

# Regulation of Activity in Desert-Living Striped Mice: The Importance of Basking

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Received: November 7, 2006

Initial acceptance: December 22, 2006

Final acceptance: January 20, 2007

(J. Schneider)

doi: 10.1111/j.1439-0310.2007.01361.x

## Abstract

Deserts represent challenging, energy restricted environments for small mammals, but offer ample exposure to sunlight that might be used for energy saving during basking. The Succulent Karoo desert in southern Africa is a seasonal environment with cold moist winters, followed by maximum food availability in spring and dry hot summers with food shortage. The striped mouse (*Rhabdomys pumilio*) from the Succulent Karoo desert is diurnal and its activity is influenced by photoperiod in captivity. However, in contrast to standardized laboratory conditions, it can be expected that several factors other than photoperiod influence its activity pattern in the field. We expected that striped mice behave in a way that indicates that they use basking to passively warm up and thus reduce endogenous energy expenditure. We studied activity and basking patterns in 56 social groups of striped mice for a period of 4 yr, comprising 1534 observation sessions at their nests. Mice generally started activity around the time the sun illuminated their nest and terminated activity when their nest was no longer sunlit, i.e. they were strictly diurnal. The onset of activity was delayed on days when ambient temperature was colder and when group sizes were smaller. During the breeding season when food availability was high, striped mice usually left the nest before it was sunlit without basking. Outside the breeding season, they emerged and basked in front of nests mainly after nests were sunlit. These findings concur with the view that striped mice trade-off between active energy gain via foraging and passive energy acquisition by sun basking.

## Introduction

Prevailing weather conditions influence an animal's activity pattern, reproduction, survival and thus fitness (Corsini et al. 1995; Eifler & Slade 1998; Lovegrove et al. 1999; Bacigalupe et al. 2003; Geiser & Drury 2003). However, while many researchers recognize that the behavior of their study animals is influenced by weather and climatic changes (Kenagy & Vleck 1982), there are surprisingly few detailed

published field studies about this relationship. An exception are the reptiles, which control their body temperature behaviorally and are inactive when it is too cold (e.g. Christian & Bedford 1995; Bauwens et al. 1996). However, short-term changes in weather conditions also affect the behavior of mammals. For example, the activity of degus (*Octodon degus*) is influenced by ambient temperature, with reduced activity both under cold and hot conditions (Bacigalupe et al. 2003). Many mammals change their

activity seasonally (Corsini et al. 1995; Eifler & Slade 1998; Schwaibold & Pillay 2006) or even terminate activity during cold periods via torpor (e.g. Lovegrove et al. 1999; Geiser & Drury 2003) or hibernation (Carey et al. 2003; Humphries et al. 2003).

The influence of weather conditions might be more acute in habitats, such as deserts, with limited resources and large daily fluctuations in ambient temperature. Small endotherms, such as birds and rodents, are particularly vulnerable to heat loss because of their large surface area to volume ratio. Therefore, small mammals in deserts often display specialized physiological and behavioral strategies to deal with thermal challenges. For instance, a population of the golden spiny mouse *Acomys russatus* inhabiting high mountains of the southern Sinai desert (which experiences extremely cold winters), had a higher non-shivering thermogenesis capacity compared with a population from the Dead Sea shores (hot all year round; Haim & Borut 1981). The round-eared elephant shrew (*Macroscelides probiscideus*) from arid areas of South Africa conserves energy by entering into torpor during winter nights, when food abundance and temperatures are low (Lovegrove et al. 1999). Common behavioral strategies include avoiding extremes of heat and cold by remaining in dens and burrows (Du Plessis et al. 1992) and utilizing radiant solar energy by basking (Mzilikazi et al. 2002; Geiser & Drury 2003).

The striped mouse *Rhabdomys pumilio* from the Succulent Karoo of southern Africa is a medium sized (average 40–60 g; Schradin & Pillay 2005a), diurnal (Schradin 2006), group-living rodent (Schradin & Pillay 2004). Mice of one group share one territory and one nest which they defend against mice from other groups (Schradin & Pillay 2004, 2005c; Schradin 2004). In the mornings and afternoons, mice sunbask in a group in front of their nest, but forage alone during the day (Schradin 2006). While it seems that basking is an important behavior for striped mice, which might be a mechanism to save energy by passively heating up (Geiser et al. 2002; Mzilikazi et al. 2002; Geiser & Drury 2003), detailed studies are absent, both in relation to the factors which influence basking, and the putative benefits of basking. In the present study, we present field data collected over 4 yr to test predictions about the factors influencing the start and end of activity of striped mice and the occurrence of basking:

1. If striped mice trade-off between active energy gain (foraging) and passive energy gain (sun basking), this would mean mice should bask instead of foraging when the energy gain per time unit is

higher for basking than for foraging. Although we could not directly measure energy intake, this lead to following predictions of behavioral correlates with this trade-off hypothesis: (a) mice should bask more when ambient temperature is low, as this would yield a relatively greater energy gain; (b) mice should bask more in the morning, when temperatures are below the thermo-neutral zone (about 30°C, Scantlebury et al. 2006), but less often during evenings, when ambient temperatures are higher; and (c) mice should bask less (and forage more) when food is abundant, i.e. during the breeding season (Schradin & Pillay 2006), when energy demands are high, especially for pregnant and lactating females.

2. To facilitate sunbasking, the start of activity should be dependent on the onset of sunshine on the nest rather than on the time of day. Thus, we predicted: (a) seasonal differences in the onset of activity in relation to seasonal differences in sunrise, i.e. a correlation between activity and onset/end of time nests are sunlit; (b) mice from nests that experience later onset of sunshine will start activity later. This was testable because our study population was located in a valley in which the geographic configuration of the surrounding hills shaded different nests at different times.

## Materials and Methods

### Study Area and Period

The study was conducted in Goegap Nature Reserve near Springbok in the Northern Cape Province, South Africa (S 41.56, E 1.60, elevation 950 m). The vegetation type is Succulent Karoo (Cowling et al. 1999). The dominant shrub species is *Zygophyllum retrofractum* and there are many and often large patches of sand, containing different species of small succulents and annuals in spring, providing important food sources for mice (Schradin & Pillay 2006). For pictures of the field site see <http://www.striped-mouse.com>. The area is arid with an average rainfall of 160 mm per annum, with rain mainly occurring in winter (Rösch 2001). Minimum night and maximum day temperatures at the field site are –1.5 and 24°C in winter and 5 and 40°C in summer (C. Schradin, unpubl. data).

The study was performed from Sep. 2002 until Dec. 2002, Jul. 2003 to Jan. 2004, and Jun. 2004 to May 2005. The breeding season coincides with fresh plant growth flush (Schradin & Pillay 2005a), which is dependent on precipitation. The breeding season

(estimated from when juveniles were first and last observed) differed among years. In 2002 and 2004, breeding occurred from the middle of August until the beginning of December. In 2003, the breeding season was delayed as a consequence of a severe drought during the previous winter (Schradin 2005), and took place from September to December. Unexpected rain in Jan. 2005 (normally the dry season) enabled breeding from Mar. to May 2005, which did not take place in 2001, 2002, 2004 and 2006 (no juveniles were trapped during this time).

The study area was situated in a valley, approx. 600–700 m wide. The study population occurred around a dry riverbed in the valley, which flows once every 5–20 yr. The topography of the surrounding landscape was hilly. The duration of sunshine (i.e. start and end times) differed between nests, depending on the position of nest sites in relation to the surrounding hills.

The study area varied in size between years due to changing population densities. The study area was 1 ha in 2001, 3 ha in 2002, 30 ha in 2003, and 10 ha in 2004/2005.

#### Trapping and Marking of Animals

Striped mice were trapped using locally produced metal live-traps ( $26 \times 9 \times 9$  cm; similar in design to Sherman traps), baited with a mixture of bran flakes, currants, sea salt and salad oil. Traps were placed in the shade under bushes that were used as nesting sites (revealed by direct observations and radio-tracking). Traps were checked at least every 2 h and trapping was done only during mornings and afternoons, but not during the hottest times of the day. Trapped mice were sexed, weighed and individually marked with ear tags (National Band and Tag Co., Newport, KY, USA, 2 mm long) as well as hair dye for individual recognition during field observations (see photo in Schradin & Pillay (2004) or at <http://www.stripedmouse.com>).

#### Nest Observations: Determination of Start/End of Activity Period and Basking

Nests were observed in the mornings and afternoons to record start/end of activity and behavior at the nest. Data were collected on a standardized check-sheet. Observations were done from a distance of 5–10 m; mice were well habituated to and not disturbed by the presence of observers (Schradin & Pillay 2004; Schradin 2006). Nest observations lasted for at least 45 min or until mouse activity ended (in

the afternoon), starting 10 min before the expected start of activity and ending 5–10 min after termination of mouse activity (i.e. when mice left to go foraging in the morning or when they withdrew into their nest in the evening). This method of observations was validated by radio-tracking, i.e. mice were radio-tracked inside the nests before the start of morning observations and radio-tracked inside the nests after afternoon observations four to six times every week (Schradin & Pillay 2005b). Depending on the seasonal differences in daylight, nest observations started between 5.30 and 8.00 in the morning and 17.00 and 19.15 in the afternoon. Nest observations were routinely made at our field site to determine group composition, parturition, and the emergence of pups (Schradin & Pillay 2003, 2004, 2005c). In total, we made 1534 nest observations for 56 groups, 775 in the morning and 759 in the afternoon. The following data were collected: (1) the onset/end of sunshine on the nest; (2) weather condition (sunny vs. cloudy); (3) time of the emergence of the first mouse in the morning and of the withdrawal of the last mouse in the afternoon; (4) group size (number of individuals present); (5) whether juveniles were present or not (individuals below estimated body size of 30 g); and (6) whether or not mice were sun basking (sitting motionless in the sun, often pilo-erecting).

The categorical data from our nest observations were not as accurate as continuous data would have been. This was due to our standard protocol of nest observations that also involved data collection of group composition, parturition and emergence of pups for other studies (Schradin & Pillay 2004, 2005b; Schradin 2005, 2006). A great benefit of this protocol has been our ability to collect data for 4 yr and more than 1500 nest observations, which exceeds other studies of which we are aware. Another shortcoming might be that data were collected on a group basis instead of an individual basis. Group size could influence the onset of activity, as in larger groups it might be more likely that an individual leaves the nest early or withdraws later. However, by including group size as a covariate into our model (see below), we controlled for a possible group effect. Moreover, we collected data on a group basis since: (1) it was often too complicated to collect data on an individual basis, as groups contained up to 30 adult mice; and (2) by collecting data on a group basis we avoided pseudoreplication as we included only one data point per nest observation. The repeated nature of the data (several observations of each group) was taken into account in the

analysis by including group ID as a random factor and correcting for the numbers of degree of freedom (see below).

Temperature data were obtained from a weather station in Springbok, located 20 km away from the field site, as the weather station in Goegap failed to work from 2003 onwards; weather data from the Springbok weather station and data collected at our field site correlated highly significantly (e.g. Sept–Nov. 2002,  $r_s = 0.80$ ,  $p < 0.0001$ ,  $N = 20$ , for minimum night temperatures).

### Statistical Analyses

The software packages Instat and SAS (version 8.2; SAS Institute, Cary, NC, USA) were used. When general linear mixed models (LMM) were fitted to normal data (SAS, proc MIXED), residuals were accepted as being normally distributed when both Kolmogoroff–Smirnov and Shapiro–Wilk statistics yielded  $p > 0.05$ . Generalized linear mixed models (GLMM, macro GLIMMIX) were fitted to binomial data using logistic link functions and REML estimation, a scale for binomial variance, and F-statistics for significance testing (cf. Krackow & Tkadlec 2001). Error degrees of freedom (df) were calculated corresponding to the subject-by-effect interaction for categorical effects, and as sample size minus model df for covariates. Effects were tested using type III (simultaneous) modeling, i.e. in multiple effects models, variance components or likelihoods for each independent variable are corrected for all other effects in the model. Parameter estimates (regression coefficients, means) are given as estimate  $\pm$  standard error (SE); effects are considered significant for two-tailed  $p < 0.05$ .

### Basking

Observations were classified according to whether or not at least one individual basked after the group emerged (mornings) or before the group retired into the nest (afternoons). We tested the effects of ambient temperature and season (breeding vs. non-breeding) on the occurrence of basking. We introduced a random effect of group identity on the intercept. GLMM models included only data collected under clear skies as mice could not bask under overcast skies.

### Timing of activity

To evaluate which factors influence the start and end of activity in striped mice, we constructed LMMs

both for the start of activity (the time, in minutes past midnight, of the first animal to emerge from nest in the morning) and the end of activity (the time of the last animal to enter the nest in the evening) as the responses. We introduced a random effect of group identity on the intercept, as many uncontrolled variables, like nest topology, disease status, etc., could sum up to random variation of baseline values between groups. We tested the dependency of start and end of activity on time of sunrise or sunset (min past midnight), respectively; ambient temperature ( $^{\circ}\text{C}$ ), weather condition (sunny/overcast), season (breeding vs. non-breeding season), and group size.

An additional analysis was done to test for an influence of nest location on start of mouse activity. For this, we used only data for non-cloudy days when mice sun basked. Of these data, days were chosen on which more than one nest was observed during the morning and then only the nest with the earliest and latest onset of sunshine were chosen to achieve the maximum difference in the data. This resulted in 83 data pairs from 83 d from Oct. 28, 2003 to Apr. 8, 2005.

## Results

### Factors Determining Basking

Striped mice were significantly more likely to bask outside the breeding season, and when groups were larger, both during mornings and afternoons (Table 1). Mice were also more likely to bask when it was colder during afternoons, but this relationship was not quite significant for the mornings ( $0.05 < p < 0.06$ ; Table 1).

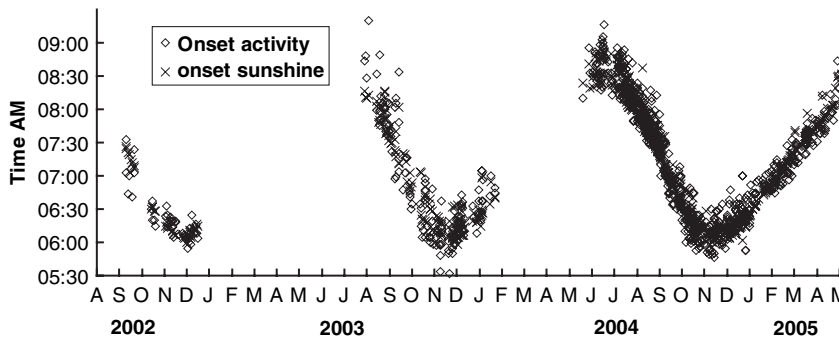
On 295 occasions, the same group was observed both during the morning and afternoon of sunny days. Taking mean values per group to avoid pseudoreplication, 14 groups basked more often in the morning than in the afternoon, two more often in the afternoon, and there was no difference for four groups ( $T = 2$ ,  $p = 0.004$ , Sign Test).

### Factors Determining the Start and End of Activity

The start of activity was most strongly determined by sunrise (Fig. 1). Season had a significant influence on the onset of activity, with mice becoming active significantly earlier during the breeding season (Table 2). Animals became active earlier when ambient temperature was higher, while weather condition and group size had no significant effect on the onset of activity (Table 2).

**Table 1:** Fixed effects on the probability of basking ( $P_b$ ) in the morning ( $N = 697$ ) and evening ( $N = 709$ ), from a GLMM\* (see text). Coefficients are regression slopes or mean differences of logits,  $Y = \ln(P_b/(1 - P_b))$ . Predicted probabilities of basking,  $\hat{P}_b = e^{\hat{y}}/(1 + e^{\hat{y}})$  at average values of covariates, during breeding and non-breeding season are 72.8% vs. 82.4% for morning sessions and 69.2% vs. 78.6% for afternoon sessions

	Morning session						Afternoon session					
	Coefficient	SE	ndf	ddf	$F_{ndf,ddf}$	P	Coefficient	SE	ndf	ddf	$F_{ndf,ddf}$	P
Intercept	-0.04	0.39					2.45	0.50				
Temperature	-0.04	0.02	1	653	3.64	<0.06	-0.11	0.02	1	662	33.69	<0.0001
Season	-0.56	0.23	1	23	6.00	<0.03	-0.49	0.22	1	20	4.95	<0.04
Group size	0.26	0.04	1	653	38.09	<0.0001	0.19	0.04	1	662	27.43	<0.0001



**Fig. 1:** Start of sunshine on nest and start of mouse activity in the morning from Aug. 2002 to May 2005. The earlier the sun started shining on nests (crosses), the earlier mice became active (diamonds)

**Table 2:** Fixed effects on time of start of activity ( $N = 757$ ) and end of activity ( $N = 694$ ), from an LMM<sup>a</sup> (see text). Coefficients are slopes for regressors and differences of means (direction indicated in parenthesis) for class effects, respectively

Parameter	Start of activity (morning session)						End of activity (afternoon session)					
	Coefficient	SE	ndf	ddf	$F_{ndf,ddf}$	P	Coefficient	SE	ndf	ddf	$F_{ndf,ddf}$	P
Intercept	4.95	5.56					-18.16	14.49				
Sunrise/sunset	0.99	0.01	1	712	7683.04	<0.0001	1.00	0.01	1	638	5270.92	<0.0001
Temperature	-0.31	0.10	1	712	8.93	<0.003	0.82	0.08	1	638	113.71	<0.0001
Weather (cloudy)	-1.81	1.69	1	17	1.15	>0.29	-7.08	2.02	1	11	12.26	<0.005
Season (breeding)	-6.83	1.05	1	22	42.69	<0.0001	1.31	0.78	1	18	2.81	>0.11
Group size	0.02	0.13	1	712	0.02	<0.89	0.20	0.10	1	638	3.87	<0.05

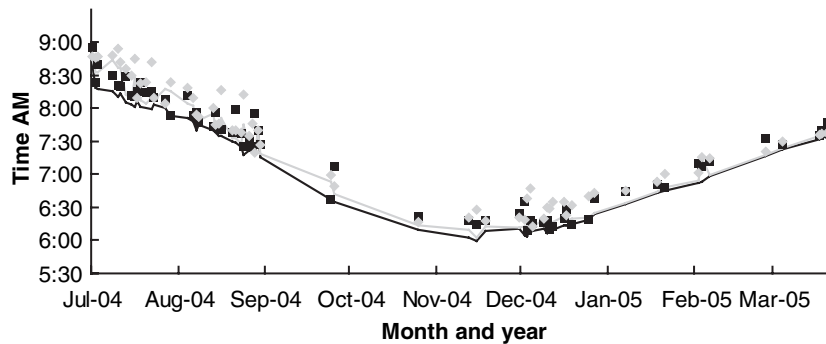
<sup>a</sup>Variance between groups exceeded expectation from the residual variation in morning ( $z = 1.88$ ,  $p < 0.031$ ) and afternoon sessions ( $z = 1.99$ ,  $p < 0.025$ ).

The end of activity was strongly determined by the end of sunshine on the nest (Table 2). Mice ended activity significantly later when it was warmer, when it was not cloudy, and when groups were larger (Table 2). Season had no significant effect.

The importance of the start of sunshine on nests for the start of activity was also demonstrated when comparing nests that experienced differential shading by the hills surrounding the study site. Mice from nests that were sunlit earlier became active earlier than mice from nests that were shaded for longer ( $t_{82} = 4.762$ ,  $p < 0.0001$ ,  $N = 83$ , paired t-test; Fig. 2). There was no difference in the latency to start of activity in relation to the start of sunshine

on the nest ( $T = 1572.5$ ,  $p = 0.82$ ,  $N = 83$ , Wilcoxon-test; Fig. 2), i.e. mice in nests with a later onset of sunshine emerged after a similar delay to mice from nests with earlier onset of sunshine. Accordingly, the delay in start of mouse activity between the early and the late nests (measured in minutes) was significantly correlated with the delay in the onset of sunshine on both nest types (measured in minutes;  $r = 0.62$ ,  $p < 0.0001$ ,  $N = 83$ , Pearson).

On 13 occasions, mice did not emerge from their nest in the morning, even though we knew from radio-tracking that they were in the nest. Observations were continued for at least 30 min longer compared with other sessions before being terminated. Instances when mice did not emerge in the morning



**Fig. 2:** Start of mouse activity in relation to the start of sunshine on their nest from Jul. 2004 to Apr. 2005. For each day, activity data from one nest with early start of sunshine (black square) and one with late start of sunshine (grey diamond) are shown. The time of the start of sunshine on 'early' nests are shown with a black line and for 'late' nests with a grey line. Only data from nests where mice basked and emerged after the start of sunshine are shown. From Sep. to Nov. 2005 (breeding season) most mouse groups emerged earlier and often did not bask, which resulted in fewer data points for this period

were significantly more common on cloudy days; of the 13 d when mice did not emerge, 11 were cloudy, whereas of the 739 d when mice emerged 74 were cloudy ( $p < 0.0001$ , Fisher test). Additionally, days when mice did not leave the nest were  $2.6 \pm 2.2^\circ\text{C}$  colder than the previous day ( $T = 0$ ,  $p < 0.001$ , Sign Test,  $N = 13$ ).

## Discussion

The Succulent Karoo desert of southern Africa represents a challenging environment for its inhabitants, because of its cold, moist winters and dry, hot summers. Food availability is correlated with these seasonal changes and is highest in spring, while summer is a period of food shortage (Schradin & Pillay 2005a, 2006). Changes are not only obvious over seasons, but also within seasons, when both cold and warm/hot periods can occur. The striped mouse has to cope with these changes, especially as its small size makes it prone to energy loss because of its high surface area to volume ratio. Therefore, we expected that striped mice change their behavior as a response to these environmental changes.

### Reasons for Basking

Striped mice sun basked during most mornings and afternoons in front of their nest, demonstrating the importance of this behavior. Our analysis of factors influencing basking support our assumption that basking serves to save energy: mice were more likely to bask when it was cold, when basking to gain heat passively would be more beneficial (prediction 1a). This also explains why basking occurred more often

during mornings than during afternoons (prediction 1b): increased solar radiation during the day increases ambient temperatures during the afternoon, and even in the shade, temperatures might be closer to the thermo-neutral zone of striped mice. Furthermore, striped mice were more likely to bask during the non-breeding season, when food is scarce (Schradin & Pillay 2006) and energy saving due to basking would thus be more important (prediction 1c).

Striped mice spend the night in huddling groups (Schradin & Pillay 2004; Schradin et al. 2006). Nest temperature is likely to be influenced by group size, which was highly variable in our study. However, in small mammals, thermoregulatory benefits due to huddling, a direct result of higher nest temperature created by huddling groups, do not increase at group sizes above 5 (Canals et al. 1989). Moreover, in striped mice there is almost no difference between energy savings due to huddling for groups of four, six, or eight individuals (Scantlebury et al. 2006). Thus, in most cases, striped mouse groups were large enough to reach the maximum nest temperature. Therefore, the fact that mice nevertheless prefer to sunbask than to remain in the huddling groups during mornings suggests that the surface area of the shrubs in which the mice nest warms up quicker in the sun than does the nest hidden inside the shrub. But why do mice bask in the afternoon when  $T_a$  is much higher than during mornings? The trade-off hypothesis predicts that mice should bask when basking yields more energy than foraging. Basking might be advantageous even under relatively high  $T_a$  when the potential energy gain through foraging is very low. In small mammals, food intake is restricted by stomach size, and when mice return to the nest

with a full stomach, such that future foraging is not possible, basking would be beneficial.

### Onset and End of Activity

The onset and end of activity in mammals is often influenced by photoperiod. Onset of activity is correlated with sunset for the serotine bat (*Eptesicus serotinus*; Catto et al. 1995) and crested porcupines (*Hystrix cristata*; Corsini et al. 1995). Black bears (*Ursus americanus*) become active 30 min after sunrise and stop activity 2 h after sunset (Lariviere et al. 1994). Sunlight also has a profound effect on the activity of the diurnal Brant's whistling rat (*Parotomys brantsii*; Jackson 1998), a rodent occurring sympatrically with striped mice in our study area. While the general effect of photoperiod on activity has been shown in many species and also for the striped mouse in the laboratory (Dewsbury & Dawson 1979; Schumann et al. 2005), the ecology and fine tuning of activity has so far been ignored. In our field study, we noted the importance of photoperiod, but we also studied several other cofactors influencing start and end of activity. Striped mice were active later when it was cold and sometimes did not leave their nest at all during rainy days. Thus, they reduced their activity when the weather was harsh. Group size appeared to have no effect on the start of activity but was important at the end of activity. The delayed end of activity in larger groups might be due to one individual returning later to the nest in larger groups than in smaller groups. Thus, it was important to include group size as a covariate into the model. However, striped mice are highly social and the breeding males, in particular, greet other group members returning to the nest in the afternoon (Schradin & Pillay 2003, 2004). A larger group would therefore engage in higher levels of social interaction, delaying withdrawal into the nest. In fact, mice often withdraw together into the nest, but as we collected data on a group basis it was not possible to test for a social effect. Another social interaction within groups that could influence activity is aggression. However, this is unlikely in the egalitarian striped mouse in the Succulent Karoo: no dominance hierarchy is obvious in free living and captive groups and even experimentally induced competition for preferred food (peanut butter) did not reveal a dominance hierarchy (Schradin & Schubert, unpubl. data).

The time that the sun actually started shining onto the nests was most important for the onset of activity (prediction 2a). Sunrise at the study site occurred

about 30–45 min before nests were sunlit. This was due to the hills shading the nests in the valley after sunrise. Outside the breeding season, it appeared that the activity of striped mice was 'switched on and off' by sunshine. In the morning, as soon as the sun started shining on a nest, the mice emerged and basked in front of their nests. In the afternoon, mice returned to the nest to bask for about 30 min before direct sunshine on the nest ended, and all mice retreated into the nests. The importance of direct sunshine on mouse activity is also demonstrated by comparing nests with different geographic positions in the valley: those located in nests that received sunshine earlier generally were active earlier (prediction 2b).

During the breeding season, mice were active earlier in the day, leaving the nest to forage even before it was sunlit. The breeding season is characterized by an abundance of protein-rich young plant growth (Schradin & Pillay 2006). Therefore, instead of starting the day basking, during the breeding season, striped mice started activity by foraging, thereby exploiting protein-rich food to meet their increased energy needs (pregnancy, lactation in females and patrolling of territory boundaries in males; Schradin 2006). Activity budgets might also differ during the breeding season due to mating behavior and parental care. However, mating behavior was rare even during the breeding season and mice visited the nest mainly during the hottest part of the day (midday) when  $T_a$  in the shade is within the thermoneutral zone of striped mice (Schradin 2006). Thus, our finding that striped mice left earlier during the breeding season can neither be explained by mating behavior nor parental behavior.

Another factor that might influence activity is predation. The main predators of striped mice in the Succulent Karoo are birds of prey, jackals and wild cats, while snakes are less important (Schradin, unpubl. data). It was not possible to study this factor, as these predators avoided the human observers. However, we have no indication that predation pressure changes seasonally, and predation is very likely to be unpredictable for striped mice, as predators attack unexpectedly. Therefore, we do not believe that predators would have dramatically altered the behavior patterns observed in our study.

Previous studies of activity were restricted to general triggers and zeitgebers, such as photoperiod influencing animal activity (Corsini et al. 1995; Eifler & Slade 1998; Bacigalupe et al. 2003). However, it can be expected that animals show a much more flexible behavioral response toward changes in

weather and climate conditions to save energy by avoiding activity during suboptimal conditions (Schwaibold & Pillay 2006). Such fine tuning of activity can be regarded as a very important means of influencing and reducing energy expenditure and would thus deserve as much attention as foraging and reproductive behavior. It is therefore surprising that so few studies exist that examine the influence of several environmental factors which might regulate activity and promote energy-saving. Here, we demonstrated that the flexible regulation of the start and end of activity in the striped mouse can be regarded as an adaptive response to its seasonally and daily changing Succulent Karoo desert environment. Striped mice respond flexibly to changes both in weather conditions and in food availability, indicating a trade-off between active energy gain through foraging and passive energy gain through sun basking.

### Acknowledgements

We thank the University of the Witwatersrand, the National Research Foundation RSA (grant number 2053514 to NP), the Schweizerische Gesellschaft der Naturwissenschaften (CS) and the Fonds zur Förderung des akademischen Nachwuchses of the University of Zurich (CS) for financial support. CS was supported by grants from the Swiss National Science Foundation (2002), the German Science Foundation (2003) and the Claude Leon Foundation (2004/2005). We are grateful to M. Scantlebury and N. Bennett for important comments on the manuscript. We would also like to thank Northern Cape Department of Agriculture, Land Reform and Environment for their assistance, and the staff at Goegap Nature Reserve. We are grateful to students that assisted in collecting data during nest observations over the years. The study received clearance from the animal's ethics committee of the University of the Witwatersrand (AESC 2001/32/3, extended by 2003/106/3).

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