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Does a mouse have a friend? Mixed evidence for individual recognition in the African striped mouse (*Rhabdomys pumilio*)

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Abstract

Individual recognition, the ability to discriminate between members of a social group according to their distinctive characteristics, is a sophisticated form of social recognition. Several laboratory studies demonstrated individual recognition in rodents, but not under natural conditions. We combined behavioral observations and an experiment to assess individual recognition in free-living African striped mice *Rhabdomys pumilio*. Striped mice live in groups that share a nest, but forage alone during the day. Interactions among group members are typically amicable and take place at the nest. In order to determine whether striped mice have individualized relationships, we analyzed whether focal mice interacted repeatedly more often with one specific group member. Data from 58 focal individuals from 15 groups revealed that the individual with which amicable interactions occurred the most was often alone in one mode of the data distribution, indicating that behavior toward this specific individual differed compared to the behavior to all other group members. Striped mice consistently preferred this specific individual during the following weeks. Preferred social partners of both breeders and younger non-breeders were young non-breeders. Sex-specific effects were obtained only for young adult males and breeding females, which both associated more often with the opposite sex. For 11 young adults from 11 groups, the preferred social partner was trapped and removed, either overnight (experiment) or only during the day (control), when striped mice forage solitarily and usually do not interact with group members. Striped mice interacted on average more with their preferred social partner after it returned in the experimental group compared to the control (7 of 11 experiments), but the difference was not significant ($P = 0.16$). Our study indicates that striped mice might have individualized relationships, although they failed to significantly indicate individual recognition during experimental removals. Future studies will have to test the adaptive function of individualized relationships in African striped mice.

Introduction

It is essential for successful social interactions that they are directed toward the appropriate individual. This requires the ability to recognize others. Different forms of social recognition exist, defined by the nature of the object that is being discriminated (Sherman, Reeve & Pfennig, 1997). In species recognition, individuals are able to discriminate between conspecifics and heterospecifics (Breed & Moore, 2012). In sex recognition, an individual is capable of discriminating males from females (Breed & Moore, 2012). Social group recognition is the ability to distinguish between familiar and unfamiliar individuals, while kin recognition describes the ability to identify and tell apart close kin, distant kin and non-kin (Halpin, 1991; Breed & Moore, 2012), as found in the house mouse *Mus musculus* (Yamazaki *et al.*, 1988). Yet, with all these recognition systems alone, individual recognition is not possible.

Individual recognition is defined as the ability to discriminate between individuals based on their individually distinctive characteristics (Beecher, 1989; Tibbetts & Dale, 2007; Breed & Moore, 2012). In mammals, individual recognition is known to play a major role in recognition of territorial neighbors (Johnston, 2003) and in parent-offspring recognition, as in mammals and colonial birds (Searby & Jouventin, 2003). Essential for individual recognition is a signaler that sends unique individual recognition cues and a receiver who is able

to learn and memorize such cues to identify the signaler in the future (Tibbetts & Dale, 2007).

Individual recognition has been suggested for a wide range of taxa (Johnston, 2008) and can be used to discriminate all other categories of individuals (species, sex, social group and kin). Demonstrating individual recognition, however, requires to provide evidence that the animal is associating individually distinctive characteristics with a particular individual and not with a class of individuals, using sex, social group or kin recognition to identify, for example, a nest mate or a territorial neighbor. The distinction between class-level recognition and individual recognition has been profoundly controversial. A practical way to identify individual recognition is to determine whether an animal is able to recognize multiple individuals within a given class (Thom & Hurst, 2004).

Individual recognition requires both identity discrimination (can be performed on known or unknown individuals) and memorizing specific individuals. These two aspects have been studied in several laboratory rodent species. Hopp, Owren & Marion (1985) demonstrated that male rats discriminate between the odors of individual littermates. In house mice, Hurst *et al.* (2001) showed that despite other genetic differences between outbred wild-derived mice, the pattern of the major urinary proteins (MUPs) was essential for individual discrimination. Later, Cheetham *et al.* (2007) found strong evidence for the hypothesis that females use MUPs to discriminate individual males, regardless of other differences that influence an individual's scent, including MHC. Several experimental studies have thus demonstrated individual discrimination under captive conditions in laboratory or wild-derived rodents (Gheusi *et al.*, 1994), and investigated in detail its proximate mechanisms (e.g. Wolton, 1984; Gouat, Patris & Lalande, 1998; Colombelli-Negrel & Gouat, 2006). True individual recognition and memory for at least five individually distinctive odors has been demonstrated using the habituation–discrimination paradigm for golden hamsters *Mesocricetus auratus* (Johnston & Bullock, 2001; Johnston & Peng, 2008). However, what is currently missing is the demonstration that rodents use this ability under natural conditions. Rodents tested under the restricted conditions in captivity might show behavior patterns that are not observed in the field, as has been discussed in detail for paternal care (Brown, 1993). Here, we present a field study on individual recognition in a free-living mouse species, using a combined approach of observations and experiments.

Animals use their ability to recognize others in the wild, but we know little about which social category traits influence individualized relationships. For example, adult spectacled parrotlets, *Forpus conspicillatus*, preferred to respond to the contact calls of their mate, while subadults preferred the contact calls of their siblings (Wanker *et al.*, 1998). In general, individuals might prefer other individuals of the same age cohort they grew up with, and individuals of the opposite sex. However, in studies on individual recognition, these aspects have rarely been addressed, as the question was rather whether individuals can recognize other individuals and by which proximate mechanism.

In the present field study, we examined whether the group living, communally breeding African striped mouse, *Rhabdomys pumilio*, exhibits individual recognition. This species is well suited for observational studies in its natural environment, because it is diurnal, inhabits an open habitat and is easily habituated to the presence of observers (Schradin *et al.*, 2012). Striped mice form extended family groups of up to 30 adult males and females (Schradin & Pillay, 2004). They show amicable behavior toward group members, but act aggressively toward strangers (Schradin & Pillay, 2004). Although sharing the same territory and nest, they forage and feed solitarily during the day (Schradin, 2006). Thus, social interactions predominantly occur at the nest (Schradin & Pillay, 2004).

In order to determine whether striped mice have individualized relationships, we analyzed whether focal mice spent repeatedly more time over a period of two weeks with one specific group member and consistently showed more social interactions with this individual compared to other individuals. We defined such an individual as preferred partner. We then tested whether in the subsequent two weeks this determined partner was still preferred over other group members. Capitalizing on the fact that striped mice interact almost exclusively at their nest, we then tested whether wild striped mice modify their social behavior when the preferred social partner was removed from the group for 36 h (a time long enough to allow for the removed individual to be experienced as 'missing') or for 10–12 h (control period, with removal during the day, when no social interactions take place). Finally, we tested whether free-living striped mice differentiate by age, social category and by sex when establishing individualized relationships, predicting that social partners are mainly chosen from individuals with whom they grew up in the nest (the same age cohort) and the opposite sex.

Materials and methods

Study site and period

Data were collected in Goegap Nature Reserve (29°41.714′ S–18°01.564′ E) in South Africa. The vegetation type is classified as Succulent Karoo and is dominated by many ephemeral species and leaf succulent shrubs. The field site of approximately 10 ha is characterized by a dry river bed.

Study species

Striped mice in the Succulent Karoo form extended family groups that usually consist of one breeding male, one to four breeding females, and young adult philopatric males and females (offspring of the breeders) (Schradin & Pillay, 2004). Striped mice are diurnal and start activity at the time the sun shines over their nest (Schradin *et al.*, 2007). After up to 45 min sun basking, they leave their nest in order to forage for food solitarily, before returning to their nest in the afternoon (Schradin, 2006). At the nesting site, individuals show social behaviors, for example, sniffing each other, grooming or sitting in body contact with each other (Schradin & Pillay, 2004). In the hot dry season (January to May) with reduced food availability, no reproductive competition occurs and groups are stable (Schradin, König & Pillay, 2010). Data were collected during the dry seasons between 2007 and 2009, and in the dry season 2014.

Behavioral observations

Data were collected from 15 focal groups. Groups are permanently monitored via trapping, observations and radio-tracking, such that group composition and individual life histories (date of birth, age, social tactic) are known (Schradin & Pillay, 2004). Striped mice were trapped with Sherman-like metal traps (26 × 9 × 9 cm) that were baited with a mixture of bran flakes, sunflower oil and raisins. Traps were placed in the shade directly at the nesting site of a focal group and checked after 45–60 min. The trapped mice were weighed, sexed and received permanent ear tags with individual numbers (National Band and Tag Co., Newport, KY, USA). For easy identification in the field, each group member was individually marked with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa). The age of striped mice was estimated from their body mass at first trapping, using a population specific growth curve. One striped mouse of each focal group was equipped with a radio collar (Holohil, Carp, Ontario, Canada; 2.5–3.2 g). We used AOR 8000 wide range receivers (AOR USA Inc., Torrance, CA, USA) to determine the sleeping sites of the focal groups.

For behavioral observations, we chose four focus mice in each group: the breeding male, one breeding female, one young adult male and one young adult female. Breeders were individuals that had bred in the previous breeding season (September to December), young adults their offspring from the previous breeding season. Groups were observed with binoculars at their nests in the field from a distance of 10 m. Behavioral observations were done when mice were basking at their nest, that is, in the morning before the mice went foraging, and in the evening before the mice retired into their nest. Each focal group was observed over a period of 2 weeks, 5 days a week, morning and afternoon, which resulted in a total of 20 observations. Observations in the morning started with the first appearance of a focus mouse and were terminated when all focus mice had left for foraging or after a total observation time of 45 min. Mice bask for shorter periods during the hotter evenings, and observations started 30 min before the sun stopped illuminating the nest and were terminated with all the focus mice being out of sight for at least 5 min (having entered the nest). Because of the complexity of the situation with several mice coming to or leaving the nest, being visible or hidden inside the shrub, one zero recording was used with a matrix in which the presence or absence of each individual was recorded. Every 60 s it was recorded whether the focus mice were present, which other mice were present, and what social interactions were shown by and toward the focus mice. The following behavioral patterns in which the focus mice were involved in were recorded: (1) Sniffing each other; (2) sitting in body contact; (3) grooming.

Removal experiment

This removal test was done to determine whether the individuals that had been determined as preferred partner during the previous observations were really preferred. As such, we predicted that these preferred individuals would still be the preferred individuals during the observations performed during both controls and following experimental removal.

In order to avoid effects based on different social categories, the young adult male of each group was chosen as focus animal for the removal experiment, except for one group, where the male had disappeared (most likely due to predation), and the young female was used instead. After the behavioral observations period, the individual who had the most social interactions with the focus mouse was selected to be removed. This preferred social partner was trapped at the nest in the morning and was transported to the research station where it was transferred to a plastic cage (365 × 205 × 140 mm type III Perspex cage) in a separate room. The plastic cage was bedded with sand and enriched with one-half of an egg container, an empty toilet paper roll, some hay and toilet paper. The removed preferred social partner was fed twice a day with 2.5–3 g of hamster food (Brennco, Pretoria, South Africa) right after trapping and a small piece of fruit (apple or grape) one hour before it was taken back to the field. Water was provided *ad libitum*.

During controls, the removed mouse was released at its nest again after approx. 10 h, 1 h before evening observations began, to allow the individual to settle again in its home area. This procedure was repeated for 5 days. During the experimental treatment, the preferred social partner was only released after 36 h, staying overnight at the research station. This provided the focus mouse with the information that its preferred social partner was absent, as it did not return to the nest for one afternoon, night and morning. The experimental treatment was also repeated five times.

For half of the groups, first, the control treatments and then the experimental treatments were done; for the other ones, the order was reversed. All social behaviors between the focus mouse and its preferred social partner were recorded using the same protocol as during behavioral observations. Only the behaviors initiated by the focus mouse (not the removed social partner) were considered. While we cannot exclude that the behavior of the removed mouse had been affected by the removal, we observed no obvious change.

Statistical analysis

The software R (R Core Team, 2014) was used for statistical analysis. Data from 58 individuals from 15 groups of wild striped mice were analyzed for behavioral observations. We used the package lme4 (Bates, Maechler & Bolker, 2012) to perform a linear mixed effects analysis of the relationship between interaction scores of focus mice with group members and the category of social interaction partner. Interaction scores between a focal mouse and a partner were calculated as the sum of all social behaviors (sniffing, sitting in body contact, grooming) that were recorded during observations divided by the number of occasions the focal and the partner were present simultaneously. The group member with the highest interaction score was considered the preferred social partner.

We predicted a bi- or multimodal distribution of the observational data with the preferred individual alone representing

one mode, if a focal mouse has a specific preferred social partner. Bimodality was assessed by calculating the kurtosis and the skewness of the distribution of interaction scores. Skewness and kurtosis were calculated following Crawley (2007), while unimodality/bimodality was estimated using recommendations provided by Pearson. For validation, we compared our estimates of unimodality/bimodality with the density distribution plots (see Appendices S1 and S2). In each distribution plot, we marked the identified preferred social partner. We then determined for each focal individual whether the data of its preferred social partner was both (1) in a separate peak that (2) did not include data from any other group members (see Appendices S1 and S2). Thus, we determined whether the preferred social partner differed from all other group members (tested via Sign test).

We tested whether focus mice preferred to interact with the preferred social partner compared to all other group members by using all available data from all potential interaction partners and all 15 groups in one analysis, resulting in 7381 data points. One data point consisted of the focal individual and one of its potential (present) social partners, for each of the 20 observations. Partner type (preferred vs. non-preferred) was the independent categorical variable. Individual ID of the focus mouse was entered as random factor. *P*-values were obtained by likelihood ratio test (referred to as LRT) of the full model with the effect in question (partner type) against the model without the effect (package pbkrtest, Halekoh & Højsgaard, 2013). In order to exclude the large sample asymptotic assumption, we additionally compared the two models using a parametric bootstrap method (referred to as PBtest). For comparison and to demonstrate statistical consistency of observed effects, *P*-values obtained for the analysis of linear mixed models are presented for both tests, LRT and PBtest.

We used sign tests to determine whether social category, age and sex influenced individualized relationships. Data for 50 focal animals were available because eight focal individuals had to be excluded from analyses as data availability was incomplete.

Data from 12 out of 15 groups of wild striped mice were analyzed for removal treatments. Three groups yielded incomplete datasets and were therefore excluded from analysis. As above, we used LRT and PBtest for comparisons between social interaction frequencies of focus mice. We predicted that the individual that was identified as preferred social partner during observations will still receive most of the interactions afterwards, both in the control and in the experimental treatment. We tested for an effect of treatment (control and experiment) on social interaction frequencies.

Results

Kurtosis and bimodal distribution of data

In 46 out of the 58 focal mice, calculation of the modality distribution (relationship between skewness and kurtosis) was in agreement with our visual examination of the density distribution plots ($P < 0.001$, Sign Test), indicating that the two methods identified the same distributions (see Appendices S1 and S2). Our calculations indicated a unimodal distribution for 21 individuals, a bimodal distribution for 33 individuals and a multimodal distribution, for four individuals. The overall distribution of bi- or multimodal distributions within all cases (37 of 58) was significantly different from chance ($P = 0.048$, Sign Test). However, in only 32 out of the 58 cases were the data of the preferred social partner in a separate mode ($P > 0.05$, Sign test). For breeders alone, the distribution differed from chance (for 19 breeders, the data from the preferred social partner was alone in its own mode, for 10 breeders this was not the case; $P < 0.005$, Sign test), but not for young adults (only 13 out of 29, $P > 0.05$, Sign test).

During controls of the experiment, the data of preferred partners was in its own mode in nine out of 11 cases ($P = 0.07$, Sign test), and after experimental removals in seven out of 11 cases ($P = 0.54$, Sign test). Combining data from controls and experimental removals, the *P*-value approached significance (in 16 out of 22 cases the data of preferred individuals were in their own mode; $P = 0.052$, Sign test).

Behavioral observations

Using data from all observed focal mice, partner type affected interaction score (LRT: $\chi2(1) = 43.38$, $P < 0.001$; PBtest: test statistic 43.38, $P < 0.001$; Table 1). Interaction scores with preferred social partners were on average $5.85 \pm 0.88\%$ higher (estimate of the model $\pm$ SE, Fig. 1). For the subsample of young adults, which were used for further experiments, the same effect was found (LRT: $\chi2(1) = 13.75$, $P < 0.001$; PBtest: test statistic 13.75, $P = 0.002$; Table 1), with interaction scores with preferred social partners being on average $6.24 \pm 1.68\%$ higher.

Young adults associated significantly more often with other young adults than with breeders (males: $P < 0.001$; females: $P < 0.001$; Table 2), while no significant effect was found for breeders (males: $P = 0.092$; females: $P = 0.11$). No sex-specific effect was found for breeding males ($P > 0.99$), whereas breeding females associated significantly more often with males ($P = 0.012$; Table 2). Sex-specific effects were also obtained for young adult males ($P = 0.008$), which associated significantly more often with the opposite sex, but not for young adult females ($P = 0.79$). Young adults did not associate significantly more often with other mice of the same age (with which they possibly had shared the nest as pups; males: $P > 0.99$; females: $P = 0.75$).

Table 1 Relationships between interaction scores and partner type

		P-value	
Stage	Focus mouse category	LRT	PBtest
behavioral observations	50 of all categories	< 0.001	< 0.001
behavioral observations	15 young adults	< 0.001	0.002
removals: control	12 young adults	< 0.001	0.009
removals: experiment	12 young adults	< 0.001	< 0.001

P-values obtained by likelihood ratio test (LRT) and *P*-values obtained by parametric bootstrap method (PBtest) are shown for comparison.

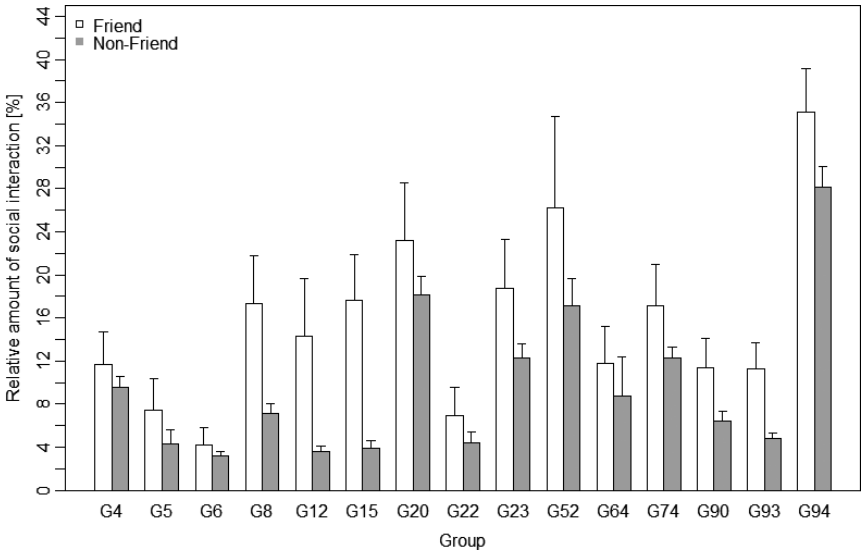

Figure 1 Mean (± SE; %) per group (G4–G94) of relative amount of social interaction scores of focus mice from 15 different groups with preferred social partners compared to all other group members during behavioral observations.

Removal experiment

Focal mice interacted significantly more with the individual that had been identified as preferred social partner during behavioral observations when compared to all other group members. This was the case both for the control treatment (LRT: $\chi2(1) = 7.6$, $P < 0.001$; PBtest: test statistic 7.6, $P = 0.009$; Table 1), as well as during the experimental treatments (LRT: $\chi2(1) = 37.814$, $P < 0.001$; PBtest: test statistic 37.814, $P < 0.001$; Table 1). Interaction scores with preferred social partners were on average 9.99 ± 3.61% higher during control and 19.72 ± 3.08% higher during experimental treatments.

Interaction scores with the preferred social partner during the experimental treatment were 7.69 ± 5.91% higher than during controls, but did not differ significantly (LRT: $\chi2(1) = 2.11$, $P = 0.15$; PBtest: test statistic 2.12, $P = 0.16$; Fig. 2). Seven of the 12 focus mice showed significantly more interactions with their preferred social partner during experimental than during control treatments, one did not differ significantly and four showed significantly more social interactions during controls than during the experiments.

For each male, data from observations, controls during experiments, and after experimental removal were plotted and compared with each other (Appendix S2). The individual identified as the preferred social partner during the first observation remained in its position within the plot of eight of the focal males both during controls and experiments, while for two focal males, its position remained similar, though the plot changed due to changes of other individuals ($P = 0.008$, Sign test with $N = 8$, number of exceptions = 0, 2 males excluded).

Table 2 Traits of potential importance for partner preference

focus mouse category	trait	preference	*k*	*N*	*P*-value
Young adult males	Age cohort	None	5	11	0.99
	Sex	Females	5	15	0.008
	Social category	Young adult	13	13	<0.001
Young adult females	Age cohort	None	6	10	0.75
	Sex	None	6	14	0.79
	Social category	Young adult	13	13	<0.001
Breeding male	Sex	None	6	13	0.99
	Social category	None	3	11	0.092
Breeding female	Sex	Males	1	11	0.012
	Social category	none	3	10	0.11

Age cohort: same (birth date less than 15 days apart, such that they could have shared the nest as pups) or different age cohort. Age was not included for breeders, as typically no other breeders of the same age cohort (born within 15 days of each other) was present. Social category: breeders versus young adult. The direction of the preference is indicated. *N*: sample size; *k* = number of exceptions; *P*-value two tailed, calculated via Sign Test.

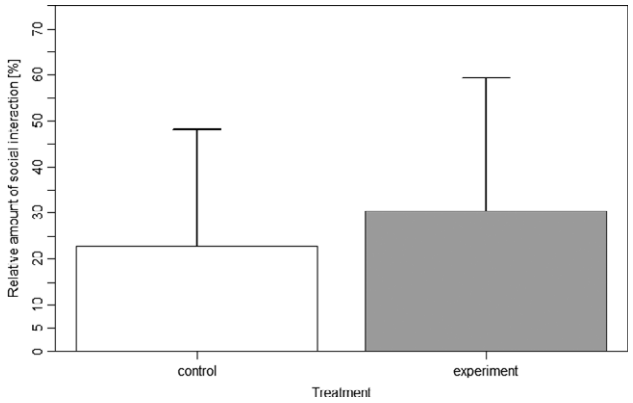

Figure 2 Mean (± SE; %) of relative amounts of social interactions of focus mice with preferred social partners during control and experimental treatments, LRT: $P = 0.15$, PBtest: $P = 0.16$.

Discussion

We found evidence that group living, diurnal African striped mice exhibit individualized relationships, consistently preferring a specific social partner, at least over a period of 4 weeks (2 weeks behavioral observations plus 2 weeks experiments; Table 1; Appendix S2). For most of the individuals, the data of the preferred social partner were in its own mode, indicating that they behaved differently toward this single individual when compared to all other group members. When the preferred social partner was removed for 36 h and then released again, striped mice on average increased the frequency of social interactions with it (Fig. 2), but the increase was not significant ($P = 0.16$). This is the first field study finding some support for individualized relationships in a free-roaming rodent, though striped mice failed to statistically prove individual recognition during experimental removals.

For every focus mouse, we could determine one preferred social partner, with which it had the highest interaction score in comparison to all other group members. This at first simply represented descriptive statistics, as there will always be one individual having the highest mean of interaction scores. However, we could show that the observed mean values with the determined preferred social partner differed significantly from the group`s mean. This analysis does not indicate how many preferred social partners existed (there could have been more than one). However, the modality data distribution for most focal individuals indicates that there was in fact often one preferred social partner (Appendix S1). Further, we then predicted that the identified preferred social partner would still be preferred over the next weeks, and we found this both during control and experimental treatments (Table 1). Importantly, the data distribution remained similar over all three observation periods (Appendix S2). Thus, we found a preference over at least 4 weeks, a significant period of time in a species that in the field does not live much longer than 1–1.5 years (with 30%–70% of individuals dying before being 1-year-old). It is also important to note that other individuals of the same social class (young adult male or female, female breeder) were typically spread over the rest of the data distribution and not concentrated in one node not shared by other social classes. This indicates that our results cannot be interpreted as evidence of class recognition, but are better explained by the existence of individualized relationships and individual recognition.

Removal of the preferred social partner for 36 h, such that the focus mouse could not interact with it for one afternoon, one night and one morning, did not significantly increase the social interaction score toward this partner. As a control, the social partner was removed during the day, when mice forage solitarily and do not interact with each other. The reasons for the absence of a significant effect could be a too low statistical power for the complex field conditions, as at least the mean difference was going into the predicted direction. For example, events within the group or within the home range might have had an effect on the results. Other confounding factors might have been changes in weather, especially ambient temperature and wind. In sum, the results of our experiments were inconclusive regarding the question of whether focus mice showed behavioral changes induced by the absence of their preferred social partner.

Our hypothesis that social partners are mainly chosen from the same age cohort and the opposite sex was only partly confirmed. Young adults associated preferentially with other young adults, but independently whether those were from the same age cohort (and thus were raised together in the nest) or not. The fact that they associated less with breeders could simply be a statistical effect, as striped mouse groups in the dry season have more young adults than breeders (Schradin & Pillay, 2004). If that would be the case, then this effect should be even stronger in breeders. However, breeders had as often other breeders as preferred social partner as young adults. Interestingly, male breeders and young females did not show any preference regarding the sex of their social partner, while both female breeders and young males preferred the opposite sex. In sum, striped mice did not prefer individuals with which they were raised in the nest, but young adults often preferred other young adults, while the sex of the social partner played a minor role.

Conclusion

This study was conducted in African striped mice in their natural environment and neither relied on trained animals, nor on food or water deprivation, as used in most operant conditioning experiments done in the context of recognition studies. The hypothesis that free-living striped mice have individualized relationships was tested by analyzing the relative amount of social interactions. The results revealed that the focus mice had prominent associations with one specific group member. Accordingly, the data of this preferred individual was often in its own mode within the data distribution, indicating that interactions with this preferred social partner stood out. However, striped mice did not significantly increase social interactions when the preferred social partner returned to the group after 36 h of experimental removal compared to a 10 h separation in the control situation. Our study did not aim at identifying benefits of individualized relationships, and future studies have to test whether in striped mice the formation of dyadic individ-

ualized relationships could improve benefits of group living, for example, during communal breeding, or might be important in recognizing individual neighbors. The ability of individual recognition is well documented for laboratory rodents, and we provide the first evidence that this might also occur in free-ranging rodents.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Behavioral observations.
Appendix S2. Comparison of modality plots for young focal males.