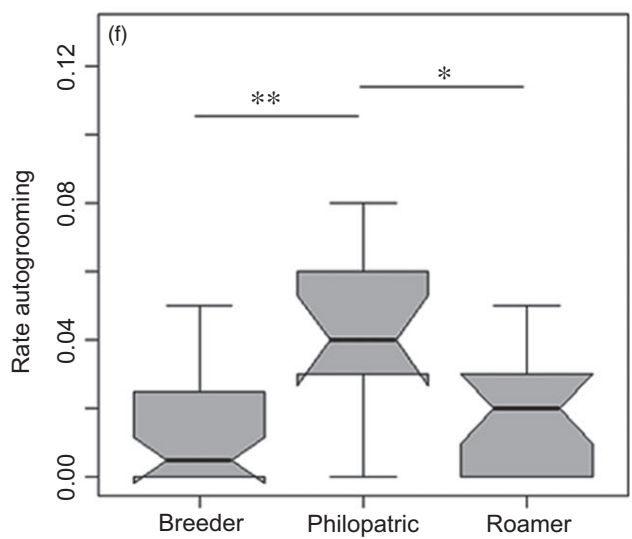
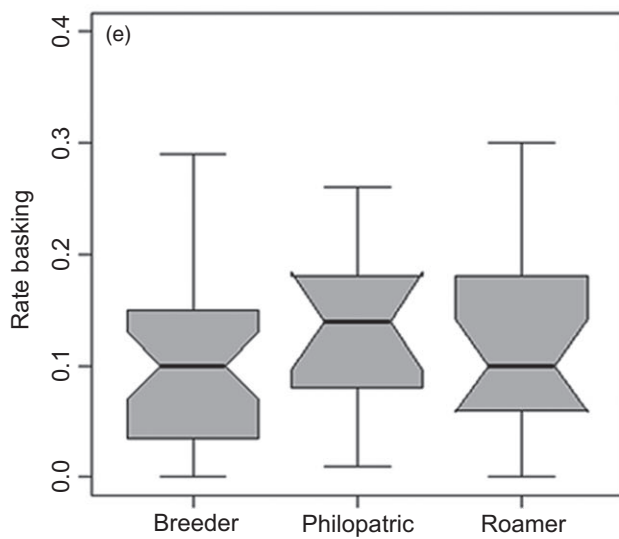
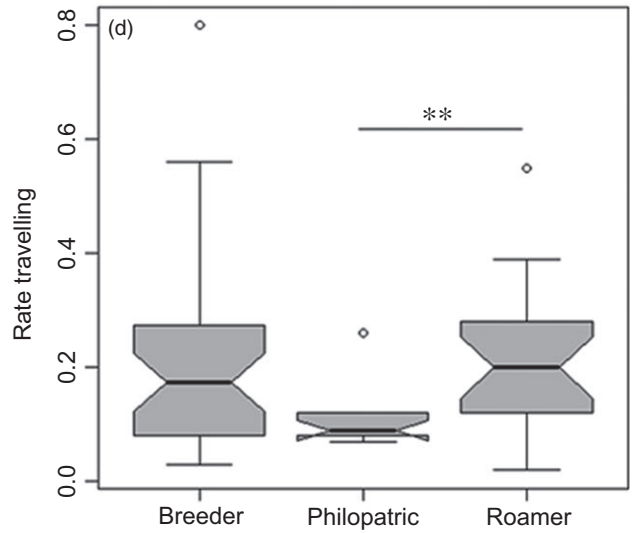
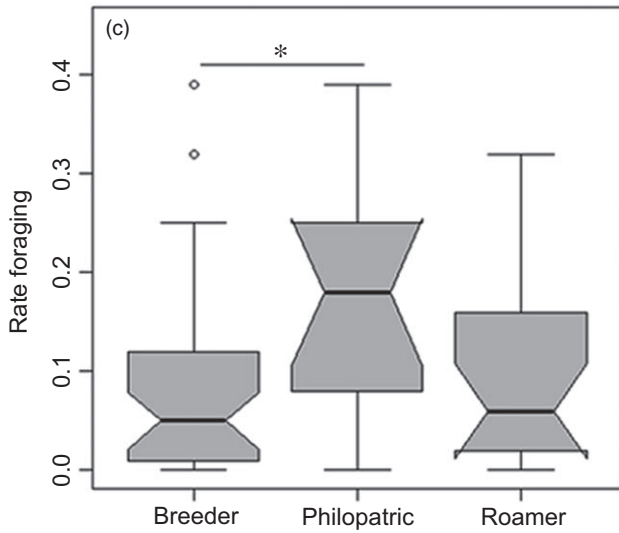
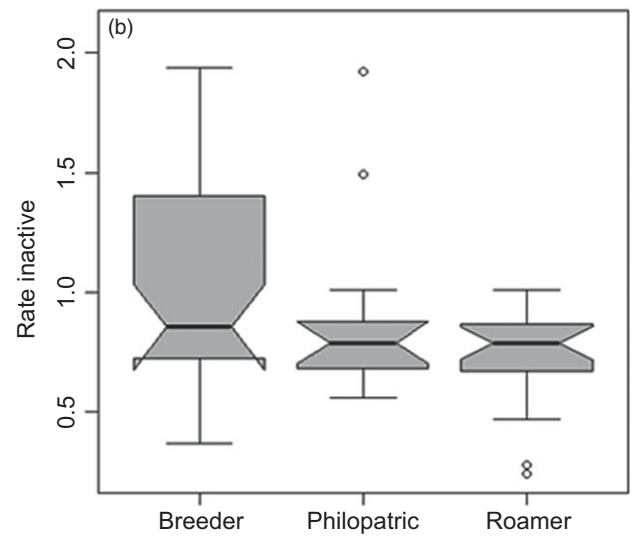
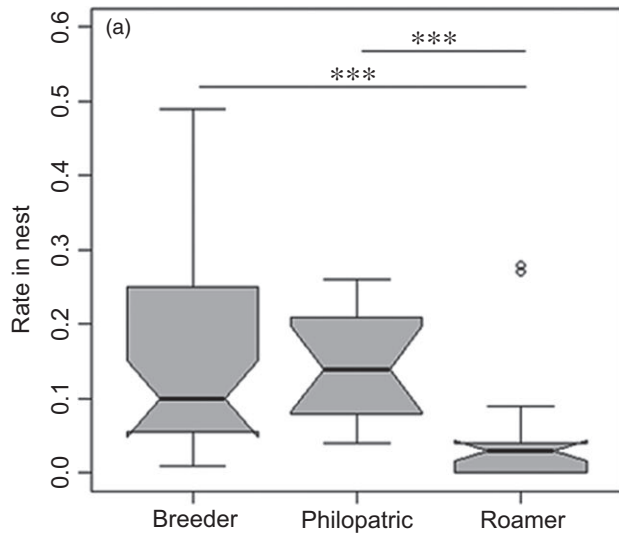
## Discussion

We found that activity budgets differed between male striped mice following ARTs. Roamers and breeders allocated time in behaviours which increase mating possibilities, and breeders additionally into territory defence. Philopatrics allocated time to foraging, indicating that they invested in gaining body mass, which would increase their chance to switch to a tactic with a higher reproductive success. Thus, philopatrics showed a risk avoiding tactic and might have invested in allo-parental care. Our study suggests that during the breeding season males display adaptive alternative activity budgets corresponding to their prevailing tactic.

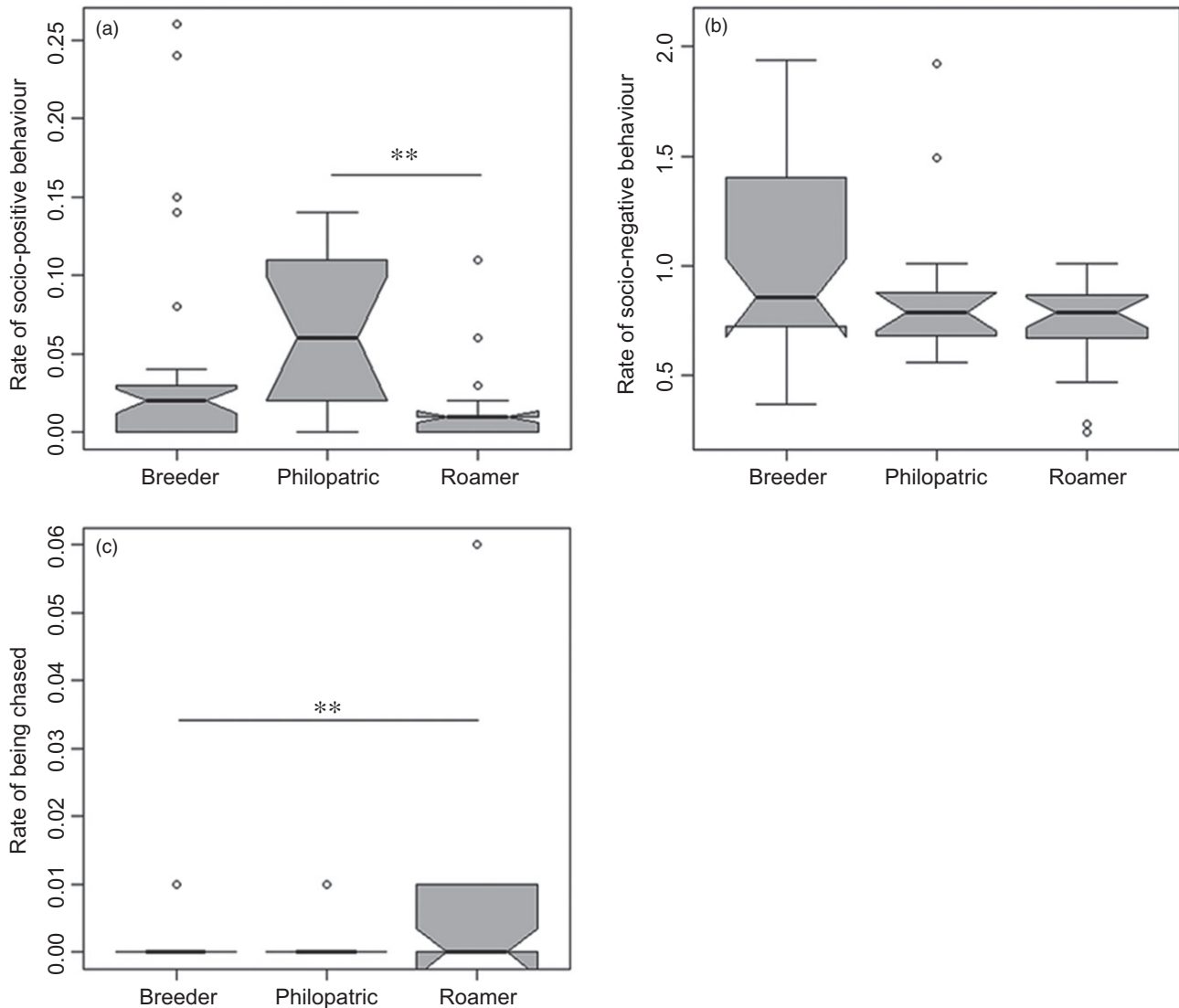
Overall, breeders and roamers showed similar activity budgets. They travelled similar distances, had similar-sized daily ranges, and did not differ concerning rates of resting, foraging, basking and time inactive. These similarities likely reflect territory patrolling by breeders and searching for receptive females in roamers during the breeding season. However, there were three marked differences between breeders and roamers. First, as predicted, breeders spent more time in their nest than roamers. Due to the lack of data on behaviour inside the nest, we could not tell why breeders returned to their nest. They might have been providing paternal care to their pups, which improves offspring growth (Schradin & Pillay, 2005), and thereby increase their fitness. Alternatively, group-living males (i.e., breeders and philopatrics) may return to the safety of their nest to rest, whereas solitary roamers did not seem to prefer their nest to other shrubs. Second, although the three tactics showed similar rates of socio-negative behaviour, roamers were chased more often than breeders, indicating that searching for receptive females increased the likelihood of encountering territory holders and philopatrics, which defend the territory against intruders (Schradin, 2004). Similarly to roaming striped mice, prospecting male meerkats receive much aggression from males following a bourgeois tactic (Mares *et al.*, 2012). Third, breeders were older and heavier than roamers, but did not differ with regard to body mass changes. The lack of body mass increases by roamers may partly explain why only one quarter

switched to the breeder tactic. Although the bourgeois tactic has the highest reproductive success, being heavy alone does not increase fitness because females do not seem to prefer mating with heavy males (Schradin & Lindholm, 2011). In contrast to our expectations, breeders did not show more socio-positive behaviour than roamers. This may be due to the fact that during the breeding season, breeders typically leave the nest earlier than other group members to patrol their territory. Most of the observable social behaviour between group members occurs at the nest during basking in the mornings and evenings (Schradin & Pillay, 2004), and thus, breeders may miss the opportunity of interacting with group members during basking at the nest. However, breeders spent more time in their nest than roamers, potentially engaging in social interactions with other group members. Breeders had lower foraging rates than philopatrics. The heavier body mass of breeders may be essential in enabling them to make a trade-off between energy intake and expenditure due to relatively lower energy requirements of body maintenance when compared to body mass gain. Continuously increasing body mass would induce costs in breeders, such as reduced ability to flee from predators (Lima, 1986; Houston, McNamara & Hutchinson, 1993), which could explain why they did not invest in further increasing body mass. In summary, during the breeding season breeders allocated their time in a manner that increases mating possibilities, aids territory defence and potentially paternal care.

Similar to breeders, philopatrics spent more time in their nest than roamers, which may indicate that they provided allo-parental care for pups (Raynaud & Schradin, 2014), which can result in inclusive fitness benefits for helpers (Jennions & Macdonald, 1994). Philopatrics can benefit from remaining in their natal group through access to the food resources present in that territory (Schradin, 2004). Remaining in a familiar territory may enable them to quickly gain body mass to switch tactic. In support of this hypothesis, our results show that philopatrics allocated more time to foraging than breeders and significantly increased their body mass. Philopatrics also had the smallest daily ranges and travelled short distances, avoiding risks associated with long-distance travel. Similar results have been



**Figure 1** Activity budgets of breeders, philopatrics and roamers. Panels show rates of behaviours (number of events divided by 360 min of focal observation): (a) in nest, (b) total inactive, (c) foraging, (d) travelling, (e) basking and (f) autogrooming [black lines indicate the median, notches show the confidence intervals, whiskers show minimum and maximum values of non-outlier data (data inside 1.5 times the interquartile range above the upper quartile and below the lower quartile), and open circles show outliers]. Significant differences between tactics are illustrated ( $*P \leq 0.05$ ;  $**P \leq 0.01$ ,  $***P \leq 0.001$ ).

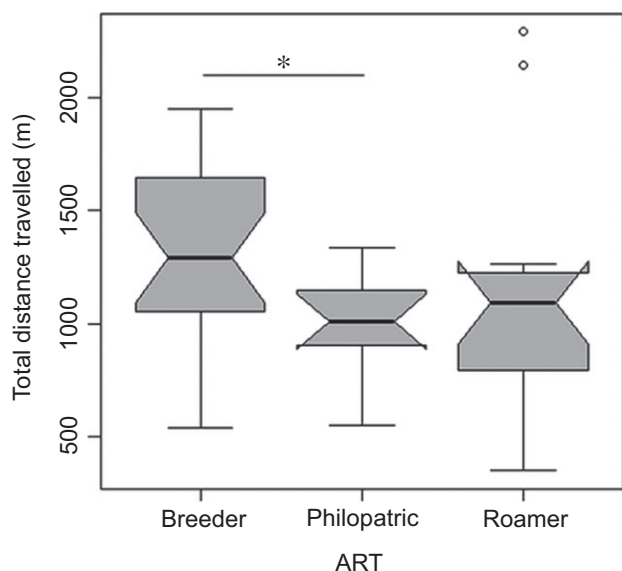


**Figure 2** Social behaviour of breeders, philopatrics and roamers. Panels show rates of behaviours (number of events divided by 360 min of focal observation): (a) socio-positive behaviour, (b) socio-negative and (c) being chased [black lines indicate the median, notches show the confidence intervals, whiskers show minimum and maximum values of non-outlier data (data inside 1.5 times the interquartile range above the upper quartile and below the lower quartile), and open circles show outliers]. Significant differences between tactics are illustrated ( $*P \leq 0.05$ ;  $**P \leq 0.01$ ,  $***P \leq 0.001$ ).

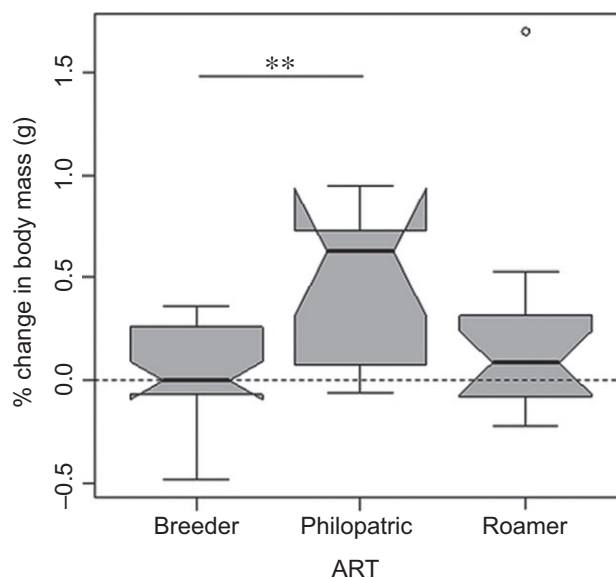
**Table 5** Median (1st–3rd quartile) body mass (in g) at the time of the focal observation (initial  $M_b$ ) and 4 weeks later (final  $M_b$ ) and daily range sizes (95% and 99% kernel contour sizes) of individuals following alternative reproductive tactics

Tactic	Initial $M_b$	Final $M_b$	95% kernel size	99% kernel size
Breeder	58.0 (53.5–62.1)	58.2 (55.0–61.5)	0.20 (0.16–0.35)	0.28 (0.22–0.45)
Philopatric	31.0 (30.0–36.4)	38.0 (37.0–43.0)	0.14 (0.10–0.17)	0.19 (0.14–0.25)
Roamer	53.1 (50.1–58.0)	56.2 (51.2–59.8)	0.26 (0.12–0.51)	0.35 (0.22–0.70)

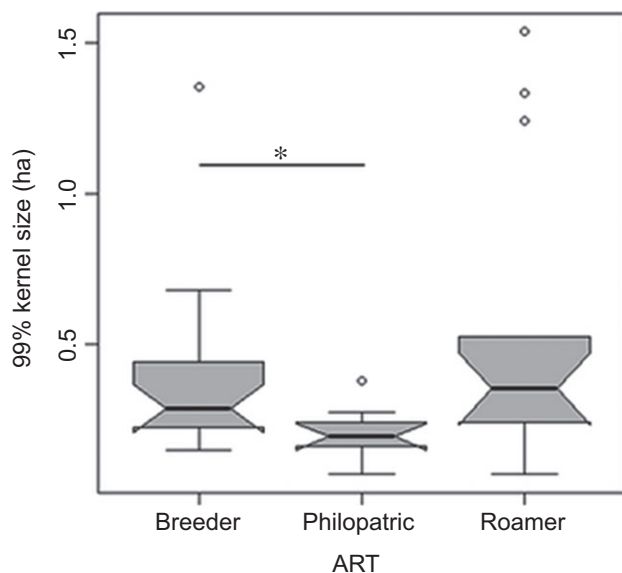
For significant differences see Table 4.



**Figure 3** Distance travelled (m) by breeders, philopatrics and roamers (black lines indicate the median, notches show the confidence intervals, whiskers show minimum and maximum values of non-outlier data (data inside 1.5 times the interquartile range above the upper quartile and below the lower quartile), and open circles show outliers). Significant differences between tactics are illustrated (\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ).



**Figure 5** Percentage body mass change per day of breeders, philopatrics and roamers [black lines indicate the median, notches show the confidence intervals, whiskers show minimum and maximum values of non-outlier data (data inside 1.5 times the interquartile range above the upper quartile and below the lower quartile), and open circles show outliers]. The dashed line indicates 0% change in body mass. Significant differences between tactics are illustrated (\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ).



**Figure 4** Daily range size (99% kernels, in ha) of breeders, philopatrics and roamers [black lines indicate the median, notches show the confidence intervals, whiskers show minimum and maximum values of non-outlier data (data inside 1.5 times the interquartile range above the upper quartile and below the lower quartile), and open circles show outliers]. Significant differences between tactics are illustrated (\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ).

reported for two ground squirrel species (Scantlebury, Waterman & Bennett, 2008; Vasilieva *et al.*, 2014). Our results suggest that philopatric striped mice follow an energy saving tactic, which enabled them to gain body mass, which would allow them to sooner change to a tactic of higher reproductive success (Schradin *et al.*, 2009; Schradin & Lindholm, 2011). Likewise, in yellow ground squirrels *Spermophilus fulvus* yearling males follow a passive tactic, which enables them to continue growing (Vasilieva *et al.*, 2014). Basking behaviour did not differ between ARTs, indicating that basking is a similar important energy saving mechanism for all three ARTs (Schradin *et al.*, 2007; Scantlebury *et al.*, 2010) during the breeding season, when ambient temperatures are low. Similarly, sun-basking to reduce the energetic cost of thermoregulation has been described in many other small mammals (Schwaibold & Pillay, 2006; Brown & Downs, 2007). Philopatrics showed more socio-positive behaviour than roamers. A high level of socio-positive behaviour may further help to prolong their stay at the natal nest, which can increase their survival probability (Komdeur, 1992; Taborsky & Grantner, 1998). Philopatric striped mice have higher corticosterone levels than males of the two other tactics (Schradin *et al.*, 2009), which may explain the high rates of autogrooming compared to roamers and breeders. Many animals increase self-directed behaviour (i.e. autogrooming) when experiencing physiological stress (Honest & Marin, 2006). In addition, elevated corticosterone levels can decrease immune function (Charbonnel *et al.*, 2008), making individuals more susceptible to (ecto-)parasites, which



may be removed through autogrooming. However, future studies need to determine whether males following ARTs differ in parasite load. Overall, during the breeding season philopatrics allocated their time in a manner that promotes survival and body mass gain, while avoiding risks that could compromise survival.

While a previous study found that roamers have larger home ranges than males of the other tactics (Schradin *et al.*, 2009), we had no information about how they were using their home ranges. In accordance with our predictions, roamers travelled more than philopatrics. Surprisingly, however, they did not travel longer distances and although the median daily range sizes of roamers were the largest, differences between roamers and the other tactics did not reach significance. This indicates that roamers are effective in covering large areas without increasing the travel distance, which should facilitate searching and encountering receptive females, with which they can mate even though they have a lower body mass compared to breeders (Schradin & Lindholm, 2011). In summary, roamers, similar to breeders, allocated their time in a manner that increases their mating success.

Our study contributes to the understanding of the movement ecology of male small mammals. Philopatrics allocated their time in a manner that directs energy towards survival and body mass gain, by allocating time towards foraging, and less towards travelling. Thereby philopatrics likely increase their survival probability and will be able to switch tactic once they have reached the requisite body mass. In contrast, roamers and breeders allocated their time towards activities related to reproduction. Therefore, following a specific ART is associated with specific activity budgets in male striped mice during the breeding season. It is known that ARTs differ considerably in their physiology (hormone profile and metabolic rate: Scantlebury *et al.*, 2006b; Schradin *et al.*, 2009; Young & Monfort, 2009), and future studies should investigate whether these physiological differences are causes or effects of the behavioural differences described here. We encourage studies of activity budgets and movement ecology in other species with ARTs, including species with female ARTs, to come to a more comprehensive understanding of the alternative costs and benefits as well as trade-offs to which alternative tactics are exposed.

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