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NEST-SITE COMPETITION IN TWO DIURNAL RODENTS FROM THE SUCCULENT KAROO OF SOUTH AFRICA

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Species that occupy the same area and use the same resources must either compete with each other or find ways to minimize competition. For rodents, 1 important resource is nesting sites. In this study I present data from direct behavioral observations in the succulent karoo of South Africa that show aggressive interactions between bush karoo rats (*Otomys unisulcatus*) and striped mice (*Rhabdomys pumilio*). Because both species nest in shrubs, the potential exists for interspecific competition for nesting sites. Because of a severe drought in 2003, the bush karoo rat became locally extirpated. As a result, striped mice nested significantly more often in shrubs that contained bush karoo rat nests than in 2001 and 2002, when the population density of bush karoo rats was high. Furthermore, I observed that striped mice never nested in the shrub *Lycium cinerum*, the favorite nesting site of bush karoo rats, when bush karoo rats were present, but regularly used these nesting sites after bush karoo rats became extirpated. I conclude that striped mice and bush karoo rats compete actively for access to preferred nesting sites in the succulent karoo.

Key words: interspecific competition, nest, *Otomys unisulcatus*, *Rhabdomys pumilio*, succulent karoo

Reproductive success of animals is restricted by their access to important resources such as food, mating partners, and shelter. Shelters provide protection against predators and harsh environmental conditions such as extreme temperatures, wind, and rain. Thus, shelters offer safe sleeping and nesting sites. If these are of limited supply, competition for this resource will occur. For example, intraspecific competition for nesting sites is common in fish (Draud and Lynch 2002; Kroon et al. 2000), and the same has been reported for small mammals (Dooley and Dueser 1996; Radespiel et al. 2003).

Territoriality to defend space against members of the same species also functions to defend nesting sites within territories (Schradin 2004; Stamps 1994). However, suitable nesting sites might not only be used by conspecifics, but also by other species that occur sympatrically. For example, in mouse lemurs, sympatric species can avoid competition by choosing different categories of sleeping sites (Radespiel et al. 2003). Nest-site selection also can be dependent on the presence of other species. For example, the white-footed mouse (*Peromyscus leucopus*) prefers to nest in trees, as does the closely related cloudland deer mouse (*P. maniculatus nubiterrae*). However, when both species occur together, the cloudland deer mouse displaces the white-footed mouse from preferred arboreal nesting sites (Dooley and Dueser 1996).

The succulent karoo of South Africa is a semidesert with winter rain of on average 150 mm per annum at my field site and extreme daily fluctuations in temperature, which can be $<0°C$ in winter and $>40°C$ in summer (Cowling et al. 1999). Two diurnal rodent species occur sympatrically here: the bush karoo rat (*Otomys unisulcatus*) and the striped mouse (*Rhabdomys pumilio*). The bush karoo rat is a strict folivore (Plessis et al. 1991), whereas the striped mouse is an omnivore, thus reducing competition between the 2 species. However, both species nest in shrubs. Striped mice build nests with soft hay in shrubs above ground, and large shrubs can contain more than 1 nest, although 1 shrub is always exclusively used by a single striped mouse group that uses only 1 nest at a time (Schradin and Pillay 2004). Bush karoo rats build extensive stick lodges in shrubs; these lodges can be >1 m high and there is always only 1 stick lodge per shrub (Brown and Willan 1991; Jackson et al. 2002). Stick lodges offer protection against the extreme climatic conditions of the succulent karoo and probably more protection than the simple hay nests of striped mice. Temperature variation in nests of bush karoo rats is much less pronounced than ambient temperature variation, with temperatures during cold winter nights being about 4°C higher than outside and during hot summer days being 14°C lower than outside (Plessis et al. 1992). Thus, striped mice might take

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advantage of deserted bush karoo rat nests that offer better protection against climatic harshness than their own simple hay nests and I often observed striped mice nesting in abandoned bush karoo rat nests.

In this study, I investigated factors influencing nest-site choice of both species and the potential for interspecific aggression and competition. I had 3 objectives. The 1st was to present behavioral data on aggressive interactions between striped mice and bush karoo rats. Because bush karoo rats (body weight about 120 g) weigh 2–3 times as much as striped mice (adult body weight 40–80 g—Schradin and Pillay 2005c), and because physical strength and body weight often are correlated (Parker 1974; Schradin and Lamprecht 2002), I predicted that bush karoo rats would win aggressive encounters. The 2nd was to investigate how bush karoo rats choose their nesting sites, that is, to determine which factors distinguish shrubs used as nesting sites compared to shrubs not used. The factors investigated were the circumference and height of the shrub, the grade of foliage of the shrub, the shrub species, and the number of other shrubs in the surrounding area. Third, I wanted to test whether bush karoo rats might displace striped mice from their preferred nesting sites, that is, whether the presence of bush karoo rats influences where striped mice nest. Because bush karoo rats nests are likely to offer better protection than striped mouse hay nests, I predicted that striped mice would take over bush karoo rat nests if the heavier bush karoo rats were absent from the study site. I was able to test this prediction during the 3rd field season in 2003, when bush karoo rats were absent at my field site because of a severe drought that led to a larger decrease in the bush karoo rat than in the striped mouse population.

Materials and Methods

Study area and period.—Data were collected during the breeding season of both species in spring 2001, 2002, and 2003 (each year from September until December). The study was conducted in Goegap Nature Reserve near Springbok in the Northern Cape of South Africa. The vegetation is characterized as succulent karoo (Cowling et al. 1999; Rösch 2001), a biodiversity hot spot (Myers et al. 2000). The main vegetation consists of shrubs (mainly *Zygophyllum retrofractum* and *Lycium cinerum*) and sandy areas covered by succulents such as *Mesembryanthemum guerichianum* and ephemerals (Rösch 2001). The climate of the succulent karoo is semiarid to arid. In Goegap, annual rainfall is approximately 150 mm and occurs mainly during winter (Rösch 2001). Temperatures regularly fall below 0°C during winter and spring nights, but can be >40°C during summer days. Daily temperature fluctuation is about 0–25°C in spring, and 10–35°C in summer.

Trapping and marking of animals.—All parts of the study involving live animals followed guidelines of the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp) and were approved by the Animal Ethics Committee of the University of the Witwatersrand. Both study species are diurnal. Adult striped mice at my field site have an adult body weight of 40–80 g, and males are slightly heavier than females (Schradin and Pillay 2005c). The bush karoo rats at my study site have an average adult body weight of 121 g. Striped mice and bush karoo rats were livetrapped with metal traps (locally produced Sherman traps; 26 × 9 × 9 cm) at the field site of 150 × 200 m. Traps were placed around shrubs where striped mice and bush karoo rats were nesting. Locations of nests were known from previous observations. Traps, baited with a mixture of bran flakes, currants, sea salt, and salad oil, were placed in the shade and checked every 30 min. The trapped animals were sexed, weighed, and individually marked. A number given to each trapped animal was written with a fine brush on the side of each animal with black hair dye (Inecto Rapid, Rapido, Pinetown, South Africa; photograph in Schradin and Pillay [2004] and at http://www.stripedmouse.com). Striped mice were trapped and marked all 3 years, whereas bush karoo rats were only marked in 2001.

The year 2003 was the driest since 1984 (information from weather station in Springbok, 20 km from our study site). Only 5 mm of rain was recorded in autumn and winter (April–July), the main rainy season, whereas the average for the same period since 1960 (when the weather station began operation) was 102 mm ± 51.5 *SD*. This drought severely affected the vegetation, which normally starts to grow in autumn (May) and has its peak growth season in July and August. In contrast, in 2003, no green plant material was present in July or August. After heavy rains finally fell at the end of August, plant growth started. Although no direct measurements were made, we estimated that green plant production in 2003 was less than 50% that in 2001 and 2002. This drought led to a significant decline in population density of both species. Although a population of the omnivorous striped mouse survived, the folivorous bush karoo rat was nearly extirpated, that is, no bush karoo rat was observed or trapped at the field site. It became evident that the small population of striped mice that had survived was found along the dry riverbed that runs through the field site. Thus, to obtain enough data for striped mice, in 2003 I also trapped along 1 km of the dry riverbed.

Behavioral observations.—Behavioral observations were only performed in 2001. As striped mice left their nest early in the morning to forage throughout their territory (Schradin 2005), they were observed by focal animal sampling (Altman 1974). In contrast, bush karoo rats are much more tied to their nest and would leave only for short foraging excursions, always returning to their nests. Thus, for this central-place forager, focal nest observations were performed.

Striped mice individually marked with hair dye were observed in the field by direct observation and by using 10 × 42 binoculars. Observations were performed during the peak activity period of striped mice, that is, during mornings (0600–1100 h) and afternoons (1600–1930 h—Schradin 2005). Every time a striped mouse was identified, focal animal sampling observations were performed and the individual was carefully followed for a distance of about 10 m until it disappeared. Altogether, 210 h were spent in the field, during which focal observations could be performed for 52.1 h. The rest of the time no focal animal was present. Altogether, 477 focal observations were performed with a duration of 1–45 min ($\bar{X} = 6.5$ min). Here I report all interspecific interactions observed (observations of intraspecific interactions are reported in Schradin and Pillay [2004]).

In addition to focal observations of striped mice, 17 individually marked bush karoo rats were observed. Focal observations were made at 9 occupied nests, with each nest being observed 6 times for 45 min. During this time, bush karoo rats spent a total of 80 min adjacent to their nests, enabling the collection of behavioral data; the rest of the time they were in their nests.

Two behavioral patterns were recorded both during focal animal and focal nest sampling. These were a striped mouse in proximity to a bush karoo rat, that is, within 2 body lengths; and 1 species chasing the other.

Determination of nesting sites of striped mice.—Hay nests of striped mice are hidden inside shrubs and it cannot be determined from outside whether a shrub contains a nest. Because striped mice basked adjacent to their nests in the mornings and afternoons, it was possible to detect nesting sites by observations in the field (Schradin and Pillay 2003, 2004). I used this method during all 3 years. In 2002 and 2003, I additionally determined nesting sites by radiotracking striped mice at night, when they were inactive in their nests (Schradin and Pillay 2005a). A total of 56 striped mice (21 males and 35 females) were radiotracked during 36 nights in 2002 and 51 striped mice (26 males and 26 females) during 80 nights in 2003. Each year, I recorded the species of shrub the striped mice were nesting in and whether nesting sites contained a bush karoo rat nest or not.

Random sample of shrubs in areas previously occupied by bush karoo rats.—In spring 2001 and 2002, the field site was inhabited by about 30 bush karoo rats/ha. In spring 2003, after the severe drought of the previous winter, the bush karoo rats were absent, that is, no bush karoo rats were observed or trapped, and no stick lodges showed indication of being inhabited by a bush karoo rat (no droppings or food plants carried to the nests). However, the stick lodges they had built as nests were still intact and visible, such that it was possible to study bush karoo rat nesting sites in 2003. Shrubs were sampled in an area of 47 ha, including the field site and surrounding areas. To get a representative sample, shrubs were chosen at random, measuring 1 shrub every 15 m while walking through the area along lines 15 m apart. A total of 424 shrubs were sampled. For each shrub, the following 6 parameters were recorded: the presence of a bush karoo rat nest, using 4 categories, 0 (no nest), 1 (a small nest with a height below 20 cm), 2 (a medium-sized nest with a height 20–50 cm), and 3 (a large nest that occupied nearly the entire shrub, with a height above 50 cm); the circumference of the shrub in cm; the height of the shrub in cm; the number of other shrubs in a radius of 5 m, using 3 categories, 1 (0–5 shrubs), 2 (6–10 shrubs), or 3 (more than 10 shrubs); grade of foliage, using 5 categories, 0 (no foliage), 1 (25% of foliage), 2 (50% of foliage), 3 (75% of foliage), and 4 (full foliage); and the species of the shrub.

Dissection of 1 bush karoo rat nest inhabited by a striped mouse group.—In December 2001, 1 shrub (*Z. retrofractum*) containing a medium-sized bush karoo rat nest that was used by a striped mouse group as nesting site was dissected. Because dissection of shrubs leads to habitat destruction, only 1 nest was dissected and no permit for dissecting more shrubs was issued. By using hedge clippers, I carefully removed 1 branch after another, until the hay nest of the mouse group was laid open.

Data analyses.—All tests performed are 2-tailed. The Mann–Whitney *U*-test is abbreviated as *U*-test, Fisher's exact test as Fisher test, the Wilcoxon matched pairs rank sign test as Wilcoxon test, and the Kruskal–Wallis test, which was followed by Dunn's posttest, as KW-test. To analyze the factors that might influence how bush karoo rats chose their nesting sites, I performed multiple regressions for the 2 main shrub species that were used as nesting sites (*L. cinerum* and *Z. retrofractum*), with nest size being the dependent variable and circumference, height, grade of foliage, and number of shrubs in the surrounding area being independent variables. For striped mouse nests, data for the years 2001 and 2002 were combined for the period with bush karoo rats and compared to data from 2003, when bush karoo rats were absent. These periods are abbreviated as "BKR present" and "BKR absent" (BKR for bush karoo rat), respectively. Date are presented as mean ± *SEM*.

Results

Objective 1: aggressive interactions between bush karoo rats and striped mice.—Focal animal observations of striped mice revealed that striped mice came in proximity to bush karoo rats 18 times. All 18 cases resulted in aggression (sign test: $P < 0.001$). Striped mice were chased 16 times by bush karoo rats and an adult male striped mouse was observed to chase a bush karoo rat twice. Bush karoo rats significantly more often chased striped mice than vice versa (sign test: $\chi = 2$, $P = 0.002$; $n = 18$).

Focal observations of bush karoo rats revealed the same result. Altogether, striped mice were in proximity to bush karoo rats 11 times and all cases resulted in the bush karoo rat chasing the striped mouse (sign test: $\chi = 0$, $P < 0.001$; $n = 11$).

Objective 2: choice of nesting sites by bush karoo rats.—Of the 424 shrubs sampled, 23% contained a bush karoo rat nest (Table 1). Of these, 42% were small nests, 49% were medium-sized nests, and 16% were large nests (Table 1).

TABLE 1.—Random samples of shrubs in the succulent karoo of South Africa and the size of bush karoo rat (BKR) nests found in the shrubs.

	Zygophyllum retrofractum	*Lycium cinerum*	*Deverra aphylla*	Other shrub species	Total
No BKR nests	258	51	5	14	328
Small BKR nests	27	6	0	4	37
Medium-sized BKR nests	25	18	0	3	46
Large BKR nests	4	7	0	2	13
Total shrubs	314	82	5	23	424
Total BKR nests	56	31	0	9	96

I compared whether the probability of finding a bush karoo rat nest within a shrub differed between shrub species (*Z. retrofractum*, $n = 314$; *L. cinerum*, $n = 82$; other shrub species, $n = 28$), and found an overall significant difference (KW-test: KW $= 19.7$, $P < 0.0001$; Table 1). Post hoc analyses revealed that bush karoo rats nested significantly more often in *L. cinerum* than in *Z. retrofractum* (Dunn's posttest: rank difference $= -47.4$, $P < 0.001$; Table 1). All other comparisons were nonsignificant.

A multiple regression for factors influencing nest-site choice for *L. cinerum* revealed a significant result ($P < 0.03$; Table 2), with 13.6% of the variance being explained by the model. The only significant factor influencing whether a shrub was used as a nest was the number of shrubs in proximity, with bush karoo rats nesting significantly more often in areas where more vegetation was present ($P < 0.02$). The multiple regression for *Z. retrofractum* was significant ($P < 0.0001$; Table 2), with 33.3% of the variance being explained by the model. Bush karoo rats nested more often when the circumference of the shrubs was larger ($P < 0.0001$) and when more green foliage was present ($P < 0.01$).

Objective 3: do striped mice take over bush karoo nests?—For striped mice, 28 nesting sites were found when bush karoo rats were present and 75 when bush karoo rats were absent (Table 3). Comparisons between striped mice and bush karoo rats showed that striped mice nested significantly more often in *Deverra aphylla* (Fisher test: $P = 0.0001$). In contrast, bush karoo rats nested relatively more often in *Z. retrofractum* (Fisher test: $P = 0.008$), and in *L. cinerum* than did striped mice (Fisher test: $P < 0.0001$). However, under the BKR absent situation, striped mice nested as often in *L. cinerum* as

TABLE 2.—Characteristics of shrubs from the random sample, shrubs with bush karoo rat nests of different sizes, and striped mouse nests when bush karoo rats (BKR) were either present or absent in the succulent karoo of South Africa.

	Sample size	Circumference (in cm)	Height (in cm)	Grade of foliage[a]	Grade of surrounding vegetation[b]
Random sample	424	531 ± 9.7	77.3 ± 1.8	1.1 ± 0.0	1.6 ± 0.0
No BKR nest	328	483.5 ± 9.6	72.1 ± 2.1	1.0 ± 0.0	1.7 ± 0.1
Small BKR nest	37	637.5 ± 23.6	81.2 ± 3.2	1.2 ± 0.1	1.6 ± 0.1
Medium-sized BKR nest	43	699.5 ± 27.4	97.1 ± 3.2	1.4 ± 0.1	1.7 ± 0.1
Large BKR nest	13	842 ± 72.0	124.1 ± 11.1	1.4 ± 0.3	1.5 ± 0.2
Striped mouse nest with BKR	7[c]	1,060 ± 255.4	114.1 ± 12.0	2.7 ± 0.4	1.0 ± 0.2
Striped mouse nest without BKR	72[d]	965.2 ± 48.5	110.1 ± 5.0	2.3 ± 0.1	2.2 ± 0.1

[a] 0: no foliage, 1: 25%, 2: 50%, 3: 75%, 4: full foliage.
[b] Measured as other shrubs within a radius of 5 m: 1 (0–5 shrubs), 2 (6–10 shrubs), or 3 (more than 10 shrubs).
[c] Data for the other 21 nesting sites are not available.
[d] Nesting sites within grass fields of *Juncus acutus* are not included because this would lead to an overestimation of circumference.

bush karoo rats had done in previous years (Fisher test: $P = 0.17$). Striped mice used *L. cinerum* significantly more often as nesting sites when bush karoo rats were absent (Fisher test: $P = 0.006$).

Striped mice nested significantly more often in shrubs containing bush karoo rat nests under the BKR absent than under the BKR present situation (Fisher test: $P < 0.01$; Fig. 1). Seven of 28 striped mouse nests were in shrubs containing a bush kaoo rat nest under the BKR present situation (25% of cases), whereas 42 of 75 striped mouse nests were in shrubs containing a bush karoo rat nest under the BKR absent situation (56% of cases). I never observed that striped mice and bush karoo rats shared a shrub as a nesting site. Under the BKR present situation, nesting sites of striped mice did not contain bush karoo rat nests more often (7 of 28 or 25% of cases) than did the random sample of shrubs at the study area (96 of 424 or 22% of all shrubs contained bush karoo rat nests; U-test: $U = 6{,}009$, $m = 26$, $n = 424$; $P > 0.4$). However, under the BKR absent situation significantly more striped mouse nesting sites were in shrubs with bush karoo rats nests (42 of 75 or 56% of cases) than the random sample (U-test: $U = 11{,}533$, $m = 89$, $n = 424$; $P < 0.0001$).

Dissection of 1 bush karoo rat nest inhabited by a striped mouse group.—The dissection revealed that the mice had built their hay nest inside the nesting chamber of the bush karoo rat nest.

DISCUSSION

This study found evidence for interspecific competition for nesting sites in 2 sympatric diurnal rodent species in the succulent karoo of South Africa. Bush karoo rats and striped mice used the same places as nesting sites and interacted aggressively toward one another during encounters. The heavier bush karoo rats won nearly all encounters. The presence of bush karoo rats had a significant impact on what nesting sites were used by striped mice. Thus, it seems that bush karoo rats kept striped mice away from preferred nesting sites.

Nesting sites are an important resource for small mammals. This is especially true in arid environments such as the succulent karoo. Although I found that only 22% of sampled shrubs contained bush karoo rats nest, this does not mean that nest sites where an abundant resource. Bush karoo rats did not choose nest sites at random, but seemed to select them by characteristics such as shrub species, shrub diameter, and amount of cover in the surrounding area. Diameter of a shrub is important, because it might influence the amount of protection the nesting site offers. Cover provides protection against predators, especially raptors, and might also correlate with food abundance in the surrounding area. Thus, although many

TABLE 3.—Nesting sites of striped mice from the succulent karoo of South Africa in different shrubs, either when bush karoo rats (BKR) were present or when they were absent (data are number of nests).

	Zygophyllum retrofractum	*Lycium cinerum*	*Deverra aphylla*	Other shrub species	Total
BKR present	13	0	6	9	28
BKR absent	26	16	17	16	75

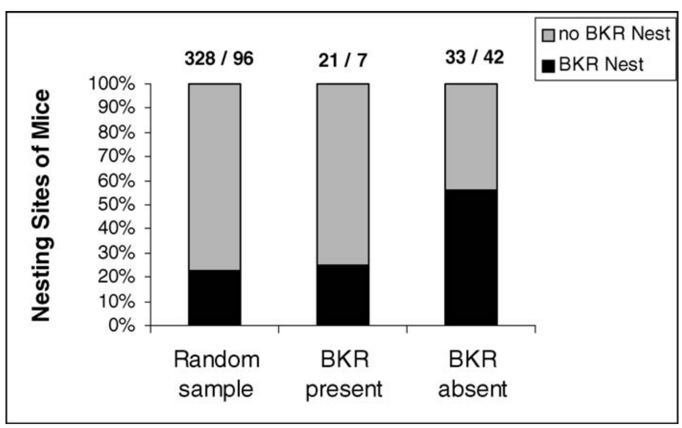

FIG. 1.—Sites of striped mouse nests relative to shrubs with and without nests of bush karoo rats and relative to presence of the rats at the site. Percentage relative to the total number of nests found. Values for a random sample of shrubs are also shown. Values above bars indicate sample sizes (without bush karoo rat nest/with bush karoo rat nest). BKR nest: shrub contained a bush karoo rat nest; no BKR nest: shrub contained no bush karoo rat nest; BKR present: data for 2001 2001 and 2002 when bush karoo rats were abundant; BKR absent: data for 2003, when bush karoo rats were absent.

shrubs may be available, only few provide good nesting sites, which represent a limited resource.

Although I observed only 29 aggressive interactions between the 2 species during 53 h of observations, encounters between the species were always aggressive (see also Schradin 2005). Bush karoo rats and striped mice came in close proximity 29 times, and 27 times the bush karoo rat chased away the striped mouse. Only 1 large striped mouse male was seen chasing a bush karoo rat twice (see also Schradin 2005). I never observed both species nesting in the same shrub at the same time. Bush karoo rats at my field site weigh 120 g and are 2–3 times heavier than striped mice, which weigh 40–80 g (Schradin and Pillay 2005c). Because physical strength and dominance correlate with body weight (Parker 1974; Schradin and Anzenberger 2001; Schradin and Lamprecht 2002), their larger size may explain why bush karoo rats can dominate striped mice.

Both bush karoo rats and striped mice commonly nest in the shrub *Z. retrofractum*, probably because it is the dominant shrub species and because this species with its hard branches offers good protection against potential predators. In contrast, only the striped mouse used *D. aphylla* for shelter. These shrubs have long, strawlike, elastic green branches without leaves, which do not offer substrate for bush karoo rats to build their stick lodges. However, because the striped mouse is group living in the succulent karoo, with up to 30 individuals sharing a nest (Schradin and Pillay 2004), increased vigilance replacing thorny branches as protection against predators could explain why this nesting site is suitable for striped mice.

The preferred nesting sites of bush karoo rats were in *L. cinerum*, which has woody branches offering good attachment points for building stick lodges and leaves that provide food (Brown and Willan 1991). In 2001 and 2002, when the population density of bush karoo rats was high, no striped mice nested in *L. cinerum*. However, when bush karoo rats were absent in 2003, striped mice often nested in *L. cinerum*. The area experienced a severe drought in 2003 and the local bush karoo rat population became nearly extirpated. Thus, no interspecific competition for nesting sites occurred in 2003 because only striped mice were left. This result indicates that *L. cinerum* is preferred for nesting sites for both species, but the heavier bush karoo rats keep striped mice away from this resource (which is less common than *Z. retrofractum*; Table 1). Furthermore, the prediction that bush karoo rats outcompete striped mice was demonstrated by another result. In 2003, striped mice nested significantly more often in shrubs containing abandoned bush karoo rat nests than in the previous years. This suggests that in 2001 and 2002, bush karoo rats prevented striped mice from nesting in such shrubs.

Two reasons, which are not mutually exclusive, are possible for why striped mice preferred to nest in shrubs containing bush karoo rat nests; 1st, these nests were built in shrubs that provided better nesting sites, and 2nd, bush karoo rat nests themselves increased the quality of the nesting sites. With the data available, it is not possible to distinguish between these 2 possibilities, but it is likely that both factors play a role. Because bush karoo rats can dominate striped mice, they should be able to gain access to the best nesting sites. The extensive stick lodges further improve protection against predators and climatic harshness (Jackson et al. 2002; Plessis et al. 1992). The dissection of 1 bush karoo rat nest occupied by a striped mouse group in 2001 revealed that striped mice had built a typical striped mouse hay nest in the nesting chamber of the bush karoo rat nest, indicating that striped mice not only use the same shrub, but also use the stick lodge when taking over bush karoo rat nests.

Good nesting sites are essential for striped mice for protection against predators, rain, and hot and cold weather. In winter and spring, night temperatures are very low and an insulated nesting site could significantly influence both survival of adults and development of young (Schradin and Pillay 2005b, 2005c). Because not all shrubs are equally suitable as nesting sites, good nesting sites are a limited resource. Competition for these nesting sites occurs both between striped mice from different groups, which show a higher level of territorial aggression at nest sites than at territorial boundaries (Schradin 2004), and between bush karoo rats and striped mice.

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