



Young But Not Old Adult African Striped Mice Reduce Their Activity in the Dry Season When Food Availability is Low

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Received: April 18, 2016

Initial acceptance: June 3, 2016

Final acceptance: July 27, 2016

(L. Fusani)

doi: 10.1111/eth.12527

Keywords: time allocation, activity patterns, energy expenditure, maturation

Abstract

An individual's survival and fitness depend on its ability to effectively allocate its time between competing behaviors. Sex, social tactic, season and food availability are important factors influencing activity budgets. However, few field studies have tested their influences. The African striped mouse (*Rhabdomys pumilio*) lives in highly seasonal habitats in southern Africa, and individuals can adopt different social tactics. We investigated seasonal changes in activity budgets of different tactics and predicted that individuals will reduce their activity in the non-breeding season to save energy when food availability is low and that young non-breeding adults ('philopatrics') invest mainly in activities related to gaining body mass to increase survival probability. We predicted old adults ('breeders'), which bred during the previous breeding season, to invest mainly in maintenance of their social status. We conducted 90 focal observations during the non-breeding season and 73 during the breeding season. Activity budgets of striped mice were season and tactic specific, with philopatrics, but not breeders, reducing activity when food availability was low, possibly to decrease energy expenditure. Philopatrics of both sexes foraged and basked more in the breeding season than during the non-breeding season. Male philopatrics gained body mass and female philopatrics maintained their body mass in both seasons. Sex-specific differences occurred during the breeding season, when female breeders foraged more than male breeders, while male breeders chased other individuals more than female breeders. These findings indicate that individuals adopting different social tactics display distinct behaviors to fulfill tactic-specific energetic needs.

Introduction

Individuals allocate time to different behaviors, such as foraging, traveling and mating (Krebs & McCleery 1984), to meet their nutritional needs and to reproduce. But they face a trade-off between competing activities to avoid predation risk (Kotler et al. 1991) and hypo- or hyperthermia (Melcher et al. 1990; Kenagy et al. 2002). How individuals divide their time between different behaviors, also termed 'activity budget', is predicted to vary over time, depending on weather conditions and food availability (Cotton & Parker 2000; Kenagy et al.

2002; Schwaibold & Pillay 2006). Activity budgets also vary between the sexes, age classes and individuals in different reproductive states (Behrends et al. 1986; Loughry 1993; Ruckstuhl & Neuhaus 2002; Ebensperger & Hurtado 2005). Sex differences can arise from different energy requirements due to sexual dimorphism in body size (Ruckstuhl & Neuhaus 2002), different energetic investment into reproduction (Behrends et al. 1986; Kenagy et al. 1989; Loughry 1993), and/or they may be due to differences in parental investment, including sex-specific behavioral tactics to achieve reproductive success (for example mate searching in males vs. foraging in

females; Trivers 1972). High energetic demands of reproduction (Gittleman & Thompson 1988) can force females to increase foraging time (Clutton-Brock et al. 1982; Pépin et al. 1991), while males may reduce foraging time to instead search and guard females (Komers 1994; Girard-Buttoz et al. 2014).

Energy-demanding periods, such as growth and maturation, further affect individual activity budgets. Individuals in different developmental stages (e.g., unweaned, juvenile or adult) or following different social tactics (e.g., non-breeding philopatric or breeder) have different energetic requirements (Kenagy et al. 1989; Scantlebury et al. 2008). Accordingly, distinct energetic requirements should result in discrete activity budgets (Robinson 1986; Melcher et al. 1990; Scantlebury et al. 2008). Young individuals, for example, often spend more time foraging than adults to sustain somatic growth (Robinson 1986; Shi et al. 2003). While much is known about behavioral tactics of helpers regarding helping (Reyer 1980; Goldizen 1987; Taborsky & Grantner 1998), only few studies directly compare activity budgets of individuals following different social tactics (but see: Dammann et al. 2011; Schielke et al. 2012).

The African striped mouse (*Rhabdomys pumilio*) exhibits different social tactics, thus providing the possibility to study tactic-specific differences in activity budgets. Striped mice are small, diurnal, murid rodents that inhabit the semi-arid Succulent Karoo in southwestern Africa, an environment with pronounced seasonal changes food and water availability (Schradin & Pillay 2006). Inhabiting this seasonal habitat makes striped mice a good model species for examining seasonal changes in their activity budget. It is the only mouse species that has been observed for several hours directly in the field (Schradin 2006). As most mammals are rodents and mouse like and are often dominant models in biomedical research, it is important to obtain more information about their natural behavior. Striped mice live in extended family groups with one breeding male, several breeding females and philopatric adult non-breeding offspring of both sexes (Schradin & Pillay 2004). They breed in spring, which coincides with high levels of food availability (Schradin & Pillay 2005, 2006). Offspring typically reach adulthood in the same breeding season (Schradin & Pillay 2004) and then have to survive the following hot dry season in summer with reduced food availability (Schradin & Pillay 2005), before they can reproduce in the next spring.

The aim of this study was to compare the activity budgets of free-living striped mice between the breeding and non-breeding season. More specifically, we

aimed to assess how activity budgets differ between (i) social tactics (breeder vs. philopatric) and (ii) the sexes in both (iii) seasons (breeding vs. non-breeding). (i) Social tactic. Because philopatrics have to survive the non-breeding season to breed in the subsequent breeding season, we expected them to invest in survival and somatic growth. Consequently, we predicted that they would spend more time basking and foraging, and less time traveling compared with breeders. We also expected philopatrics to increase body mass in the breeding season and to maintain body mass in the dry season, indicating that their activity budgets were adapted to enable somatic growth. (ii) Sex. As gestation and lactation impose high energetic requirements on females, we predicted breeding females to spend more time foraging than breeding males during the breeding season. We did not expect sex differences during the non-breeding season because energy requirements would be similar for both sexes. (iii) Season. Because food availability is low in the non-breeding season (Schradin & Pillay 2006), we predicted that striped mice reduce activity levels compared with the breeding season to reduce energy expenditure. For the same reason, we expected sun-basking to increase during the non-breeding season, as passively heating up through basking can reduce energy expenditure (Scantlebury et al. 2010). As striped mice show biparental care and philopatrics are helpers at the nest (Schradin & Pillay 2003, 2004), we expected individuals to spend more time in the nest during the breeding season than during the non-breeding season. During the breeding season, courtship and mating occur and group sizes increase (Schradin & Pillay 2005), all of which may lead to an increase in the occurrence of social interactions. Thus, we expected individuals to show more sociopositive behavior with group members during the breeding season than during the non-breeding season. During the breeding season, breeding males patrol their territories (Schradin 2006), and philopatrics of both sexes and breeding females also participate in territorial defense by chasing away intruders (Schradin 2004; Schradin & Pillay 2004). Thus, we expected individuals to show more chasing behavior during the breeding season than during the non-breeding season.

Material and Methods

Study Site and Animals

We collected data during the breeding season (Aug.–Nov.) of 2003, 2008, 2009, 2010, 2011 and 2013 and

during the non-breeding season (Jan.–June) of 2009, 2010, 2011 and 2012 at the Succulent Karoo Research Station in Goegap Nature Reserve (S 41.56, E 1.60, elevation 950 m). In the Succulent Karoo, a semi-arid region in southwestern Namibia and the Northern Cape Province of South Africa, temperatures vary from below zero to 25°C during winter and spring (breeding season), and from 5 to 40°C during summer (non-breeding season; Schradin & Pillay 2004; Scantlebury et al. 2006). The region experiences winter rainfall, with an average annual rainfall of 190 mm at our field site (C. Schradin, unpublished data). The breeding season typically lasts 3–4 months, in which females can give birth to 2–3 l (Pillay 2000), at an average of 5 pups per litter (Schradin & Pillay 2005).

Trapping, Marking and Radio-Tracking of Striped Mice

We trapped striped mice using Sherman-style live-traps (26 × 9 × 9 cm) baited with wheat bran flakes, raisins, sea salt and sunflower oil. We placed traps close to a group's nest in the morning and the late afternoon and checked them 30–45 min later. We weighed captured individuals using an electronic scale and recorded their reproductive state (males: whether they were scrotal; females: whether nipples were visible and/ or their vagina was perforate). For individual recognition, we marked mice permanently with ear tags (National Band and Tag Co., Newport, KY, USA) and temporarily with hair dye (Rapido, Pinetown, South Africa). To locate individuals during behavioral observations, we equipped them with radiocollars (Holohil, Canada). Radiocollars weighted 2.5–3.5 g, which represented <10% of the body mass. A previous study demonstrated that neither the behavior nor corticosterone levels of striped mice are affected when individuals carry radiocollars (Schradin 2008).

Determination of Social Tactic

Male striped mice are the dispersing sex, while females show a higher level of natal philopatry (Solmsen et al. 2011). We determined male breeders as scrotal males that live in groups which are not their natal group. Female breeders were identified at the first time their vagina was perforate (Schradin & Pillay 2006). Philopatrics were individuals that were trapped as juveniles (body mass <25 g) in a group and still trapped there as non-breeding adults. In this study, we refer to philopatric adult non-breeding offspring as 'philopatrics' and to individuals which have already bred as 'breeders'. We use these terms during the

breeding season as well as during the non-breeding season to prevent confusion over the term 'adult' because individuals belonging to both tactics were adults (Schradin & Pillay 2004).

Behavioral Observations

Striped mice at our field site are well habituated to the presence of observers, due to the continuous monitoring of the population. They are diurnal and occupy an open habitat, which facilitates direct observations (Schradin et al. 2012). We performed 3-h behavioral observations during the main activity periods, mornings (between 6:00 and 9:00) and afternoons (14:30 and 17:00), but not during the hottest times of the day when they are usually inactive (Schradin 2006). We used radiotracking to follow a focal mouse and to determine its position when it was not visible. In such a case, we located individuals every 3 min to confirm their position. We followed individuals at a distance of 5–10 m and recorded their behavior directly or by using 10 × 25 binoculars (Schradin 2006). Every minute, we recorded the behaviors (Table S1) of the focal mouse during the previous minute. We used 1/0 sampling (recording presence/ absence of behaviors shown within a 1-min interval), which has been shown to correlate with percent of observation time and hourly rate of a specific behavior (Leger 1977). Using this sampling method allowed for the recording of more than one behavior for every minute of focal sampling. For social behaviors, we attempted to determine the identity of the non-focal mouse, but in many cases this was not possible, and thus, sex and tactic of the interacting partner were not considered in the analyses.

We conducted a total of 326 focal observations each lasting 3 h, equally divided into mornings and afternoons. The morning and afternoon focal observations on one individual were typically conducted within 24 h of each other (median 0 days, 1st–3rd quartile: 0–1 day). To examine daily activity budgets, we combined the morning and afternoon observations per individual, and hence, our data collection resulted in a total of 163 6-h focal observations (a total of 978 h; Table 1). We conducted observations on a total of 145 different individuals (of which 18 were observed twice: five male breeders, four female breeders, two female philopatrics and four male philopatrics were observed in a breeding and a non-breeding season; 2 males and 1 female were observed first as philopatrics and again as breeders).

All focal observations of philopatrics during the breeding season were conducted in the season in

Table 1: Number of focal observations with corresponding numbers of body mass measurements and travel distances of individual striped mice following different social tactics during the breeding season and non-breeding season (body mass measurements and travel distances were taken from focal observation individuals).

	Breeding season			Non-breeding season		
	Focal observations	Body mass measurements	Travel distance	Focal observations	Body mass measurements	Travel distance
Female breeder	19	13	15	12	11	8
Female philopatric	5	4	5	23	19	19
Male breeder	36	29	23	22	18	14
Male philopatric	13	13	10	33	26	22

which they were born (i.e., during the first 3–4 months after birth), and observations of philopatrics recorded during the non-breeding season were conducted during their first non-breeding season. To monitor body mass changes of individuals, we recorded body mass of 59 individuals during the breeding season and of 74 individuals during the non-breeding season (Table 1), once around the day of the focal observation (median 0 days, 1st–3rd quartile: –4 to 3.5 days) and again 4 weeks later (median 31 days, 1st–3rd quartile: 27–35 days; Table 2). To account for variation in days between measurements, we calculated the percentage change of body mass per day between both measurements.

For the data analyses, we converted all behaviors into percentages of all events recorded during a focal observation (i.e., 6 h of observation). We also calculated rates of behaviors (number of events divided by 360 min of focal observation), which gave comparable results (for results see Tables S4 and S5). To examine whether social tactics differed in the overall time they spent inactive, we pooled resting, time in nest and in shrub into a fourth category “total inactive”. Social behavior occurred infrequently, and we divided it into two categories (Table S1), sociopositive (proximity, close proximity, sniffing, body contact, grooming, mating) and socionegative (chasing, being chased, fighting, biting). We analyzed chasing and being chased separately. Fighting and biting occurred very rarely and were thus excluded from the analyses.

Table 2: Mean \pm SD body mass (in g) at the time of the focal observation (initial M_b) and 4 weeks later (final M_b) of individuals following different social tactics during the breeding and non-breeding season.

Social tactic	Breeding season		Non-breeding season	
	Initial M_b	Final M_b	Initial M_b	Final M_b
Female breeder	48.8 \pm 9.7	57.9 \pm 9.7	46.5 \pm 5.0	46.8 \pm 5.4
Female philopatric	34 \pm 2.8	38.5 \pm 5.0	35.7 \pm 4.0	37.2 \pm 5.0
Male breeder	58.5 \pm 6.2	58.9 \pm 5.3	57.8 \pm 6.2	58.6 \pm 5.4
Male philopatric	33.5 \pm 4.5	40.2 \pm 6.1	42.5 \pm 7.1	45.3 \pm 8.4

Travel Distance

During 116 behavioral observations (6 h per individual), a GPS (Garmin etrex) was mounted on the belt of the observer, automatically recording a track. We recorded 53 tracks during the breeding season and 63 during the non-breeding season (Table 1). We turned the track function on simultaneously with the start of the focal observation and turned it off when we terminated it. As the observer followed the focal individual at a distance of 5–10 m, this track provided a proxy of the distance traveled by the focal mouse.

Ethical Note

All applicable institutional and/or national guidelines for the care and use of animals were followed, and all methods complied with the ABS/ASAB guidelines for ethical treatment of animals. Animals were captured and handled following the protocol approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2007/40/01).

Statistical Analyses

All behavioral variables differed significantly from normality (Shapiro–Wilk W-test, all $p < 0.001$). Thus, we fitted GLMs with a poisson distribution using the ‘glm’ function from the lme4 R-package (Bates & Maechler 2010). We controlled for overdispersion of the data (dispersion parameters: 4.39–15.02) by fitting one negative binomial model (‘glm.nb’ function in MASS package (Venables & Ripley 2002)) per behavioral category. To examine whether sex, tactic and season influenced body mass changes, we used a LMM (Baayen 2010) with a Gaussian error distribution. We used individual ID as a random factor in the LMM. In all models, we used sex, tactic and season as fixed factors and included interactions between season and sex, tactic and season, and tactic and sex. To

select the best model, we then used a stepwise backward method (Zuur et al. 2009) using the 'step' function. We verified all models by inspecting Q-Q plots, by plotting model residuals against fitted values, and we checked variance inflation factors (Zuur et al. 2009, 2010) using the function 'vif' in the car package (Fox & Weisberg 2011).

For significant factors of the minimal adequate model, we examined seasonal differences in behavioral categories, total distance traveled and changes in body mass within social tactics using pairwise Wilcoxon rank sum tests *post hoc*. We used paired t-tests to examine within-season body mass changes of individuals and tested for between-tactic differences in behavioral categories and differences in body mass changes within the same season using 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). We conducted all statistical tests in R2.15.1 (R Development Core Team 2012).

Results

The results of the models examining whether sex, season, and social tactic influence activity budgets of striped mice showed that they display seasonal differences concerning traveling time, time spent in a shrub, being chased by other mice, and changes in body mass (Table 3). Sex was a significant predictor of the time individuals spent in the nest, resting, in a shrub, chasing other mice, and changes in body mass (Table 3). Social tactic was a significant predictor of body mass changes in striped mice (Table 3). The interaction between tactic and season was a significant predictor for the behavioral categories time spent in nest, total inactive, resting, foraging, basking, sociopositive behavior, and total distance traveled, and the interaction between tactic and sex was a significant predictor for the behavioral category foraging (Table 3).

Seasonal Differences within Tactics

Philopatrics of both sexes spent more time foraging (Fig. 1a) and basking (Fig. 1c) during the breeding season, and more time inactive during the non-breeding season (Fig. 1d, Table S2). Philopatrics of both sexes and breeding males traveled more during the breeding season (Fig. 1b, Table S2). Male philopatrics spent more time in a shrub during the non-breeding season (Table S2). Female philopatrics rested in the shade more during the breeding season than the non-breeding season (Table S1). Philopatrics of both sexes were involved in more sociopositive behaviors during

the breeding season, whereas the opposite was true for male breeders (Fig. 2c, Table S2). During the breeding season, breeders and philopatrics of both sexes traveled similar distances, but distances traveled by philopatrics of both sexes were significantly shorter during the non-breeding season (Fig. 3, Tables S2 and S3). Breeders of both sexes did not show seasonal differences in the time they spent foraging (Fig. 1a), basking (Fig. 1c), and inactive (Fig. 1d). Breeders of both sexes and male philopatrics did not show seasonal differences in the time they rested (Table S1). None of the social tactics showed seasonal differences in the time they spent in the nest, chasing other mice, or were chased by other mice (Fig. 2a+b, Table S2).

In the breeding season, philopatric males ($t = -4.66$, $df = 12$, $p = 0.0005$) and female breeders ($t = -2.61$, $df = 12$, $p = 0.022$) significantly increased their body mass, while female philopatrics ($t = -2.19$, $df = 3$, $p = 0.11$) and male breeders ($t = -0.52$, $df = 28$, $p = 0.60$) did not change their body mass (Table 2, Fig. 4). Only philopatric males ($t = -2.75$, $df = 25$, $p = 0.01$) significantly increased their body mass in the non-breeding season (female breeders: $t = -0.21$, $df = 10$, $p = 0.83$; male breeders: $t = -0.67$, $df = 17$, $p = 0.50$; female philopatrics: $t = -1.36$, $df = 18$, $p = 0.18$; Table 2, Fig. 4). Male philopatrics gained significantly more body mass during the breeding season than during the non-breeding season, but breeders of both sexes and philopatric females showed no seasonal differences (Table 2, Fig. 4, Table S2).

Differences Between Tactics During the Breeding Season

Female breeders and male philopatrics foraged more than male breeders (Fig. 1a, Table S3a). Female philopatrics basked more than female breeders (Fig. 1c, Table S3a). Females spent more time in the nest than males of the same tactic (Table S3a). Male breeders chased other individuals more often than female breeders and male philopatrics (Fig. 2a, Table S3a). Philopatrics of both sexes showed more sociopositive behaviors than breeders of the same sex (Fig. 2c, Table S3a). Male breeders traveled larger distances than male philopatrics (Fig. 3, Table S3a). Male philopatrics gained more body mass than male breeders (Table 2, Fig. 4, Table S3a). There were no sex differences between breeders or philopatrics concerning sociopositive behavior (Fig. 2c, Table S3a). There were no differences between individuals of both tactics and sexes concerning traveling time, time spent inactive, in a shrub, resting in the shade, and being

Table 3: Results of negative binomial models and a linear mixed model (for body mass changes) to assess whether sex, social tactic and season influenced how striped mice allocated their time to different behavioral categories and their changes in body mass. Variables that significantly influenced a behavioral category appear in bold.

Behavioral category	Estimate	SE	z value	p
Forage				
Intercept	2.1434	0.2323	9.226	<0.001
Tactic	0.2832	0.4217	0.672	0.5018
Season	0.4287	0.2541	1.688	0.0915
Sex	-0.3060	0.2594	-1.180	0.2381
Tactic*season	-1.4974	0.4174	-3.588	0.0003
Tactic*sex	0.7738	0.3905	1.981	0.0475
Travel				
Intercept	3.4434	0.1889	18.228	<0.001
Tactic	-0.6342	0.3543	-1.790	0.0735
Season	-0.6486	0.2786	-2.328	0.0199
Tactic*season	-0.3282	0.4254	-0.772	0.4403
Bask				
Intercept	2.7321	0.1576	17.339	<0.001
Tactic	0.4877	0.3763	1.296	0.1949
Season	0.1361	0.2645	0.514	0.6069
Tactic*season	-1.5252	0.4478	-3.406	0.0006
Total inactive				
Intercept	8.4002	0.1279	65.652	<0.001
Tactic	-0.8754	0.2574	-3.401	0.0006
Season	-0.3688	0.2052	-1.798	0.0722
Tactic*season	2.0186	0.3332	6.059	<0.001
Nest				
Intercept	4.3932	0.3226	13.617	<0.001
Tactic	-0.0616	0.4334	-0.142	0.8869
Season	0.0607	0.3419	0.178	0.8589
Sex	-1.1601	0.3191	-3.636	0.0002
Tactic*season	1.8935	0.6025	3.142	0.0016
Rest				
Intercept	3.2828	0.4098	8.010	<0.001
Tactic	-2.1806	0.4954	-4.402	<0.001
Season	-1.9953	0.4542	-4.393	<0.001
Sex	0.4122	0.2010	2.051	0.0403
Tactic*season	1.6481	0.5605	2.940	0.003
Shrub				
Intercept	6.2210	0.2056	30.260	<0.001
Season	0.4853	0.2116	2.293	0.0218
Sex	0.6006	0.2161	2.779	0.0054
Sociopositive				
Intercept	1.7591	0.2604	6.755	<0.001
Tactic	0.5345	0.5147	1.038	0.2991
Season	0.9441	0.3374	2.798	0.0051
Sex	-0.1472	0.2992	-0.492	0.6227
Tactic*season	-1.7718	0.5467	-3.241	0.0011
Tactic*sex	0.2860	0.4109	0.696	0.4863
Chasing				
Intercept	0.2228	0.0898	2.482	0.0131
Tactic	-0.1342	0.1303	-1.030	0.3031
Sex	0.2384	0.1106	2.156	0.0311
Tactic*sex	-0.2259	0.1638	-1.379	0.1678

Table 3 (Continued)

Behavioral category	Estimate	SE	z value	p
Chased				
Intercept	0.3576	0.0582	6.112	<0.001
Season	-0.1593	0.07876	-2.024	0.043
Total distance traveled				
Intercept	33.944	1.798	18.882	<0.001
Tactic	-1.589	3.267	-0.486	0.6268
Season	-1.631	2.841	-0.574	0.5659
Tactic*season	-9.398	4.083	-2.302	0.0213
Body mass change				
Intercept	0.2630	0.0099	2.634	0.0074
Tactic	0.4316	0.1239	3.481	0.0006
Season	-0.3043	0.1432	-2.125	0.0346
Sex	-0.2380	0.1183	-2.012	0.0448
Tactic*season	-0.2449	0.1615	-1.516	0.1294
Season*sex	0.2624	0.1568	1.672	0.0920

chased by other individuals (Figs 1b+d and 2b, Table S3a).

Differences Between Tactics During the Non-breeding Season

Breeders of both sexes foraged (Fig. 1a), traveled (Fig. 1b), basked (Fig. 1c), rested in the shade, and showed more sociopositive behavior (Fig. 2c) than philopatrics of the same sex (Fig. 1a, Table S3b). They also traveled larger distances than philopatrics of the same sex (Fig. 3, Table S3b). Male philopatrics traveled more than female philopatrics (Fig. 1b, Table S3b). Philopatrics of both sexes spent more time inactive than breeders of the same sex, but neither breeders nor philopatrics showed sex differences (Fig. 1d, Table S3b). Male philopatrics spent more time in the nest than male breeders (Table S3b). Male breeders chased other individuals more often than male philopatrics (Fig. 2a, Table S3b). There were no differences between the tactics or sexes in the time they spent in a shrub, were chased by another individual (Fig. 2b), or concerning their body mass changes (Table 2, Fig. 4, Table S3b).

Discussion

Our results indicate that striped mice adaptively trade off the time they allocate to different activities. Both season and social tactic influenced how individuals allocated their time to different activities, and most sex differences appeared during the breeding season. Philopatrics of both sexes showed similar activity budgets, which enabled philopatric males to gain and

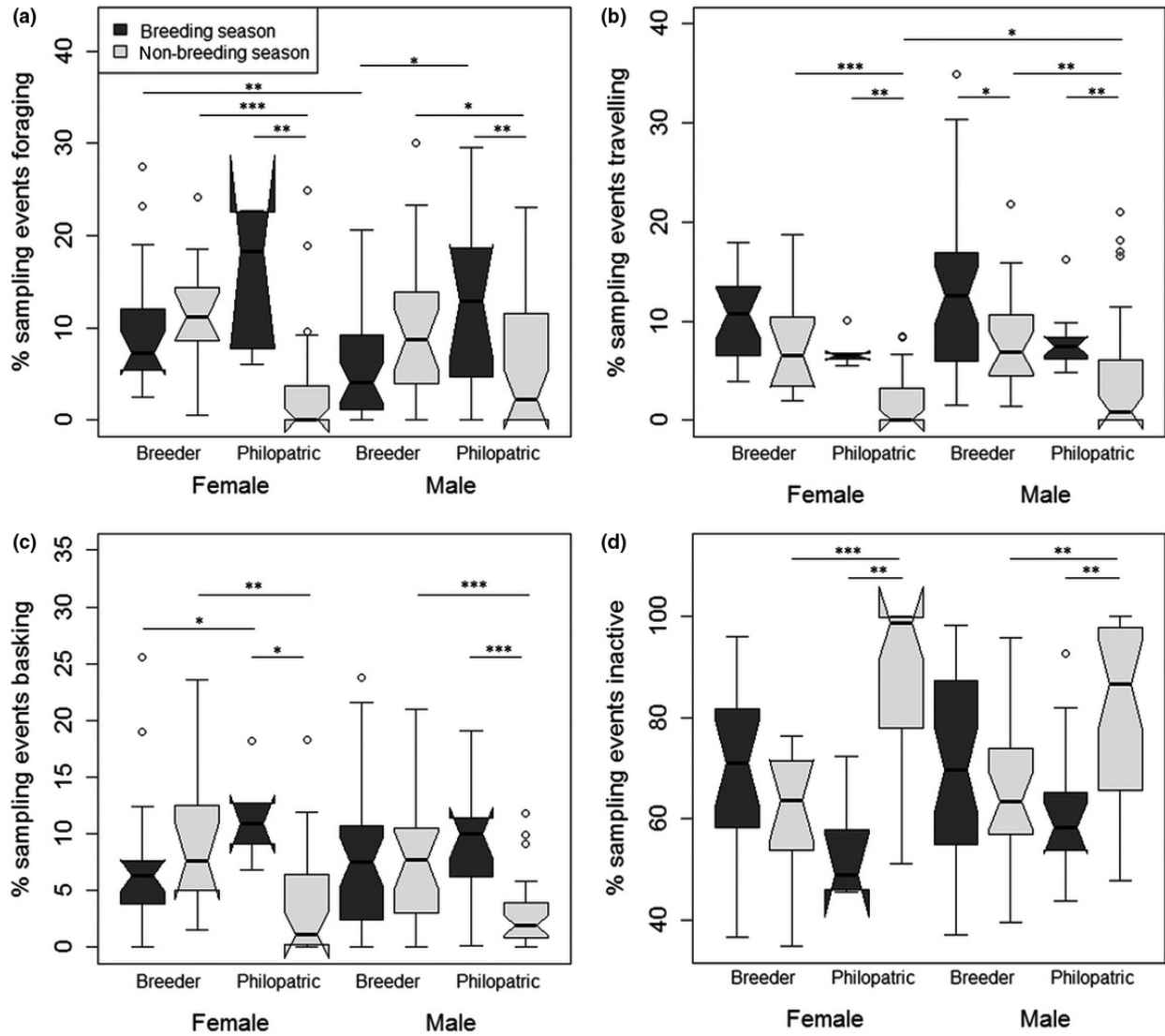


Fig. 1: Activity budgets of different striped mice social tactics (breeding female, philopatric female, breeding male, and philopatric male) during the breeding season (dark gray notches) and the non-breeding season (light gray notches). Panels show the percentage of all sampling events of a focal observation individuals allocated to (a) foraging, (b) traveling, (c) basking, and (d) total inactive (black lines indicate the median, notches confidence intervals, whiskers 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 within and between tactics are illustrated (* $p \leq 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$).

female philopatrics to maintain their body mass in both seasons. Breeders showed fewer seasonal adjustments than philopatrics, and overall, seasonal patterns contrasted between breeders and philopatrics. This study therefore reveals that striped mice display tactic-dependent activity budgets, and suggests that during the breeding season, activity patterns of breeders shift in a sex-specific way. In sum, individuals adopting different social tactics display distinct behaviors to fulfill tactic-specific energetic needs.

Seasonal Differences within Tactics

Philopatrics of both sexes displayed similar activity budgets and similar seasonal shifts, but contrasted with those of breeders (Fig. 5). Similarly, young prairie dogs (*Cynomys ludovicianus*) showed no sex differences in activity budgets (Loughry 1992). As predicted, philopatric mice showed a lower level of activity during the non-breeding season, most likely to reduce energy expenditure when food availability

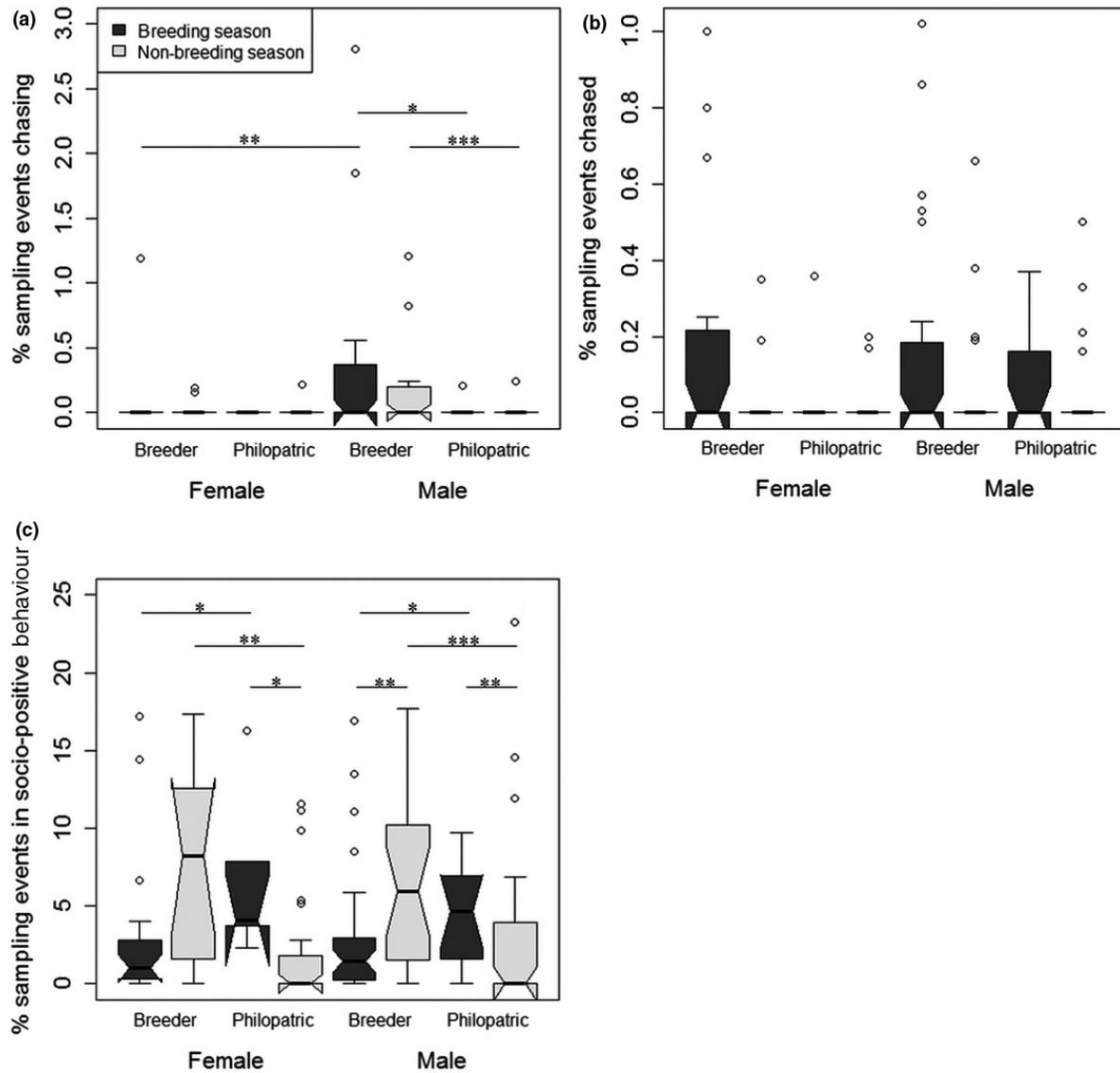


Fig. 2: Social behavior of different striped mice social tactics (breeding female, philopatric female, breeding male, and philopatric male) during the breeding season (dark gray notches) and the non-breeding season (light gray notches). Panels show the percentage of all sampling events of a focal observation individuals allocated to (a) chasing other individuals, (b) being chased by another individual, and (c) in sociopositive behavior (black lines indicate the median, notches confidence intervals, whiskers minimum and maximum values of non-outlier data, and open circles show outliers). Significant differences within and between tactics are illustrated (* $p \leq 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$).

is low. Reduction in activity in response to low resource availability has been previously reported in other mammals (Cornish & Mrosovsky 1965; Brinkmann et al. 2014). During the breeding season, philopatrics foraged more than during the non-breeding season, which was associated with an increase in body mass in males, but not females. However, this is likely a result of the small sample size for females ($N = 4$) as most females classified initially as philopatric showed signs of reproduction early in the season. Philopatrics

typically delay their first reproduction to the next spring (Schradin & Pillay 2004) and consequently have to survive the dry non-breeding season prior to the breeding season (Schradin & Pillay 2005). Investing in somatic growth is likely to improve survival probability and body condition when entering the breeding season. Body mass is especially important for males, as heavier males can adopt a reproductive tactic with greater fitness (Schradin & Lindholm 2011). Likewise, in ground squirrels (*Spermophilus saturatus*)

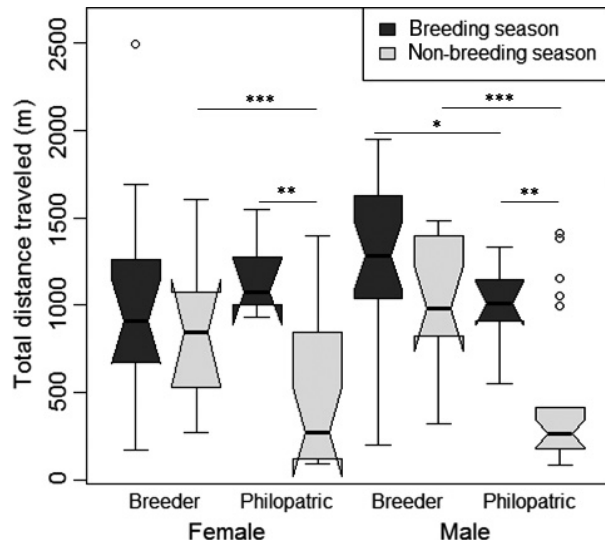


Fig. 3: Total distance traveled by striped mice following different social tactics (breeding female, philopatric female, breeding male, and philopatric male) during the breeding season (dark gray notches) and the non-breeding season (light gray notches; black lines indicate the median, notches confidence intervals, whiskers minimum and maximum values of non-outlier data, and open circles show outliers). Significant differences within and between tactics are illustrated (* $p \leq 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$).

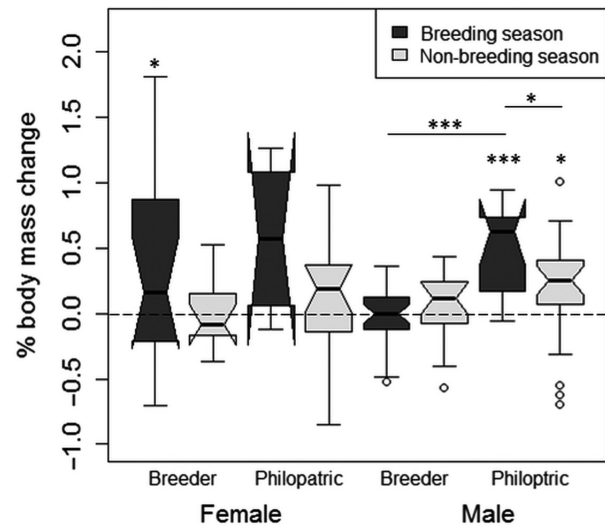


Fig. 4: Percentage change in body mass per day by striped mice following different tactics (breeding female, philopatric female, breeding male, and philopatric male) during the breeding season (dark gray notches) and the non-breeding season (light gray notches; black lines indicate the median, notches confidence intervals, whiskers minimum and maximum values of non-outlier data, and open circles show outliers). The dashed line indicates 0% body mass change. Significant differences within and between tactics are illustrated (* $p \leq 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$).

male yearlings allocated substantially more energy to somatic growth than older males, thereby increasing their condition for future reproduction (Kenagy et al. 1989).

During the breeding season, when ambient temperatures are low, philopatrics basked more than during the hot non-breeding season. Exploiting solar radiation to overcome nocturnal hypothermia and to reduce the energetic cost of thermoregulation has been described previously in striped mice (Schradin et al. 2007; Scantlebury et al. 2010) as well as in other small mammals (Geiser & Drury 2003; Schwabold & Pillay 2006; Brown & Downs 2007). Generally, many mammals increase basking time when ambient temperatures decrease (Rathbun & Rathbun 2006; Hanya et al. 2007; Warnecke et al. 2010). As predicted, philopatrics showed more sociopositive behavior during the breeding season, when group sizes were larger compared with the non-breeding season (Schradin & Pillay 2004, 2005). However, in contrast to our expectations, striped mice showed no seasonal differences concerning the time spent inside their nest. Nonetheless, during the breeding season, females of both tactics spent more time in the nest than males following the same tactic, possibly displaying (allo-)parental care for pups. However, we had no data for when pups were actually present, and thus at least during some observations, no pups might have been present.

Overall, breeders showed fewer seasonal changes in their activity budgets than philopatrics (Fig. 5). Breeders traveled similar distances and showed no seasonal differences regarding travel distance, which likely reflects similar territory sizes in both sexes (Schradin & Pillay 2004). Interestingly, and in contrast to philopatrics, male breeders (female breeders showed a similar trend) showed less sociopositive behavior during the breeding season. Reasons for this are currently unclear, but it is most likely due to groups being smaller when observations were conducted on breeders at the start of the breeding season compared with when observations were conducted on philopatrics toward the end of the season (at the onset of observations, very few adult philopatrics were present). Similar to ground squirrels (*S. saturatus*) (Kenagy et al. 1989) and degus (*Octodon degus*) (Ebensperger & Hurtado 2005), breeders showed no seasonal difference in foraging time. In the Succulent Karoo, food availability is high during the breeding season and various food types are available (e.g., new shoots with high protein content, and flowers with sugar-rich nectar; Schradin & Pillay 2006). In contrast, food availability is reduced during the dry non-

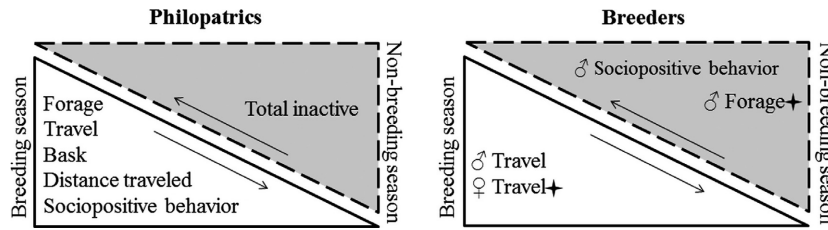


Fig. 5: Seasonal changes in activity budgets of male and female striped mice following different social tactics (philopatrics: left panel, breeders: right panel). Results of the breeding season are presented inside white, solid triangles, those of the non-breeding season in gray, dashed triangles. Triangles indicate significant decreases (along the arrow) in the time allocated to different behavioral categories (either from breeding to non-breeding season or from non-breeding to breeding season). Results which were significant only for one sex are indicated by ♀ for females and ♂ for males, and non-significant trends are indicated by †.

breeding season and striped mice mainly feed on one stable food source, fruits, and leaves of the succulent *Zygothallum retrofractum* shrubs (Schradin & Pillay 2006). At our study site, *Z. retrofractum* is the dominant plant species, but its toxins make it of low quality for striped mice (Schradin et al. 2014). Consequently, breeders (and striped mice in general) likely show a seasonal shift in plant species consumed. The absence of seasonal differences in feeding time may be a result of poor-quality foods, typically consumed in high quantities to meet physiological requirements (Zhao & Wang 2007). Further studies are needed to assess the water and (macro-)nutritional content of food plants consumed by striped mice to assess how food quality influences food choices made by individuals, and especially how these choices differ seasonally. Additionally, studies determining physiological responses (i.e., adjustments of resting metabolic rate and daily energy expenditure) to seasonal changes in food availability/ quality may help to explain the absence of adjustments in feeding time.

Differences Between Tactics During the Breeding Season

Energetic demands of females are high during gestation and lactation (Kurta et al. 1989; Pekins et al. 1998), which explains why female breeders spent more time foraging than male breeders. Males, on the other hand, may trade off foraging time to patrol their territory and guard their females from other males as has been reported for many male mammals (Komers 1994; Shi et al. 2003), including striped mice (Schradin 2006). This explanation is further strengthened by the finding that male breeders chased other individuals more often than did female breeders. Similar sex-specific patterns in agonistic interactions have also been reported for other small mammals during the breeding season (Kenagy et al. 1989; Koprowski

1998; Ebensperger & Hurtado 2005). Male philopatrics foraged more than male breeders, explaining their body mass gain. Similar differences in foraging behavior have been reported for other mammals (Zegers 1981; Robinson 1986; Shi et al. 2003). Interestingly, males and females adopting both tactics invested similar amounts of time into traveling, but male breeders traveled the largest distances. Territory patrol and defense by male breeders (Schradin 2004) are likely the main contributors to this pattern. Similarly, male yellow-bellied marmots (*Marmota flaviventris*) travel larger distances than females to patrol their territories (Armitage et al. 1996).

Differences Between Tactics During the Non-breeding Season

Philopatrics spent more time inactive, and foraged and traveled less than breeders of the same sex. These differences follow predicted patterns and support the assumption that philopatrics reduce their energy expenditure during the non-breeding season when food availability is low, which is further supported by our finding that philopatric males gained body mass and philopatric females maintained their body mass during the dry season. Likewise, Damaraland mole rats (*Fukomys damarensis*) decreased their activity in response to elevated temperatures (Oosthuizen & Bennett 2015). Male breeders chased other individuals more often than male philopatrics, demonstrating a constant investment in territory defense. Each striped mouse group has only one male breeder, which can be replaced even during the non-breeding season (C. Schradin unpublished data). Thus, as neighboring philopatric males would be willing to take over as soon as a breeding position becomes vacant (Schradin & Yuen 2011), territorial defense during the non-breeding season would be adaptive. Interestingly, we did not observe sex-specific

differences in activity patterns of breeders or philopatrics during the non-breeding season (with the exception of traveling time in philopatrics), indicating that both sexes following both tactics have similar demands outside of the breeding season.

Conclusions

Activity budgets of striped mice were influenced by both intrinsic (i.e., social tactic, sex) and extrinsic (i.e., season) factors. Philopatrics of both sexes invested in behaviors that result in body mass gain and prevent body mass loss, and which might increase survival. In contrast, breeders invested in behaviors related to reproduction during the breeding season, and maintenance of their social status during the non-breeding season. Thus, our results indicate different behavioral motivations by individuals following the two social tactics, which might be due to differential energy investments. We encourage other studies on non-migratory animals – especially species which exhibit different social tactics – living in seasonal habitats to understand how they adjust their activity budgets, and to test for the adaptive value of such changes. We also encourage researchers to examine activity budgets of rodents and especially mouse-like species, as they are important models in biomedical research and thus, information about their natural behavior is valuable.

Acknowledgements

This study was made possible by the administrative and technical support of the Succulent Karoo Research Station (registered South African NPO 122-134). We thank two anonymous reviewers for helpful comments on an earlier version of this manuscript. We thank Goegap Nature Reserve and the Department of Environment and Nature Conservation for their support. We are extremely grateful for the help of many field assistants and students with data collection. This work was supported by the University of the Witwatersrand; National Research Foundation (grant number 87769); the University of Zurich; and the Swiss National Science Foundation.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Behaviors recorded during behavioral observations.

Table S2: Comparison of the time breeders and philopatric striped mice of both sexes allocated to different behavioural categories and their changes in body mass during breeding seasons and non-breeding seasons (Wilcoxon rank sum tests, P value corrections were achieved using the Holm method).

Table S3: Comparison of activity budgets between social tactics a) during breeding seasons and b) during non-breeding seasons (Mann Whitney U tests, P value corrections were achieved using the Holm method).

Table S4: Comparison of rates of behaviours, changes in body mass and distance travelled by breeders and philopatric striped mice of both sexes during breeding seasons and non-breeding seasons (Wilcoxon rank sum tests, P value corrections were achieved using the Holm method).

Table S5: Comparison of rates of behaviours, changes in body mass and distance travelled between social tactics a) during breeding seasons and b) during non-breeding seasons (Mann Whitney U tests, P value corrections were achieved using the Holm method).