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Schradin, C

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Abstract

Understanding mammal social systems and behaviour can best be achieved through observations of individuals in their natural habitat. This can often be achieved for large mammals, but indirect methods have usually been employed for small mammals. I performed observations of the striped mouse (Rhabdomys pumilio)during the breeding season in the succulent karoo, a desert of South Africa. The open habitat and the diurnal habit of striped mice, together with the use of radio-telemetry, made it possible to collect data on activity patterns and social interactions over an entire activity period (whole-day follow). The striped mouse in the succulent karoo has been reported to form groups of one breeding male, two to four breeding females, juvenile and adult offspring of both sexes, and several litters. Accordingly, daily range size did not differ between males and females, but females spent more time foraging whereas males spent more time patrolling territory boundaries. Captive R. pumilio display biparental care, and in this study both sexes visited the nesting site during the day, possibly engaging in parental care. Mice travelled more than 900 m/day, mainly during the morning and afternoon, and rested in bushes during the hottest times of the day.

Whole day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent

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Running title: Whole day follows of striped mice

Abstract: Understanding of mammal social systems and behaviour can best be achieved through observations of individuals in their natural habitat. This can often be achieved for large mammals, but indirect methods have usually been employed for small mammals. I performed observations of the striped mouse (*Rhabdomys pumilio*) during the breeding season in the succulent karoo, a desert of South Africa. The open habitat and the diurnal habit of striped mice together with the use of radio-telemetry made it possible to collect data on the activity pattern and social interactions over an entire activity period (whole day follow). The striped mouse in the succulent karoo has been reported to form groups of one breeding male, 2-4 breeding females and juvenile and adult offspring of both sexes and several litters. Accordingly, daily range size use did not differ between males and females, but females spent more time foraging whereas males spent more time patrolling territory boundaries. Captive *R. pumilio* display biparental care, and in this study both sexes visited the nesting site during the day, possibly engaging in parental care. Mice travelled more than 900 metres per day, mainly during the morning and afternoon, and rested in bushes during the hottest times of the day.

Key words: Striped mouse, *Rhabdomys*, group living, parental care, activity pattern.

Introduction

Field studies during the previous decades have increased our knowledge about behaviour of mammals in their natural habitat. The focus of these studies has often been on large carnivores (e.g. Bertram 1975; McLeod 1990), ungulates (e.g. Brotherton and Rhodes 1996; Pluhacek and Bartos 2000) and primates (e.g. Goodall 1986; Smuts 1985) occupying open habitats, which offer favourable study conditions. Data were often collected in these studies using whole day follows (observations over an entire activity period) and radio-

telemetry. Despite the fact that rodents provide almost half of all mammalian species (Wilson and Reeder 1993), comparable data on these small mammals are rather scarce. Due to their cryptic nature, nocturnal habit and small size, studies of murid behaviour have normally been performed in captivity (reviews in Bronson 1979; Carter and Roberts 1997), under semi-natural conditions (e.g. Gerlach and Bartmann 2002; Lidicker 1976), or in nature by indirect methods such as trapping (e.g. Getz et al. 2000; Keesing 1998; Salvioni and Lidicker 1995), radio-tracking (e.g. Johannesen et al. 1997; Webster and Brooks 1981; Wilkinson and Baker 1988), the use of fluorescent pigments (e.g. Ribble and Salvioni 1990), or using genetic analyses (e.g. Ribble 1991). Only a few percentage of studies included direct behavioural observations. A pioneer in using direct behavioural observations to study small mammals the same way as others studied big mammals was Rathbun (1979) with his studies on elephant shrews. Direct observations have been done with diurnal species (Jackson 1999; Randall et al. 2000; Tchabovsky et al. 2001), some large nocturnal species (Sommer 2000) and even a few small nocturnal species (Agren et al. 1989; Wynne-Edwards 2003). However, in all the cited studies observations were either only anecdotic or over restricted time periods. To my knowledge, the only other study that has collected behavioural data over entire activity periods on small mammals in their natural habitat (apart from ground squirrels and marmots) has been done in the Djungarian dwarf hamster (*Phodopus campbelli*; Wynne-Edwards 2003).

In this paper, I present data of whole day follows of a murid rodent, the striped mouse (*Rhabdomys pumilio;* as the genus *Rhabdomys* is monotypic, this species is referred to *Rhabdomys* hereafter), a diurnal species with an adult body weight of 30 to 80g which can be directly observed at the field site in the arid to semi-arid succulent karoo, South Africa (Schradin and Pillay, 2003; Schradin and Pillay, 2004). Here, *Rhabdomys* lives in groups with typically one breeding male and up to four breeding females that rear their offspring communally. Group members share one nest and territory, but forage alone. Intra-group

relationships are amicable but inter-group interactions are aggressive (Schradin 2004). Offspring of both sexes remain in their natal group until the next breeding season in spring, and participate in territorial defence and nest construction. After the breeding season groups can contain up to 30 adults (Schradin and Pillay, 2004). The social behaviour of *Rhabdomys* in the succulent karoo is in great contrast to the social system of the same species in moist grasslands, where it is solitary (Choate 1972; Willan and Meester 1989; Schradin and Pillay 2005-b; Schradin in press).

The main aims of this study were to perform whole day follows in striped mice, and to compare the results with previous studies that had used ad libitum sampling (Schradin and Pillay, 2003; Schradin and Pillay, 2004).

Materials and Methods

Field site

The study was performed during the breeding season of 2002, lasting from September to October (Schradin and Pillay 2005-a), in Goegap Nature Reserve near Springbok in northwest South Africa. The vegetation consists of succulent karoo (Acocks 1988), one of 25 global hotspots of biodiversity (Myers et al. 2000). The field site is characterized by shrubs of the species *Zygophyllum retrofractum* and sandy areas, on which succulents and ephemerals are growing (Rösch 2001; photo in Schradin and Pillay, 2004).

An area of 200 m by 150 m was chosen as study site. The study area was occupied by nine different *Rhabdomys* groups. Approximately 40 breeding individuals were present at the start of the study and population size increased to about 200 adult individuals after the breeding season.

Trapping

Rhabdomys individuals were trapped using 60 live traps (26 x 9 x 9cm, like Sherman traps) for five days every 5 to 6 weeks. Traps were baited with a mixture of bran flakes, sea salt and salad oil. Trapping was done only in the early morning and late afternoon, but not during the hottest times of the day. Traps were placed in the shade of bushes and checked every hour. Trapped mice were sexed and weighed. Each mouse was assigned a number which was written on their sides using black hair dye (Inecto Rapid) which was not found to have any negative effects on their behaviour (Schradin and Pillay 2004). All mice showed signs of reproduction (males being scrotal, females having a perforated vagina). All parts of this study were approved by the animal ethics committee of the University of the Witwatersrand (AESC 2002-14-3; AESC 2002-23-3).

Radio-Tracking

Radio tracking was performed using an AOR 8000 wide range receiver, a Telonics RA-14K antenna, and MD-2C radio-transmitters (Holohil, Canada). Radio collars weighed 2.5g, which was 4.3% of body weight on average (variation: 3.5-5.4%).

Altogether ten breeding females and all six breeding males from six different groups were equipped with radio-tags. There were additional breeding females which were not followed: One in groups 3, 5 and 6; two in groups 1 and 4. Individuals were equipped with radio collars for a mean duration of 14.6 days (range: 12-21 days). Fourteen of the 16 mice used in this study were still present at the end of the study (the remaining two mice were preyed on by jackal buzzards, *Buteo rufofuscus*).

Radio-tracking helped to determine the position of a mouse when it was not visible after entering a bush. The focal mouse was located every three minutes to ensure its position when it was inside a bush.

Nest Observations

Nests were located by radio-tracking mice during the night, when mice were inactive. Observations of the occupants of nests during mornings and afternoons revealed the identities of individual mice that had no transmitters.

Whole Day Follows

Each focal animal was followed one time for an entire day. Mice were observed three or more days after they were equipped with radio tags, such that they had enough time to get used to them. Mice were followed by two consecutive observers from the time they emerged from the nest until they entered the nest for the night, i.e. from around 6.30 until 18.30. Mice were carefully followed at a distance of 5 to 10 m. Observations were performed using 10 x 42 binoculars. Start and end of following behaviours were recorded: no activity (the mouse is hidden inside a bush); in nest (the mouse re-entered the bush that contained its nest); foraging; patroling (moving without foraging). The frequency of all social activities was recorded: sniffing at another mouse; sitting in body contact with another mouse; sexual behaviour (male tries to mount a female); feeding together with another mouse in close proximity (less than one mouse length– approximately 20cm - away from each other); chasing another mouse. For social behaviours, the identity of any other mouse was recorded, when possible.

A map of the study area was drawn using a 2 x 2 meter grid. Bushes (N=95) in the study site were used as landmarks, and marked in the field with plastic flags. Movements of the focal mouse were recorded into the map, which was then used to establish range use and distance travelled.

Statistics

The grid cell method (Kenward 1987) was used to analyze spatial data. For determination of *daily range size*, the area of squares used by each focal mouse was connected to one area like when determining home ranges (see Fig. 2). *Range use* was calculated by adding up the number of squares actually used within this *daily range size* (see Fig. 3). Thus, *daily range size* was always larger than *daily range use*, and both values depended on each other.

All tests performed were non-parametric and two-tailed (Siegel and Castellan 1988). The Fisher's exact test was used to compare a found ratio against a ratio expected by chance (50:50). Tests were either done on individuals (each individual provided one data point in the analyses) using the Mann Whitney U-test, or on groups (each group provided one data point) using the Wilcoxon matched pairs rank sign test. When tests were performed on groups to compare data from males and females, mean values were taken for females when two females were followed per group. This was done such that per group one value for the females was obtained, allowing direct comparisons with the male data (Wilcoxon-test, paired data). All correlations were performed using the Spearman rank correlation (r_s). Data are presented as mean $\pm$ SE.

Results

Social Behaviour

There was no difference in the amount of time males and females spent in the nest during the day (females: 70 ± 74min; males: 100 ± 76min; Wilcoxon-test, T=8, N=6 groups, $p>0.6$). Five of the six focal males and seven of the 10 focal females were observed together with juveniles outside their nest. Males were 1.8 ± 1.7 times associated with juveniles, females 1.4 ± 1.3 times ($p>0.7$, U=26.5, U-test).

Males rarely (N=5, two males) associated with females from other groups, but all males frequently (N=28) associated with females from their own group ($p<0.05$, T=0, N=6, Wilxocon-test). One male was observed attempting to copulate with a female from another group, but his attempts were rejected.

Three of the focal males were seen chasing other mice four times. Two of the other mice were males, one was a female and one of unknown sex, all belonging to other groups. Focal males were never chased by other mice. Only one of the 10 focal females was seen to chase three mice (two females and one male) from other groups. Seven of the 10 focal females were chased on a total of 13 occasions: by females of other groups on five occasions and by males of other groups on four occasions; in the remaining four cases, the identity and sex of the mouse doing the chasing was unknown. All chases were observed near territory boundaries (see also Schradin and Pillay 2004).

Interactions with other Species

Aggressive interactions with other rodent species were observed more frequently (N=45) than intraspecific aggression (N=20; Fisher Test, p=0.03). Whistling rats (*Parotomys littledalei*) were observed chasing female striped mice on 13 occasions but never chased males. In

contrast, one male mouse chased a whistling rat. Whistling rats chased striped mice significantly more frequently than mice chased whistling rats (Fisher Test, p=0.0261). Striped mouse males were observed chasing bush karoo rats (*Otomys unisulcatus*) on four occasions; females were never observed chasing bush karoo rats. Bush karoo rats chased striped mice on 27 occasions, nine males and 18 females. Bush karoo rats chased mice significantly more often than vice versa (Fisher Test, p=0.0023).

Activity Pattern, Range Use and Travel Distances

Figure 1 shows the activity pattern of all focal mice. Females tended to spend more time foraging (404 $\pm$ 142 min) than did males (172 $\pm$ 106 min; p=0.09, T=2, N=6 groups, Wilcoxon-Test). When the analysis was performed at the individual rather than group level, this difference was significant (U-Test, U=6, m=10 females, n=6 males, p=0.008). Males were patroling for longer periods of time (83.3 $\pm$ 48.2 min) than females (15.5 $\pm$ 14.2 min; Wilcoxon-Test, T=0, N=6 groups, $p<0.05$).

Figure 2 shows the *daily range sizes* of eight focal individuals from three groups. Ranges of the mice from the same group overlapped more with one another (72.1 $\pm$ 15.5%) than with ranges of mice from other groups (31.3 $\pm$ 9.3%; Wilcoxon-Test, T=3, N=16, p=0.0002). *Daily range size* of males (1492 $\pm$ 974 m^2) did not differ from those of females (1449 $\pm$ 615 m^2; Wilcoxon-Test, T=10, N=6 groups, $p>0.9$). There was no difference between the sexes in the overlap of their daily ranges with those of individuals from other groups (males: 31.2 $\pm$ 8.6%, females: 29.9 $\pm$ 12.4%; Wilcoxon-Test, T=9, N=6 groups, $p>0.8$).

The size of the *daily range use* of males (1052 $\pm$ 539 m^2) was not larger than that of females (972 $\pm$ 388 m^2; Wilcoxon-Test, T=10, N=6 groups, $p>0.9$). Figure 3 shows the pattern of *daily range use* of the males and one female of each of the six focal groups. Data

from the additional four females are not included in the figure, as there was substantial overlap with the *daily range use* of their group mates (see Fig. 2), making inclusion of all data on the figure untidy.

On average, females travelled 918 ±400 m/day (range: 507 – 1498m) and males 933 ± 444 m/day (range: 276 – 1618m; Wilcoxon-Test, T=9, N=6 groups, $p>0.8$). There was a significant correlation between distance travelled during the day and both range size ($r_s=0.51$, N=16, $p<0.05$) and range use ($r_s=0.574$, N=16, $p<0.03$).

Discussion

There are several limitations of this study, especially the fact that each individual was followed only once. As the breeding season is only two months long (Schradin and Pillay 2005-a), the time was limited. Thus, to get a representative sample size, I decided to follow as many individuals as possible instead of following a few individuals for several times. The fact that the behaviour of the different males and females was very similar indicates that the data collected is representative. With this data it was possible to validate data collected in a less time consuming way during other studies (Schradin and Pillay 2003; Schradin and Pillay 2004; Schradin 2004; Schradin 2005). Another aspect that cannot be easily estimated is the effect of the observer on the behaviour of the focal animals. The study animals were well habituated to the presence of observers and mice often approached us. The small distance between mice and observer did obviously not prevent mice from foraging, chasing away intruders, being associated with juveniles and initiating sexual behaviour.

Activity Pattern and Range Use

The activity pattern of *Rhabdomys* was characterized by foraging in the morning and late afternoon, and resting inside bushes during the hottest times of the day. Ambient temperature measurements at the research station 100 meters away from the field site recorded mean daily maximum temperatures of 28 °C for the study days with a maximum of 32 °C in the shade. Although it was not always possible to observe mice in bushes, on the occasions when mice were visible, the mouse was typically resting, with its belly lying flat on the ground. This behaviour is typical of rodents inhabiting hot environments and is thought to release heat from the body to the ground (Dean and Milton 1999).

The interpretation that *Rhabdomys* lives in groups was supported by a high overlap of daily ranges from mice sharing one nest but not from mice of different nests, and by males having similar *daily range sizes* as females (in contrast to rodent species where males are not group living but follow a roaming strategy and thus have much larger home ranges; Ostfeld 1990). The same has been reported elsewhere for home range sizes and overlap (Schradin and Pillay 2004; Schradin and Pillay 2005-b). The reported *daily range size* here is larger (nearly 1500 m^2) than the home range sizes reported using ad libitum sampling (mean: 975 m^2, Schradin and Pillay 2004) and radio-tracking (mean 1109m^2, Schradin and Pillay 2005-b). This is surprising, as one would expect mice to use during one activity period only a part of their home range, such that the *daily range size* should be smaller. The difference between home range size and *daily range size* is that the home range was measured over a larger time period of seven days within two weeks, during which the position of each mouse was determined six times a day (Schradin and Pillay 2005-b), whereas the *daily range size* in this study has been measured over a single day, but with continuous observations during the entire

activity period. The *daily range use*, i.e. the area actually visited by the mice, was smaller with 1052m^2 for males and 972m^2 for females, but still surprisingly large.

Similar to *daily range size* and *use*, there was no sex specific difference in the daily distance travelled. Mice travelled a surprisingly large distance over a day, more than 900 meters on average, and as much as 1618 meters in one subject. This was due to the fact that mice visited several areas many times during one day. The reasons for this are unknown, but seeking cover during foraging, and limited capacity of the stomach (mice had to digest and then come back to feed again) are potential reasons. Also, mice visited large areas without foraging, possibly to obtain information about food availability and presence of other mice in their home range. There are few other studies that measured or estimated travel distances in rodents, apart from dispersal distances (Stenseth and Lidicker 1992). In captive *Ctenomys talarum*, individuals travel on average 180 meters a day (Facundo and Daniel 2003).

Comparison of male and female reproductive strategies

It was not possible to observe parental behaviour directly inside nests, but only to measure the time mice spent in the nest during the day. Every focal mouse was observed visiting the nest during the day. As in captivity (Schradin and Pillay, 2003), I found no difference between the sexes in the amount of time spent in the nest, and males were as often associated with juveniles outside the nest as were females.

This study was conducted during the breeding season when females were simultaneously lactating and pregnant because of post-partum oestrus (Dewsbury et al. 1984). Females can rear two to three litters during the breeding season, with on average five pups per litter (Schradin and Pillay, 2005-a). Females spent more than twice as much time foraging than did males, reflecting the high energetic demands of lactation and pregnancy.

Males did not spend as much time foraging as females. It was evident that males sometimes changed their behaviour from foraging and started running along territorial boundaries, moving much faster than was done during foraging. I suggest that such behaviour would have allowed detection of strangers as well as potential extra-group mates inside their territories, as during this paroling a larger area was covered per time unit than during foraging. Whereas *Rhabdomys* is clearly a territorial species (Schradin and Pillay 2004) with males being especially aggressive towards strange males (Schradin 2004), aggressive territorial interactions were observed only infrequently in this study. In agreement with the cited previous studies, both sexes participated in territorial defence.

Interspecific relationships

Two other diurnal rodent species occur at the field site, the whistling rat (*Parotomys littledalei*), which occupies burrows, and the bush karoo rat (*Otomys unisulcatus*), which builds stick lodges inside shrubs (Jackson et al. 2002). Both rat species weigh about 120g and are thus two to three times larger as *Rhabdomys*. The commonly observed aggressive encounters between striped mice and the other rodent species cannot be explained by different population densities since *Rhabdomys* occurs in much higher numbers (pers. observ.: more than 200 marked mice at the field site compared to about 60 individuals of each rat species). Instead, the aggressive encounters may be explained by differences in range use and nesting habits. Whistling rats and bush karoo rats are relatively bound to their nests, and forage mainly in its close proximity (Jackson 2001). In contrast, *Rhabdomys* uses a much larger area. Foraging striped mice are therefore likely to pass in close proximity to burrows and nests of rats and their inhabitants. A possible functional reason for rats attacking mice is defence of nesting sites, as *Rhabdomys* uses both whistling rat burrows as well as bush karoo rat nests as

nesting sites (Schradin and Pillay 2004). In fact, in absence of bush karoo rats, *Rhabdomys* groups take their nests over (Schradin 2005).

Conclusions

The results presented here are mainly descriptive and give no explanations for the observed patterns. However, description always has to precede hypothesis generation, which would then allow for testing and explanation. To my knowledge this is the first study to provide behavioral data for the entire activity period for single individuals of a mouse species in its natural environment. This study demonstrated that the best period for focal observations of future studies of *Rhabdomys* will be early morning and late afternoon, and it generally provided support for previous field studies that had used ad libitum sampling.

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Figure legends

Fig. 1.

Main activity of the 16 focal animals from six groups during the day, from the time they emerged from the nest between 6.00 and 7.00, and withdrew into the nest between 18.00 and 19.00. F: Female, M: Male.

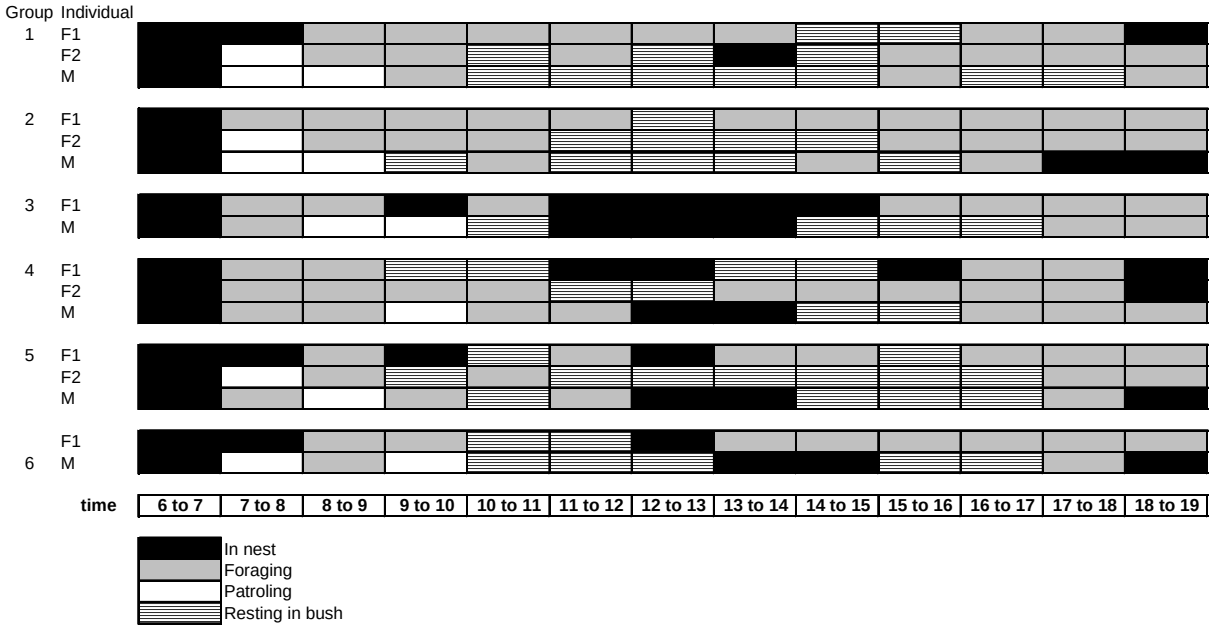
Fig. 2.

Daily range use of eight focal mice from the groups 2, 4, and 6. Mice of one group have overlapping daily ranges. The data of the other three groups are excluded for clarity. The ranges used by mice from these three excluded groups would have been between the three presented groups.

Fig. 3.

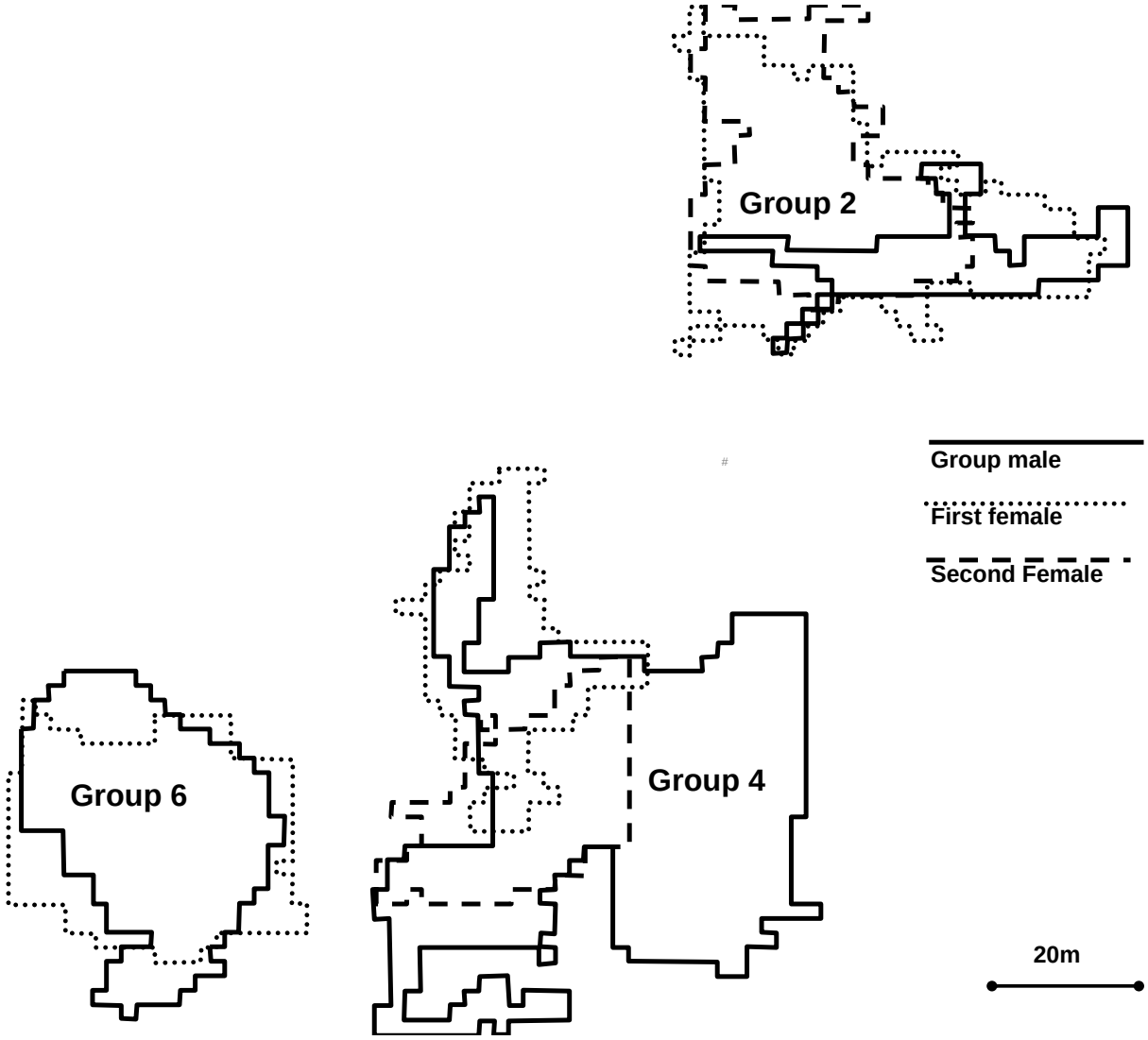
Range use by (a) one focal female per group and (b) the group males of six groups. The 2 x 2 m^2 in the study grid are shown. The quadrates used by each focal mouse are marked and the color represents how often the mouse entered the quadrate (see legend in figure). Quadrates used by more than one mouse are marked by X and no attempt was made to show how often this quadrate was used. For identification of daily used ranges, the daily range is framed for individuals, alternating with black lines, black dots, and one broken line, to make distinction between groups easier. Nest sites are indicated by “N”.

449 **Fig. 1.**


Group
Individual
1
F1
F2
M
2
F1
F2
M
3
F1
M
4
F1
F2
M
5
F1
F2
M
6
F1
M
time
6 to 7
7 to 8
8 to 9
9 to 10
10 to 11
11 to 12
12 to 13
13 to 14
14 to 15
15 to 16
16 to 17
17 to 18
18 to 19
In nest
Foraging
Patroling
Resting in bush

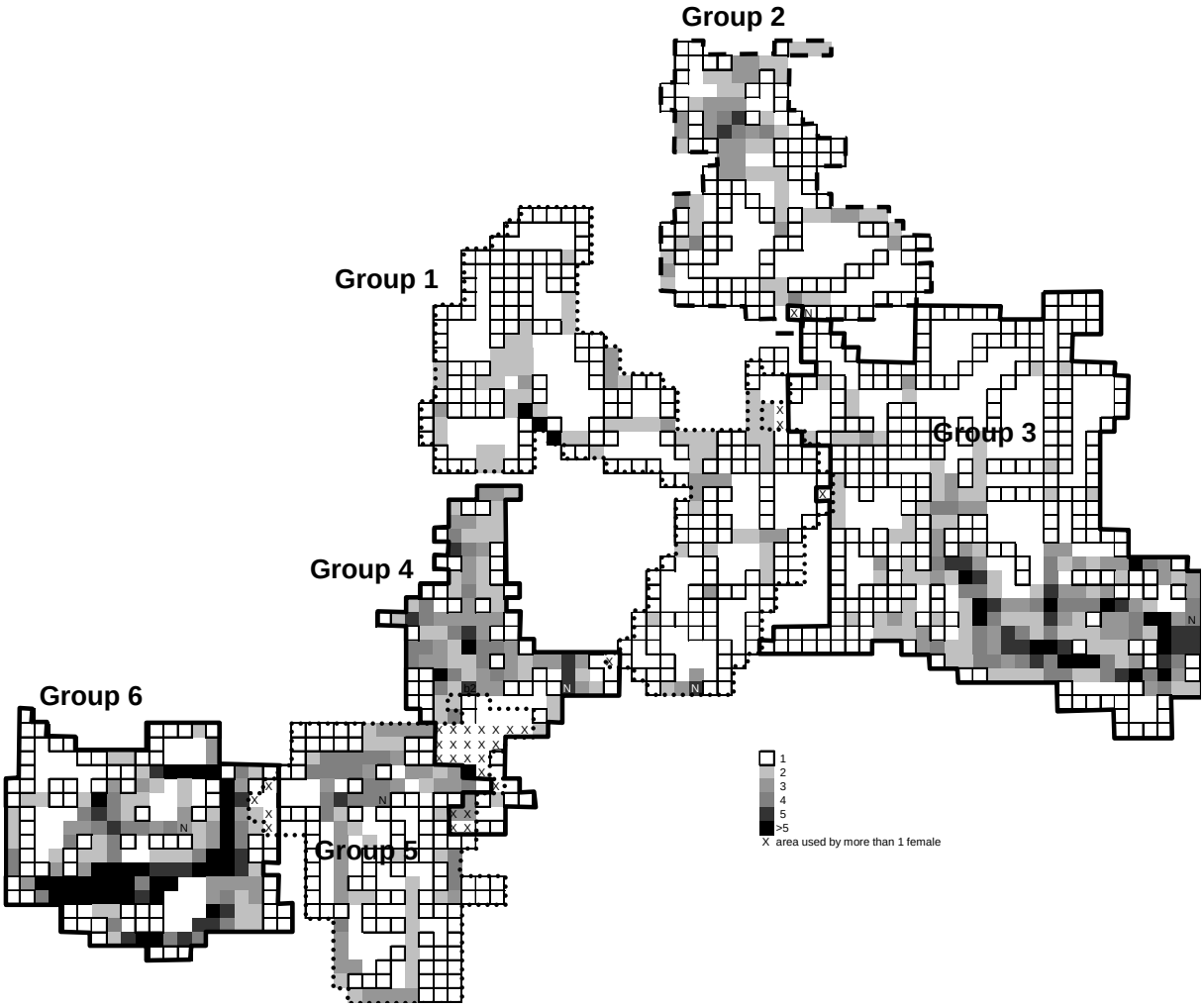
450

451 **Fig. 2.**


Group 2
Group male
First female
Second Female
Group 6
Group 4
20m

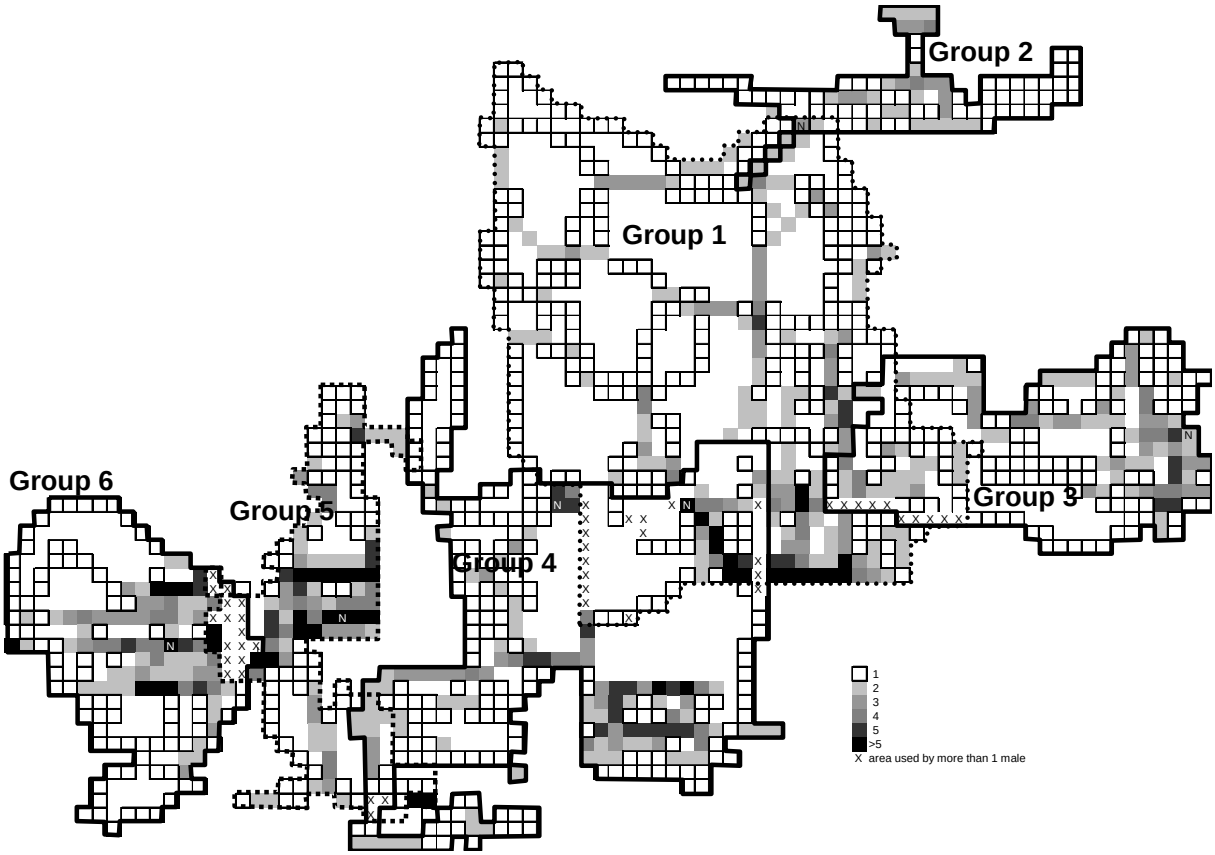
452

453 **Fig. 3a.**



454

Fig. 3b.


Group 2
Group 1
Group 6
Group 5
Group 4
Group 3
1
2
3
4
5
>5
X area used by more than 1 male