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Social Organization of the Eastern Rock Elephant-Shrew (*Elephantulus myurus*): The Evidence for Mate Guarding

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Social organization of the Eastern Rock Elephant-shrew (*Elephantulus myurus*) : the evidence for mate guarding

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ABSTRACT. Understanding the costs and benefits of defending solitary females, or mate guarding, may be the key to understanding the evolution of monogamy in most mammals. Elephant-shrews, or sengis, are a unique clade of small mammals that are particularly attractive for studies of mate guarding. We studied the spatial organization of Eastern Rock Sengis (*Elephantulus myurus*) in KwaZulu-Natal, South Africa, from August – December 2000. Our objectives were to describe the home ranges of males and females using radiotelemetry, noting the sizes and overlap of adjacent ranges and how the spatial organization changes through time. Males and females were spatially associated in monogamous pairs despite the fact that males contributed no obvious direct care to offspring. These monogamous associations persisted despite the fact that some males had home ranges large enough to encompass multiple females. Males also had more variable ranges, perhaps because they spent more time at the periphery of their ranges exploring for the presence of additional females. There was likely competition for females, as range shifts were observed when male territory holders died or disappeared. It seems likely that this species is a model study organism to investigate the costs and benefits of mate guarding.

KEY WORDS : Social organization; *Elephantulus myurus*; mate guarding, monogamy.

INTRODUCTION

Elephant-shrews or sengis (KINGDON, 1997) are a unique group of small mammals with no ecological or behavioral equivalents outside of Africa. All species feed largely on invertebrates (RATHBUN, 1979; CHURCHFIELD, 1987; KERLEY, 1995), and all are highly cursorial and capable of very fast locomotion (RATHBUN, 1979). The smaller species usually produce only one or two offspring that are born in a very precocial state. These life histories are more similar to small-bodied cursorial herbivores than similar-sized small mammals. Behaviorally, all of the 15 species of sengis from 4 genera are suspected to be monogamous (RATHBUN, 1979). Of the species studied in detail, male and female pairs have overlapping territories that result in monogamous associations, probably for life (SAUER, 1973; RATHBUN, 1979; FITZGIBBON, 1995, 1997). Territory defense is same-sex specific, and despite their nearly congruent territories, males and females spend little time together except during estrus, when the male continuously attends and follows the female (RATHBUN, 1979). Scent-marking appears to be an important component of pair bond maintenance (LUMPKIN & KOONTZ, 1986; KOONTZ et al., 1999). Males are also known to occasionally visit neighboring territories, typically resulting in intrasexual aggressive interactions (RATHBUN, 1979).

Recent molecular work indicates that sengis are a part of an early radiation of African mammals that is represented by the extant golden moles, tenrecs, the aardvark, hyraxes, sea cows, and elephants (HEDGES, 2001; MURPHY et al., 2001). Consensus is building to place all of these mammals in the Superorder Afrotheria (MURPHY et

al., 2001). All studies have indicated that elephant-shrews represent a monophyletic group (CORBET & HANKS, 1968; TOLLIVER et al., 1989), and there exists no other group of closely related mammals that are all suspected to be monogamous.

Monogamy is one of the more evolved forms of social organization in mammals and is found in fewer than 10% of mammalian species (KLEIMAN, 1977; KLEIMAN & MALCOLM, 1981). Monogamy in mammals has traditionally been proposed to be due to either the necessity for male care (obligate monogamy) or due to female dispersion (facultative monogamy; KLEIMAN, 1977, 1981; WITTENBERGER & TILSON, 1980; SLOBODCHIKOFF, 1984; BARLOW, 1988). There is no evidence to suggest sengi males engage in any direct paternal care activities, especially since the young are so precocial.

The objectives of this study were to describe the spatial organization of the Eastern Rock Sengi (*Elephantulus myurus*, Thomas and Schwann 1906) to determine if this species exhibits monogamous association patterns in natural populations. *Elephantulus myurus* is distributed in southern Zimbabwe, western Mozambique, eastern Botswana, and eastern South Africa on rocky outcrops in semi-arid savannahs (NEAL, 1995). Unlike other elephant-shrews, *E. myurus* do not travel along a network of trails; rather they use their swift cursorial gait to travel from rock to rock (RIBBLE, personal observation). The primary breeding season of *E. myurus* in southern Africa is August-March, with minimal breeding from April-July (STOCH, 1954; WOODALL & SKINNER, 1989; NEAL, 1995). Females are typically anestrus from May to July (VAN DER HORST & GILLMAN, 1941). We described the social organization of *E. myurus* by determining the home

ranges of males and females, noting the size and overlap of adjacent ranges and if the spatial organization changes through time. Since no studies on the social organization of this species had been previously conducted, we were also interested in noting any features of the social organization that would provide insight into the evolution of monogamy in elephant-shrews.

METHODS

We studied the social organization of *E. myurus* on a 10-ha rock outcrop at Weenen Nature Reserve, located in the KwaZulu-Natal province of South Africa (S28°52.5398' E030°00.2193'), from August through December 2000. Weenen is a 4183-ha game reserve with habitats characterized by open, acacia savannahs with tall grasses (e.g. *Hyparrhenia* spp. and *Themeda triandra)* and thicker woodlands (e.g. *Acacia karoo*) along valley bottoms and riparian corridors (PERRIN & TAOLO, 1999a, 1999b).

Individuals were trapped on the outcrop with Elliot aluminum traps baited with peanut butter and oats, and occasionally supplemented with chopped-up insect parts (DU TOIT & FOURIE, 1992). Captured elephant-shrews were recorded, ear-tagged, and a streak of hair dye was applied to either their back or sides for visual recognition. In the early morning, *E. myurus* were readily observed basking on rocks, which made it easy to confirm that we had marked all individuals in the population.

To document home ranges of individuals, we attached "mouse-style" radiotransmitters (SM-1, AVM Instrument Company, Ltd., Colfax, CA) around the necks of sengis with plastic cable-ties. This was accomplished by physically restraining the animals, avoiding the use of anesthesia. Radiotransmitters weighed on average 3.20 ± 0.07 (1SE) g, which was 5.3 ± 0.15 % of their average weight of 60.5 ± 1.1 g. Individuals were radiotracked with an AVM receiver attached to a 3-element Yagi antenna. Many of the radiolocations were confirmed with visual sightings (33%). During the night individuals were visible with a strong headlamp and seemed unconcerned with our presence. Some locations were determined by removing the antenna coaxial cable from the receiving antenna and waving the lead over the boulder where the elephant-shrew was taking refuge. Individuals were recorded as "active" if they were moving about or "resting" if they were stationary. The Universal Transverse Mercator (UTM) coordinates of locations were ascertained with a Garmin GPS 12 receiver (Garmin International, Inc.). The receiver was left in place at the radiolocation for 10 min to calculate the average position determined from satellites during the entire 10-min interval. We conducted experiments that indicated this 10 min point-averaging feature resulted in a reading that was within 1.8 ± 0.3 (1*SE*) m of subsequent readings at the same spot (RIBBLE, unpublished data).

After trapping the rock outcrop and conducting preliminary radio-tracking on 5 individuals in August, we attempted to radiotrack all adult individuals located in the outcrop the next 3 months. Since individuals were marked with hair dye and visible in the morning hours basking on rocks and no individuals were observed outside the rock outcrop, we were confident that we were tracking all

adults. Individuals were radiotracked for 4 – 8 days (mean $= 6 \pm 1.8$ days) during each session each month. At the start of the study, radiotransmitters were removed after each session. It became apparent that these elephant-shrews handled the radiotransmitters with no apparent problems. Pregnant females gained their expected weight and successfully weaned offspring while radiocollared. Towards the end of the study radiotransmitters were left on individuals for as long as 50 days. On average, individuals actually gained 0.14 ± 0.09 g per day while carrying radiotransmitters (range –0.03 to 0.83 g per day). Radiotracking observations were taken at all hours of the night and day because preliminary observations indicated *E. myurus* could be active at any time. Individual locations were separated by at least one hour to avoid autocorrelation of data (SWIHART & SLADE, 1985).

We collected home-range data on each radiotagged *E. myurus* during 2 to 4 (mean = 2.7) monthly sessions during this study. Animals were trapped at the beginning of each radiotelemetry session to check their reproductive status and replace radiotransmitters that quit working. The last radiotracking session was conducted in November, and animals were trapped in December in order to remove their radiotransmitters. The minimum convex polygon (MCP) of all radiolocations and trap locations during a monthly session was recorded as the home range for each individual for that month. We accepted statistical significance at $P \leq 0.05$.

RESULTS

From 10 to 14 adult *E. myurus* were observed on the study outcrop each month (Table 1). The number of males and females was most often equal except in September when the sex ratio was 7males :4 females. Females were first observed lactating in September, and the first juveniles were observed and trapped in October.

Radiotelemetry indicated that individuals were active at any hour (Fig. 1), although activity was reduced in the middle of the night (ca. 2300 – 0500h) and the middle of the afternoon (ca. 1200 – 1700h). Individuals were most active and furthest from their home range centre between 1800 and 2300h. During the morning activity period (ca. 0600 – 1100h), *E. myurus* spent most of their time basking on the tops of boulders, presumably warming their body temperature (MZILIKAZI et al., 2002).

The mean monthly home-range size for males (3958 ± 625 m^2) was larger than females (2011 ± 130 m^2; $P \leq 0.05$). Across all monthly radiotelemetry sessions, seven males had home ranges that were at least twice the size (range 8204 – 13487 m^2) of the mean monthly female home range of 2011 m^2. The average number of intrasexual overlaps each month was 0.9 and 0.4 for males and females, respectively, which was not significantly different. Intrasexual overlap was greater for males than females (18 vs. 2%; $P \leq 0.05$). The home-range data from November 2000 are representative of the monthly patterns (Fig. 2), showing the lack of overlap between adjacent females. Female ranges tended to be overlapped by only one male, but there were cases where one female range was overlapped by more than one male (see female 777 overlapped by males 724 and 738; Fig. 2).

TABLE 1

Summary of spatial and temporal relationships of *Elephantulus myurus* at Weenen Game Reserve, South Africa, 2000. Horizontal bars represent life span and location of individuals. A dotted line indicates individual was alive, but not paired. Adult individuals (boldface numbers) within same boxes were presumably paired and their offspring (italic numbers) are included in the same box. (arrow = Home-range shift; d = disappearance; X = mortality; O = offspring)

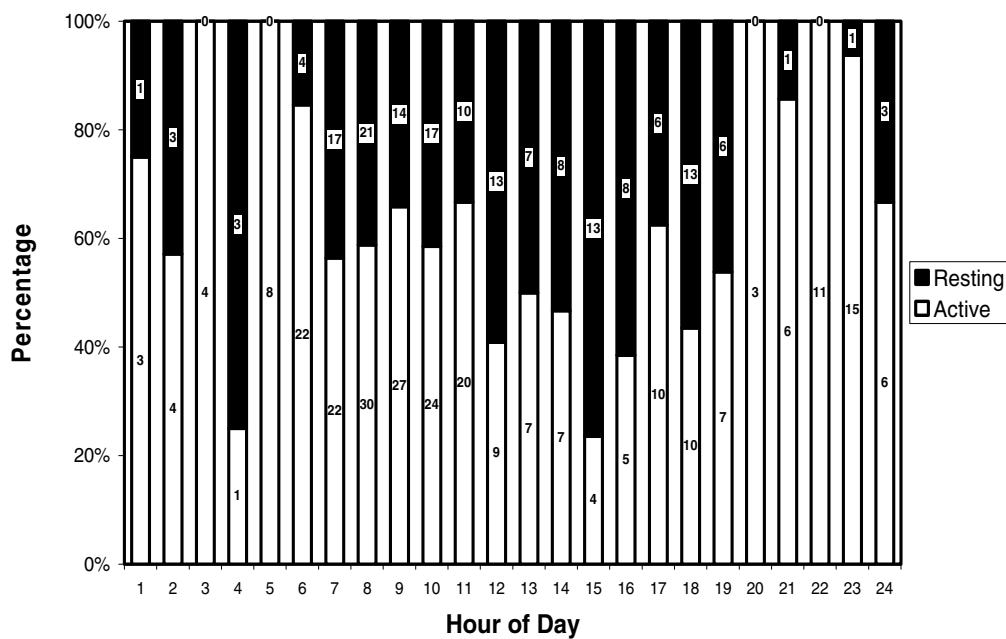| Individuals	Gender	August	Sept	Oct	Nov	Dec
719	♀	▦▦▦▦ d				
718	♂	▦▦▦				
766	♀		▦▦▦	▦▦▦	▦▦▦	▦▦
			▦▦▦	▦▦▦	▦▦▦	▦▦
783	♀				*O*▦▦ d	
784	♀				*O*▦▦▦	▦▦
720	♀		▦▦▦	▦▦▦	d	
724	♂		▦▦▦	▦▦▦	▦▦▦	▦▦
775	♂			*O*▦▦	d	
776	♂			*O*▦▦	▦▦▦	▦▦
806	♀					▦▦
777	♀			▦▦▦	▦▦▦	▦▦
738	♂		⋯⋯⋯	▦▦▦	X	
805	♂					▦▦
770	♀		▦▦▦	d		
773	♂		▦▦ d			
721	♂		⋯→	▦▦▦	▦▦▦	▦▦
774	♀			⋯⋯→	▦▦▦	▦▦
771	♀		▦▦▦	▦▦▦	▦▦▦	▦▦
723	♂	▦▦▦	▦▦▦	d		
772	♀		*O*▦▦ d			
736	♂		⋯⋯⋯	⋯→	▦▦ X	
810	♂					▦▦

Fig. 1. – Activity patterns of radio-collared *Elephantulus myurus* during the entire study. Sample sizes are indicated for each bar.
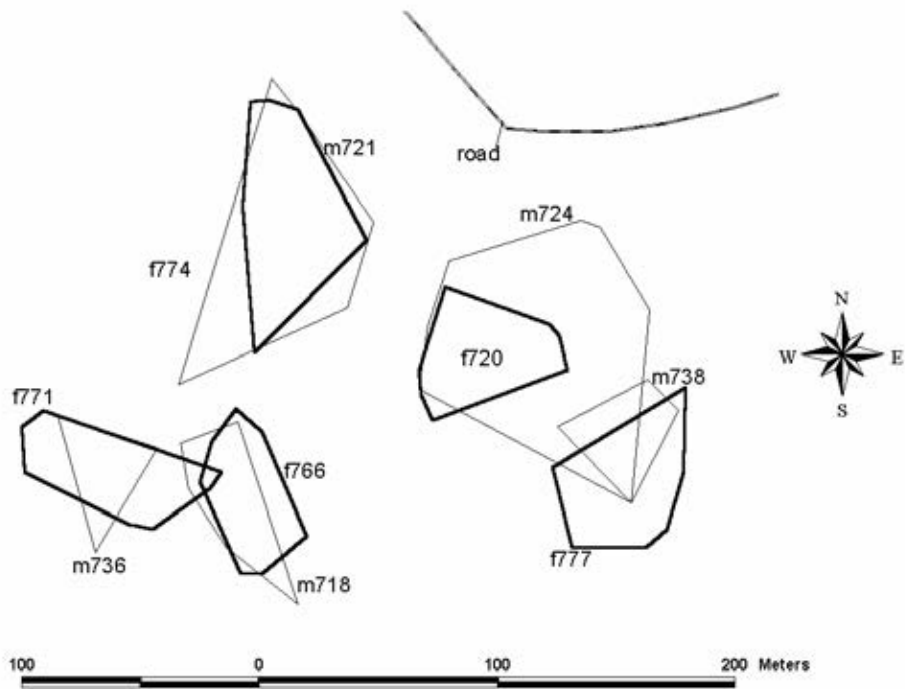
Fig. 2. – Minimum convex polygons of male (thin-lined polygons) and female (thick-lined polygons) *Elephantulus myurus* during November 2000.
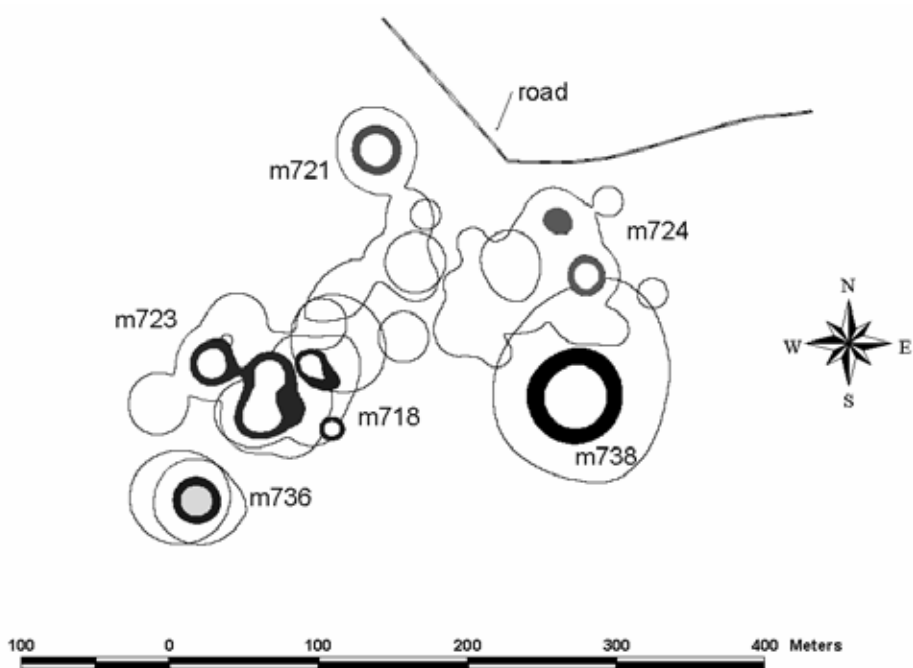

Fig. 3. – Density contours for the fixed-kernel-density estimates of males during the entire study. The thin-lined contours represent the 95% contours, and the thick-shaded contours represent the 50% contours.

Despite the cases where female ranges were overlapped by multiple males, each month there tended to be one primary male who 1) overlapped a majority of the female's range, and 2) consistently overlapped the female's home range during successive months. Based on these assertions, we assigned "putative" pairs each month (Table 1). It was apparent that when a male or female disappeared or died, another individual would quickly move

into or shift their home range to occupy the abandoned home range. For example, in October male 736 was adjacent to male 723 who was paired to female 771 (Table 1). In November, male 723 had disappeared and male 736 shifted his home range to coincide with female 771. In December, male 736 was found dead, likely due to predation. Another new male, 810, was trapped within the home range of female 771. Four cases of range shifts by adults were observed during this study, 3 by males and one by a female (Table 1).

Based on their locations when first observed, we identified offspring from 3 lactating females (Table 1). Two of these offspring, 783 and 784 (Table 1), were observed by flashlight around 2200 h one evening with their mother, female 766. While each of the 3 females were lactating we never observed any interactions between the lactating female and her presumptive mate, nor did we detect the two to be near each other with radiotelemetry.

At the end of the study, all trapping and radiotelemetry locations were combined to estimate the overall home-range size and intrasexual overlap. The fixed-kernel-density estimator (SEAMAN & POWELL, 1996) was also used to calculate home-range size using all the location data. The MCP estimates of home-range size using all data were significantly different between genders (male mean $= 9901 \pm 2593$ m^2; female mean $= 3623 \pm 367$ m^2; $P \leq$ 0.05) and significantly larger than the monthly averages ($P \leq 0.05$ and $P \leq 0.01$ for males and females, respectively). The overall home-range size for males was 150% larger, whereas females were 80% larger than the monthly average. The 95% fixed-kernel estimates were also significantly larger for males (mean $= 11065 \pm 2576$ m^2; Fig. 3) than females (mean $= 3132 \pm 220$ m^2; $P \leq 0.05$). For males, the mean number of same-sex overlaps (3.7) and the mean percentage of intrasexual overlap (67%) were significantly greater for the overall combined data than the monthly averages for males ($P \leq 0.01$). There were no differences for females.

DISCUSSION

These data indicate that male and female *E. myurus* are spatially associated in monogamous pairs, yet males were never observed in the same vicinity of females with offspring supporting the presumption that males contributed no direct care to offspring. Similar results have been observed with other species of sengis, including *E. rufescens* (RATHBUN, 1979), *Rhynchocyon chrysopygus* (RATHBUN, 1979), *Petrodromus tetradactylus* (RATHBUN, 1979; FITZGIBBON, 1995), and *Macroscelides proboscides* (SAUER, 1973). These studies have led to the conclusion that all 15 species of Macroscelidea may be monogamous, making the sengis a very unique clade of mammals in which every species is monogamous. Why all sengis are monogamous is not clear.

There is no evidence that male sengis engage in any direct parental care activities, in part because the young are so precocial. Thus, it does not appear that direct male care explains monogamy in elephant-shrews. The benefits of the presence of the male to offspring survival and female reproductive success may be more subtle than the obvious direct benefits of male care of offspring. For

example, males may defend a territory containing a female and her offspring that could increase resource availability (KLEIMAN, 1977; RUTHBERG, 1983), provide protection from infanticide (VAN SCHAIK & DUNBAR, 1990), and provide protection from predators (BARASH, 1975; DUNBAR & DUNBAR, 1980). Any of these factors could affect offspring and mother survivorship, and hence be a benefit to males in defending and mating with a solitary female. Sengis are very cursorial, often behaving more like small antelopes than typical small mammals (RATHBUN, 1984), and some species build and maintain elaborate networks of trails through the ground litter within their territories. RATHBUN, (1979) proposed that the trail-building activities of male *E. rufescens* (Rufous elephant-shrew) may indirectly benefit his female and offspring by providing efficient access to the territory for foraging and predator escape. Since *E. myurus* do not use trails, it is unlikely that females and their offspring benefit from trail maintenance activities, although there could be some other indirect benefits of the male's presence. It does seem clear, however, that the evolution of monogamy in *E. myurus* is not due to the necessity of male care (obligate monogamy).

In contrast to the necessity of male care in cases of obligate monogamy, facultative monogamy results when females exist at very low densities due to the dispersion and quality of food resources, and males can subsequently monopolize only one female (KLEIMAN, 1977, 1981; WITTENBERGER & TILSON, 1980; SLOBODCHIKOFF, 1984; BARLOW, 1988). The essential feature of facultative monogamy is that both sexes are constrained by resource quality and distribution so that monogamy is the only option available. If female ranges are widely dispersed, then individual males may only be able to access one female and mate monogamously.

If the density of females affects the strategies of males, a clear prediction of the facultative monogamy theory is that the mating strategies of males should be responsive to the density and availability of unpaired females. Recent studies of so-called facultatively monogamous species have indicated that males are not responsive to the availability of unpaired females (e.g. KOMERS, 1996), but rather males remain faithful due to the benefits of mate guarding. The evolutionary principle of mate guarding is that defending and mating with a single female during successive reproductive events is a better option than roving to mate with, or defending multiple females (PARKER, 1974; WITTENBERGER & TILSON, 1980; BROTHERTON & KOMERS, 2003). The benefits to mate guarding in mammals likely are due to the high costs of searching and or defending multiple females. Recently, mate guarding has been proposed to account for monogamy in *Madoqua kirkii* (Kirk's dik-dik). *M. kirkii* are socially and genetically monogamous (KRANZ, 1991; BROTHERTON et al., 1997), yet males exhibit no direct or indirect paternal behaviors that increase juvenile survivorship (BROTHERTON & RHODES, 1996). The dispersion of females does not appear to account for monogamy in this species either, as many males have territories large enough to encompass multiple females yet do not (BROTHERTON & MANSER, 1997), and mated males fail to respond to the presence of unmated females in adjacent territories (KOMERS, 1996). The reported costs to males of mating with multiple

females include increased predation, male-male competition, and the risk of being cuckolded by other males. Thus, the benefits of remaining with a single female and assuring access to one female during estrus outweigh the costs of mating with multiple females (KOMERS, 1996; BROTHERTON & MANSER, 1997). For females, it may be there are costs associated with harassment by extra-pair males, which results in females accepting monogamy (BROTHERTON et al., 1997).

Mate guarding may also explain the social organization of sengis. FITZGIBBON (1997) demonstrated that male *R. chrysopygus* that attempted to defend an additional female lost weight and could only temporarily defend the larger territory. This was presumably due to the costs of defending the extra female, not the extra space, as some males had territories twice the size of others (FITZGIBBON, 1997). In this study, monogamous associations of *E. myurus* persisted despite the fact that some males had home ranges large enough to encompass multiple females. The home ranges for the entire study were larger with more overlap in part due to an increase in sample locations over a longer time period. However, intrasexual overlap was significantly greater for males (67%) than females (18%; P < 0.01) for these home ranges. This indicates that over time, males have more variable and larger home ranges in which the boundaries are explored and expanded in different directions, supporting observations in other sengis that males make forays to monitor surrounding females (RATHBUN, 1979). There was likely competition for females, as range shifts were observed when male territory holders died or disappeared. It seems likely therefore, that this species is a model study organism in which to investigate the costs and benefits of mate guarding.

KOMERS & BROTHERTON (1997) argued that understanding the costs and benefits of defending solitary females, or mate guarding, may be the key issue to understanding the evolution of monogamy in mammals. Data from this study and other studies would further indicate that the monogamous members of the Macroscelidea are model organisms in which to experimentally manipulate the costs and benefits of defending solitary females and therefore advance our understanding of the evolution of monogamy in mammals in general.

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