

SHORT COMMUNICATION

Carsten Schradin

Information transfer about food locations is not a benefit of group living in the solitary foraging striped mouse (*Rhabdomys pumilio*)

Received: September 26, 2005 / Accepted: April 6, 2006 / Published online: June 9, 2006

Abstract The benefits of group living have primarily been investigated in species which form permanent groups. There are, however, several species that forage alone but still form groups that share the same territory and nest. One of these group-living solitary foragers is the striped mouse (*Rhabdomys pumilio*) from the Succulent Karoo in South Africa. I performed field experiments on this species to investigate the hypothesis that mice benefit from group living by exchanging information in social groups about the location and availability of food sources. Presenting additional food sources in the field altered individual foraging decisions. A mouse that found food at one location visited it again the next day; other mice of the same group did not arrive, however. Establishment of permanent feeding stations for 1 week affected individual foraging even 1 week after termination of feeding, a result demonstrating the strong effect trapping can have on the behaviour of study species. Results from this study suggest that information transfer about good food sources was of little importance in the evolution of group living in the striped mouse.

Key words Information centre · Social net · Rodent

Introduction

Group living can have significant costs but also advantages, for example improved foraging or avoidance of predators (Ebensperger 2001; Krebs and Davies 1993; Schradin 2000). The benefits of group living have traditionally been determined for species that form permanent groups (Inman and

Krebs 1987). Recent field studies have, however, revealed a quite different pattern of group living in several mammal species – the group living solitary forager (prosimians, Müller and Thalmann 2000; carnivores, Kays and Gittleman 2001; rodents, Schradin and Pillay 2004). In these species, group members share the same territory, meet regularly, and interact amicably with each other but react aggressively towards con-specifics of other groups.

Solitary foraging could work as a strategy for gathering information about food availability from a larger area than could be gathered by a single individual. Group living could lead to benefits, when transfer of information about the location of good food sites occurs within groups (for rats, see Galef and Wigmore 1983). For birds, colonies and communal roosts work as information centres where individuals meet. Unsuccessful foragers obtain information about who foraged successfully and subsequently follow such individuals to good feeding grounds (Brown 1986; Ward and Zahavi 1973; but see also Richner and Heeb 1995).

The same could also be true for mammalian group-living solitary foragers, for example the striped mouse, *Rhabdomys pumilio*, from the Succulent Karoo desert of South Africa. The striped mouse feeds mainly on patchily distributed plant products, for example seeds, flowers, and berries (Schradin and Pillay 2006). When food sources are distributed patchily, successful foragers could lead unsuccessful group members to good feeding sites. In the arid Succulent Karoo in the north-west of South Africa striped mouse groups can consist of up to 30 adult mice – one breeding male, up to four breeding females, and their offspring of both sexes, which remain within their natal group even after reaching sexual maturity. Group members share one nest and territory. Mice leave the nest in the morning to forage alone, resting in bushes during the hottest parts of the day. In the evening, mice of one group meet again at their nest where they withdraw for the night (Schradin 2006b). Striped mice travel on average 900 m a day, visiting, several times, the same feeding sites within their territory (Schradin 2006b), which during this study was approximately $50 \times 40 \text{ m}^2$ (Schradin and Pillay 2004). Their social centre is their nest, where the mice could transfer information about

C. Schradin (✉)
School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, South Africa
e-mail: carsten@schradin.com

Present address:
Department of Animal Behavior, Zoological Institute, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

good food sites. In this study I investigated whether mice that found a good food source during one afternoon came back to the same place the next morning, and – to test for possible information transfer – whether more members of their group arrived on the same day, compared with a control. I also tested whether mice might be able to smell what group mates ate previously and use this information to change their foraging the next day.

Materials and methods

Field site

The study was performed in November and December 2002 after the breeding season in the Succulent Karoo desert in Goegap Nature Reserve, South Africa. The end of the breeding season was also the start of the dry season with low food abundance, when mice lose approximately 12% of body mass (Schradin and Pillay 2005a). It was therefore regarded as a season when information transfer about good food sites would be beneficial for mice. The study area of 3 ha was characterised by sandy soil with patchily distributed shrubs and different species of small succulents and ephemerals.

Trapping and marking of mice

The study area was occupied by 151 mice of nine different groups, with group sizes ranging from 8 to 27 individuals (mean 16.8; Table 1). Striped mice were trapped live by use of locally manufactured metal traps ($26 \times 9 \times 9$ cm³) baited with a mixture of bran flakes, sea salt, and salad oil. Trapped mice were weighed and individually marked with hair dye.

Each group was marked with one colour: blond, red, (both Wella Viva Colour), black (Inecto Rapid), or neutral (no colour, but marking with a number, see below). Groups were marked such that groups with the same colour had the territory of a third group between them, so confusion of group association by colour was not possible. A number was also written in black dye on both sides of each mouse, enabling individual recognition. There was no indication that marking with hair dye affected behaviour or increased predation risk for the mice (Schradin and Pillay 2004).

Group association of individual mice was determined by observing shrubs containing nests during mornings and afternoons. All individuals present at each nest were recorded. Nest observations also revealed that all group members had been marked.

Experimental design

Experiments were performed with mice from nine different groups whose home ranges were known from radio tracking (Schradin and Pillay 2005b). Within the territory of each group, one location was chosen for experiments, on average 18 m away from the nest. All locations were in the middle of the group territory directly in front of a small bush (approximately 50 cm wide and 50 cm high). None of the locations, however, was on main travel routes of the mice, which were known from previous observations (Schradin 2006b). Experiments were performed 1–4 weeks after trapping at the field site had been terminated and all traps had been removed except those used for experiments (see below). Video-recordings during both experiments (see below) covered an area with a diameter of approximately 120 cm. Thus, the entire small shrub and the feeding stations of experiment II (total length: 100 cm) were in focus.

Table 1. Number of food mice and other mice from the same group that visited the different places of baiting (experiment I) or feeding stations (experiment II) during control I, after baiting in experiment I, during control II, and after baiting in experiment II

Group	Experiment I						Experiment II					
	Food mice		Other mice				Food mice			Other mice		
No.	Size	Control	Baiting	Experiment	Control	Experiment	Control	Baiting	Experiment	Control	Experiment	
1	8	0	1	0	0	2	1	1	1	8	6	
2	11	0	1	1	3	1	1	2	2	3	3	
3	27	0	1	1	0	2	2	2	2	6	5	
4	26	1	1	0	4	3	1	2	1	4	0	
5	12	0	1	1	3	2	1	1	1	10	7	
6	12	0	1	1	3	3	1	1	0	13	10	
7	22	0	3	2	3	3	0	1	1	8	8	
8	21	0	1	0	6	0	–	–	–	–	–	
9a	12	0	1	1	8	2	–	–	–	–	–	
9b	–	–	–	–	–	–	0	2	2	0 ^a	2	
Sum	151	1	11	7	30	18	7	12	10	52	41	
Mean	16.8	0.1	1.2	0.8	3.3	2.0	0.9	1.5	1.2	6.5	5.1	
SEM	2.4	0.1	0.2	0.2	0.8	0.3	0.2	0.2	0.3	1.5	1.2	

– indicates no data are available

No data are available for group 8 in experiment II, because two mice from group 9 arrived there as food mice, and so these data were used for group 9 (9b). Because of this the locations for experiment I (9a) and experiment II (9b) are different for group 9.

^aDuring this day it was raining

Experiment I

The first morning this location was filmed during the main period of foraging activity of the mice from 6.45 to 8.15, i.e. for 90 min, using a camcorder (Sony TRV140E) powered by a car battery. This was the control videotaping of experiment I (control I). At the same location, 3 g bait was presented on the same day at 17.00. Mice are trap happy with the bait we use, even during the breeding season, when food availability is highest, indicating that mice regard our bait as high-quality food. The baiting place was observed from a distance of 10 m. Bait was presented until at least one mouse arrived at the location. Each arriving mouse was allowed to eat for 3 min before bait presentation was terminated. Bait was presented in the middle of a saucer (diameter 12 cm) and care was taken that all surplus food was removed after experiment I, so that mice were not attracted by olfactory cues the next morning. The next morning the same location was filmed at the same time as the previous morning, for 90 min. No bait or saucer was present at this stage to keep the situation identical with control recordings.

Experiment II

This experiment was conducted to test whether mice do transfer information about the availability of a food source whose location is known to all mice but which was not available for the last week (mimicking a seasonal food source). A feeding station consisting of six permanently open traps placed upside down was established and baited with 12 g daily for 1 week, followed by a week without food provisioning when control II recording was performed for 90 min, as described for experiment I. It was expected that during these two weeks all mice learnt that:

- 1 food was available at this station, and
- 2 food had become unavailable during the second week.

Food was then presented again at 17.00, to make one food-mouse knowledgeable about the fact that food was available again. It was supposed that mice at the nest could learn from the smell of the food-mouse that this known but vanished food source had become available again. The next morning a new video recording was made in the same way as the morning before. No bait was present at this stage but exactly the same empty traps were present as during the control recording.

Statistics

Knowledgeable mice that had experienced food presentation were called food-mice; all other mice were called naïve mice. Video tapes were watched on a large-screen TV. I recorded which individuals visited the location during controls and after food presentations. Marking with hair dye enabled me to identify individuals. To test for information transfer, comparisons were made at the level of groups to

keep data independent ($N = 9$ groups). I counted the number of different individuals that visited each feeding station during controls and after experiments. Because data passed the normality test (Kolmogorov–Smirnov), I used parametric statistics to compare the number of naïve mice visiting between experiments and control. To test whether food-mice were more likely to come back to the feeding station after they had found food there, I combined data from both experiments. To test whether food mice were more likely to visit after experiments than during controls, I used the binomial test. Contingency tables were analysed using the Fisher's exact test. All P values are two-tailed. For post-hoc estimation of the power of non-significant results, I used the software G*power (Erdfelder et al. 1996).

Results

On one occasion during experiment I not one mouse but three mice of the same group arrived within less than 1 min and during experiment II on four occasions two mice of the same group arrived within less than 1 min. All these mice were regarded as food-mice. Food-mice ($N = 23$, both experiments combined) arrived at the bait after 14.3 ± 4.4 min (range 1–62 min). Of the 23 food mice in experiments I and II, two visited only during controls and 11 only after baiting. Significantly more individuals visited only after baiting than only during controls ($P < 0.03$, binomial test; Table 1), indicating that food mice came back to the food source they encountered the afternoon before. I also tested this by comparing, for both experiments separately, the ratio of food mice that came back the next morning to the place of baiting with the ratio of other naïve mice that visited this place by chance. After baiting in experiment I, seven of 11 food mice visited the place of baiting the next morning (ratio of 7:4). Of the total of 140 naïve mice that were part of the study groups, 18 visited the place of baiting and 133 did not (ratio of 18:133). After experiment I food mice visited significantly more often than naïve mice ($P < 0.001$, Fisher's exact test). After experiment II, 10 of 12 food mice visited the feeding station and 41 of the remaining 139 naïve mice of the focal groups ($P < 0.001$, Fisher's exact test).

There was no difference between the number of naïve mice that visited the feeding station after baiting in experiment I and in control I ($P > 0.2$, $t = 1.352$, $df = 8$, paired t test; Table 1), and on average even more mice visited during controls than after experiments. The power of this analysis was 0.27 and the same as when estimating a high-effect size.

There was no difference between the number of naïve mice that visited the feeding station after experiment II and in control II ($P > 0.09$, $t = 1.949$, $df = 7$, paired t test; Table 1) and on average even more mice visited during controls than after experiments. The power of this analysis was 0.1 and as such much smaller than the expected power of 0.27 for a high-effect size. This was because the means of control II and after experiment II were very similar, resulting in a low effect.

To test whether the establishment of permanent feeding stations affected foraging of mice in the long term (i.e. whether 1 week of feeding still had an effect on behaviour of mice after feeding had been terminated for 1 week, measured at control II), I compared the total number of mice at the feeding station during the baseline control I and control II, including food mice and naïve mice from other groups. Group 9 was excluded from this analysis, because the locations for experiments I and II were different. Mice visited the feeding station significantly more often during control II than during control I ($P < 0.02$, $t = 3.297$, $df = 6$, paired t test).

Discussion

The experiments were performed at the start of the dry season, when food abundance is low and mice lose approximately 12% of body mass (Schradin and Pillay 2005a). Thus, it would have benefited mice to follow group mates to good food sources. There was, however, little indication of information transfer about food source location in striped mouse groups: A mouse visited a food location the morning after it had discovered it the afternoon before, but other group members did not visit the same location.

One possibility could have been that only information about the general availability of a special food source was shared, but not information about the specific location. I tested this by establishing feeding stations that provided food every morning for 1 week, but not for the second week. These feeding stations resembled a seasonal food source. One week after feeding was stopped, i.e. the season of the artificial food source had ended, a control recording was made, and afterwards one mouse fed at the feeding station. It was expected that other group members would smell the typical food smell when meeting it 1 h later at the nest and might associate this food smell with the feeding stations (for evidence of this mechanism in rodents see Galef and Wigmore 1983). In my study, however, no effect was found. Instead, the change in individual foraging behaviour because of the presence of the feeding stations was very strong – even 1 week after termination of feeding nearly 30% of the mice present at the field site continued to visit these feeding stations. This shows that baiting and trapping has a long-term effect on the behaviour of rodents, a result that must be taken into account when studying animals in the wild, e.g. when determining home ranges. The strong effect on individual behaviour, i.e. mice coming back to feeding stations even after baiting had been terminated for 1 week, indicates that information transfer is not necessary, because individuals actively seek and obtain reliable information about food abundance in their territory.

The sample size in my study was relatively low. It is, therefore, not possible to accept the null hypothesis. There was, however, no indication that information transfer had

been taking place – in both experiments the means were even higher during controls than after experiments (the opposite of predictions). Even a substantially larger sample size could not have led to a significant difference. Alternative explanations for the evolution of group living in striped mice of the Succulent Karoo could include thermoregulatory benefits as a result of sleeping together in the nest (Scantlebury et al. 2006), benefits of communal breeding, and forced philopatry because of habitat saturation (Schradin 2006a).

Acknowledgments I would like to thank Northern Cape Conservation for their assistance and the staff at Goegap Nature Reserve for their support during the study. I am grateful to D. Stuartfox for comments and for correcting the English. Comments by two referees significantly improved the manuscript. This study was supported by the Swiss National Science Foundation, the Schweizerische Gesellschaft für Naturwissenschaften, the Zürcher Hochschulverein (FAN), and the University of the Witwatersrand.

References

- Brown CR (1986) Cliff swallow colonies as information centers. *Science* 234:83–85
- Ebensperger LA (2001) A review of the evolutionary causes of rodent group-living. *Acta Theriol* 46:115–144
- Erdfelder E, Faul F, Buchner A (1996) G*power: a general power analysis program. *Behav Res Meth Instrum Comp* 28:1–11
- Galef BG, Wigmore SW (1983) Transfer of information concerning distant foods: a laboratory investigation of the “information centre hypothesis”. *Anim Behav* 31:748–758
- Inman AJ, Krebs J (1987) Predation and group living. *TREE* 2:31–32
- Kays RW, Gittleman JL (2001) The social organization of the kinkajou *Potos flavus* (Procyonidae). *J Zool* 253:491–504
- Krebs JR, Davies NB (1993) An introduction to behavioural ecology. 3rd edn. Blackwell, Oxford
- Müller AE, Thalmann U (2000) Origin and evolution of primate social organisation: a reconstruction. *Biol Rev* 77:405–435
- Richner H, Heeb P (1995) Is the information centre hypothesis a flop? *Adv Study Behav* 24:1–43
- Scantlebury M, Bennett NC, Speakman JR, Pillay N, Schradin C (2006) Huddling in groups leads to daily energy savings in free-living African four-striped grass mice *Rhabdomys pumilio*. *Funct Ecol* 20:166–173
- Schradin C (2000) Confusion effect in a reptilian and a primate predator. *Ethology* 106:691–700
- Schradin C (2006a) When to live alone and when to live in groups: ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belg J Zool* (in press)
- Schradin C (2006b) Whole day follows of the striped mouse. *J Ethol* 24:37–43
- Schradin C, Pillay N (2004) The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa: a territorial group living solitary forager with communal breeding and helpers at the nest. *J Comp Psychol* 118:37–47
- Schradin C, Pillay N (2005a) Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammal Biol* 70:84–92
- Schradin C, Pillay N (2005b) Intraspecific variation in the spatial and social organization of the African striped mouse. *J Mammal* 86:99–107
- Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav Ecol* (in press)
- Ward P, Zahavi A (1973). The importance of certain assemblages of birds as “information-centres” for food finding. *Ibis* 115:517–534