



Original investigation

Social monogamy in the noki or dassie-rat (*Petromus typicus*) in Namibia

By G.B. Rathbun and Carolyn D. Rathbun

Department of Ornithology and Mammalogy, California Academy of Sciences, San Francisco, CA, USA

Receipt of Ms. 25.5.2005

Acceptance of Ms. 27.1.2006

Abstract

The noki or dassie-rat (*Petromus typicus*) is a little-studied diurnal hystricognath rodent endemic to rocky outcrops in south-western Africa. An intermittent study in Namibia of 11 radio-tagged individuals, with over 250 h of direct observation, was done between 2000 and 2004 to document their basic natural history, including their social organization. The study was terminated when noki numbers collapsed, probably due to predation by an expanding population of black mongooses (*Galerella nigrata*) that was unintentionally provisioned with food at a nearby eco-tourist lodge. Male and female adults were distributed as monogamous pairs on home ranges that were similar in size and shape. The pair bond was strong, with many coordinated behaviours. Reproduction was seasonal with litters of single highly precocial young. Multiple generations remained on the parental home range without significant aggression. Most aggression was between adult males, while adult females showed tolerance towards each other and intruding adult males. Although noki social monogamy is probably the result of male mate guarding, considerable paternal care was observed, including allogrooming and vigilance against predators. Nokis have a relatively low metabolic rate and numerous thermoregulatory behaviours that suggest that nocturnal huddling by the male with his mate and young may be an important factor in the evolution of their social monogamy.

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Key words: *Petromus*, dassie-rat, monogamy, Namibia, social organization

Introduction

The noki or dassie-rat (*Petromus typicus* A. Smith, 1831) belongs to the monospecific hystricognath rodent family Petromuridae. We use the common name “noki” because it avoids the confusion by many people with dassies (hyraxes in the mammalian order Hyracoidea) or true rats (rodent families Muridae and Cricetidae). Noki is derived from a Khoekhoegowab (=Hottentot) dialect (Shortridge 1942) and was first

mentioned in a published study by George and Crowther (1981).

Nokis are endemic to the southwest arid biogeographical region of Africa (Meester 1965) that stretches from extreme south-western Angola south through Namibia into north-western South Africa. They are restricted to rocky or boulder-strewn habitats, especially along the Namibian escarpment zone with its numerous mountains, cliff faces,

inselbergs, and kopjes or rock outcrops (Coetzee 2002). The aridity of the escarpment and closely related Namib Desert is at least 15 million years old (Ward and Corbett 1990) and the noki apparently has had an ancient association with these biomes (Meester 1965; Sénégas 2004), as demonstrated by several morphological adaptations to living in rock crevices (George and Crowther 1981; Skinner and Chimimba 2005). These features include a flattened cranium, flexible ribs, and dorso-lateral mammae.

Apart from general natural history observations (e.g., Skinner and Chimimba 2005) and reports based mostly on opportunistic observations (e.g., Coetzee 1983) or museum collections (Coetzee 2002), there are only two published field studies of noki ecology (Withers 1979; George and Crowther 1981). Recently, reproduction and behaviour of captive nokis have been studied (Mess 2002; Mess and Ade 2005) in association with research on their placentation (Mess 2003). Because of the paucity of long-term and detailed field data and the limited distribution of nokis, there is considerable interest in this near-endemic Namibian rodent (Griffin 1998). The aim of this study was to investigate the social behaviour and social organization of free-ranging nokis in Namibia.

Material and methods

Study site and study period

Our study was done near the Erongo Wilderness Lodge (21°27.679S, 15°52.523E) on Okapekaha Farm, about 10 km west of Omaruru town in the foothills of the Erongo Mountains of Namibia. The site is 1240 m above sea level and is characterized by huge rounded granite dikes that rise about 100 m above the surrounding penepain and smaller 10–20 m high granite outcrops or kopjes surrounded by intruding fingers of the surrounding bushveld. The vegetation at the study site is composed of widely spaced low trees and bushes interspersed with seasonally dense annual and perennial forbs and bunch grasses. The dominant trees include *Combretum apiculatum*, *Sterculia africana*, *Terminalia prunoides*, and *Boscia albitrunca* and the more common bushes include several species of *Grewia*, *Croton gratissimus*, *Dichrostachys cineria*, and *Mundulea sericea* (Rathbun and Rathbun 2005).

Annual mean rainfall at Omaruru Prison is 292.9 mm, with virtually all of this falling during the months of November through April. Annual average minimum and maximum temperatures at the prison are 11.4–31.0 °C, with May through August being the coolest as well as driest months (Rathbun and Rathbun 2005).

After determining the suitability of the study site in June 2000, we radio-tracked and observed nokis during four subsequent periods that covered the seasonal climatic extremes: 25 December 2000–5 January 2001, 5 September–21 November 2001, 24 April–7 July 2002, and 11 May–23 July 2003.

Trapping and marking

We captured *Petromus* with Sherman model XLF15 (11.5 × 10 × 30.5 cm folding aluminium) and Tomahawk model 201 (40.5 × 13 × 13 cm single door) live traps set during daylight hours and baited with fresh carrots or apples. To prevent hyperthermia in captured animals we positioned traps in the shade or avoided trapping during mid-day.

Trapping nokis was difficult because a few individuals became trap happy and disrupted attempts to capture trap shy individuals. Intruders were especially trap shy because of their wariness and preoccupation with exploration. When food plants were plentiful during the wet season nokis were especially difficult to trap, whereas during the dry season they were more easily attracted to fresh moist bait.

We permanently marked nokis for subsequent identification with passive integrated transponder chips (Destron-Fearing, South Saint Paul, MN) implanted subcutaneously (Schooley et al. 1993) between the shoulders, although care had to be taken because of their fragile skin (G. B. Rathbun and C. D. Rathbun, unpublished data). For visual identification we bleached pelage on different parts of the body using a mixture of 20% hydrogen peroxide and commercial hair bleaching powder mixed into a paste. We thoroughly washed the paste out of the fur with water after about 5 min. We divided nokis into three age-classes. Adults, which were capable of reproduction, were over 160 g. Subadults, which were independent but not reproductive, were less than 160 g. Young, which were neonatal through weaning, were below 100 g.

Radio tracking and visual observations

We attached radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada; model MD-2C, 2.2 g weight, 120-day battery life, 20-pound-test and 10-cm-long fishing leader wire whip antenna) with

the standard Holohil mammal collars made of antenna wire inside Tygon tubing. We radio-located nokis several times a day between 04:30 and 22:30 h, but separated consecutive fixes by at least 2 h, which was sufficient to reduce inter-fix autocorrelation. The movement of radio-tagged nokis, along with distortion of radio signals by granite rock faces and kopjes, often made triangulation difficult. Therefore, we used a combination of homing and triangulation (Kenward 2001) to determine locations (fixes). We flagged locations made at night and determined coordinates the next day. Young nokis were not radio tagged so their locations were based on sightings alone. We calculated universal transverse Mercator (UTM) coordinates for locations by determining the distance and azimuth to or from a "target" site with known coordinates, which we determined with a global positioning system (GPS) receiver at the beginning of our study. We then calculated coordinates for several other prominent target kopjes that were visible within 100 m from any spot on the study area with the computer software program UTM CALC (O'Leary 1998). The precision of our laser rangefinder (Bushnell model 400X) and sighting compass (Brunton model 16-FSM360LA-SME) was ± 1.0 m and $\pm 0.5^\circ$, respectively. The accuracy of our location calculations was less than ± 2.0 m at 100 m, which was considerably better than the GPS accuracy of ± 5.5 m that we determined from 9 fixes (1-s averaging for 3 min) taken during 24 h at a single site. The accuracy of our initial GPS location has no significance in our home range analyses because all our fixes were determined relative to the initial site. We used the software program RANGES 6 (Kenward et al. 2002) to calculate home range areas with the software's default settings.

During morning and late afternoon, when air temperatures were usually below 30 °C, and thus tolerable, we sat on top of granite boulders and with 8 × 40 binoculars observed our marked nokis. Even with the advantage of radio tags and binoculars, continuous observation was difficult due to obstructing boulders and the sheltering habits of the animals. We radio tagged and visually marked 11 individuals during the study (Tab. 1) and accumulated about 250 h of observations in addition to 2842 radio and visual location fixes.

Results

Spatial organization

Comparing the home ranges in each year of our study (Figs. 1, 2) gives an initially poor

idea of the social organization of nokis. In 2002, however, the four adults were clearly distributed as male–female pairs on highly congruent and exclusive home ranges, and each pair had a single young (Tab. 1, Fig. 1B). The social structure in the other years can only be understood in the context of several factors (age-classes of individuals (Tab. 1), individual behaviours, recent mortality, and the presence of unmarked trap-shy nokis) that are not apparent by considering the home range boundaries alone.

In 2000, our study period was short and we gathered relatively few location fixes (Tab. 1) and did not trap neighbouring nokis to the east (Fig. 1A versus B). Also, an unmarked adult female associated with adult male 209 was killed while still in a Tomahawk trap by a black mongoose (*Galerella nigrata*) on 26 December, before we had time to determine her spatial and social relationship to the other nokis.

In 2001, the number of nokis present on our study site increased to six (Tab. 1), including three from the year before. As in 2000, we again did not attempt to capture animals that we saw to the east. Male 209 was killed and eaten, probably by a black mongoose, about 10 days after we began radio tracking. This death resulted in a remarkable change in the configuration of some home ranges (Fig. 2), and was accompanied by increased aggressive encounters involving short pursuits of 1–2 m at favoured basking sites. These brief scuffles included male 141 fleeing from female 627 or female 76E, female 865 pursuing male 141, and male 141 chasing female 76E. In comparison, we did not observe this type of aggression before the death of male 209 nor within the pairs in 2002 (Fig. 1B) or 2003 (Fig. 1C). Several more intense chases were seen in 2001 after male 209 was killed and an unmarked intruder cautiously and tentatively explored the kopje and favourite basking sites. On 5 October, we watched an intruder aggressively chase male 141 for 10–20 m. On 13 October, presumably the same unmarked noki cautiously and without aggression interacted with females 865 and 206 and then later the same day exchanged nasal contact with female 865. An intruder (presumably still the same individual) was on the kopje on 15 and

Table 1. Noki home range areas (hectares), calculated using minimum convex polygon (MCP) and fixed kernel densities (K) with 95% and 100% of location fixes. In year 2001 the two blocks of rows are defined by the death of male 209 on 15 September 2001. Weight (wt.) in grams based on first capture for year. Age classes (A=adult, J=juvenile, Y=young), are based on weights and field observations (see text). Fixes are the number of locations determined by radio-tracking (except Y206 and Y864, which were not tagged – see text) and used to calculate 100% home range areas. Those identifications with an asterisk (*) were male-female pairs used to compare home ranges and overlaps. Dates are periods of time used to calculate home ranges.

Year	ID	Sex	Wt. (g)	Age class	Fixes	MCP 95%	MCP 100%	K 95%	K 100%	Dates
2000	209	m	187	A	29	0.130	0.200	0.270	0.360	29 Dec–5 Jan
2000	141	m	132	J	29	0.040	0.080	0.110	0.140	29 Dec–5 Jan
2000	76E	f	220	A	47	0.050	0.070	0.040	0.100	25 Dec–5 Jan
2001	209*	m	219	A	31	0.030	0.060	0.064	0.100	6 Sep–15 Sep
2001	865*	f	200	A	27	0.020	0.040	0.038	0.041	5 Sep–15 Sep
2001	76E	f	230	A	28	0.090	0.090	0.089	0.098	5 Sep–15 Sep
2001	206	f	111	J	11	0.010	0.030	0.015	0.016	9 Sep–15 Sep
2001	141*	m	220	A	25	0.070	0.070	0.113	0.115	5 Sep–15 Sep
2001	627*	f	132	J	28	0.060	0.060	0.023	0.023	5 Sep–15 Sep
2001	141*	m	220	A	149	0.210	0.280	0.219	0.347	16 Sep–21 Nov
2001	627*	f	132	J	140	0.090	0.161	0.116	0.219	16 Sep–21 Nov
2001	76E	f	230	A	136	0.110	0.140	0.187	0.234	16 Sep–21 Nov
2001	865	f	200	A	140	0.040	0.070	0.046	0.089	16 Sep–21 Nov
2001	206	f	111	J	137	0.050	0.120	0.043	0.154	16 Sep–21 Nov
2002	D4E*	m	230	A	322	0.190	0.290	0.115	0.290	27 Apr–29 Jun
2002	206*	f	232	A	360	0.070	0.170	0.072	0.146	24 Apr–1 Jul
2002	Y206	?	—	Y	109	0.030	0.050	0.024	0.044	8 May–1 Jul
2002	A51*	m	231	A	267	0.390	1.070	0.670	2.030	6 May–7 Jul
2002	864*	F	286	A	237	0.390	0.430	0.423	0.940	14 May–7 Jul
2002	Y864	?	—	Y	79	0.030	0.090	0.048	0.059	16 May–7 Jul
2003	401	F	179	A	89	0.050	0.110	0.056	0.099	11–23 May
2003	D4E	m	252	A	322	1.040	1.040	0.503	1.060	16 May–26 Jul
2003	F60	F	178	A	98	0.330	0.400	0.494	0.969	27 May–9 Jun

22 October, but we observed no interactions. On numerous days we attempted to trap the unmarked noki, but it was too wary. In desperation, we captured trap-happy male 141 and left him in the trap on the kopje as bait and surrounded him with several open traps. Although the intruder scolded and aggressively lunged at the trap containing male 141, and chewed the edges of his trap, it was not captured.

Upon our return in 2003 (see first paragraph in section above for 2002 results), noki numbers had declined—although male D4E from the previous year was still present (Tab. 1, Fig. 1B,C). Numbers were further reduced when female 401 was killed and eaten on 23 May and then on 9 June we flushed a black mongoose from the still warm and partially eaten carcass of female F60. Although F60 was consistently associated

with another adult in 2003, this presumed male mate was too trap-wary to capture. Similarly, we did not capture a wary occasional adult male intruder on the home range of male D4E until the end of the study period on 23 July. The nokis on our study site apparently did not reproduce in 2003.

The decline in nokis at our study site continued into 2004. When we visited the kopjes in June, we were unable to spot any nokis, although some were still observed at the nearby lodge.

It is difficult to determine whether there was any difference in the home range sizes between adult males and females because of the changes in individuals between and within years – especially in 2001. If we use only the least ambiguous five pairs (Tab. 1), the average size of male home ranges was nearly twice that of females (0.236 versus 0.134 ha,

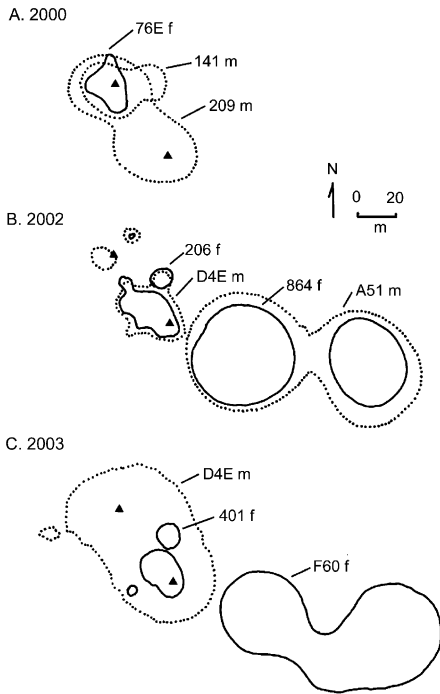


Fig. 1. Fixed kernel home range contours (95% of fixes) for adult nokis during 2000 (A), 2002 (B), and 2003 (C) at Erongo study site, Namibia. Females=solid lines and males=dotted lines. See Fig. 2 for 2001 and Tab. 1 for details. Two solid triangles represent the same paired locations in all three panes, and the scale is common to all.

respectively), but the difference is not quite statistically significant (paired *t*-test, two-tailed $P = 0.06$). We used the same pairs to calculate home range area overlap. The five female home ranges were overlapped by their associated males by an average of 81.6%, while the male ranges were overlapped by their females an average of 55.9%.

There was no overlap in the 95% fixed kernel home ranges between adjacent pairs (Figs. 1B,C), but in 2002 we radio-located male A51 once inside the home ranges of neighbouring pair male D4E/female 206. After the intruder explored several basking spots during about 10 min, he was discovered by the resident male and aggressively chased over 20 m back onto his own home range. Although the resident female had an opportunity to chase the intruding male, she did

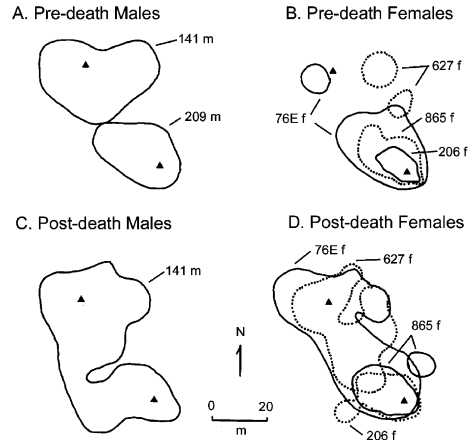


Fig. 2. Fixed kernel home range contours (95% of fixes) for adults and subadults at Erongo study site, Namibia, in 2001. Top home ranges (A and B) include data from 5 September–15 September, when predation of male 209 occurred. Bottom home ranges (C and D) include data from 16 September–21 November. For clarity, males (A and C) and females (B and D) are plotted separately and dotted lines were used for female 627 and female 865. Two solid triangles represent the same paired locations in all four panes, and the scale is common to all.

not. This incursion is not evident in the home range areas (Fig. 1B) because our analyses excluded the most peripheral 5% of locations.

Pair associations

In 2001, we examined when pair members basked within 3 m of each other and also when they were found in the same night shelter before dawn between 04:30 and 06:00 h (Tab. 2). In this year, there were no neonates present and the adult male did not associate with any of the females, but several females were found together – especially 206 and 865. In 2002, after 8 May when both pairs each had single young on their home ranges, we compared the locations of individuals in their night shelters between 04:30 and 06:00 h. Pair D4E/206 (and presumably their young) was located together on 18 nights and separate only once. Pair A51/864 (and their young?) was together on 12 nights and separate on five. We accumulated 82

Table 2. Frequency of noki associations in 2001. Data above diagonal cells with asterisks (*) are use of the same basking site (ca. 3 m diameter area) by individuals during 19 days, 21 September–20 October. A trio of 76E, 865, and 206 occurred once. Data below diagonal are use of the same night shelter by individuals during 17 days between 04:30 and 06:00 h 20 September–20 October.

ID	76E f	141 m	627 f	865 f	206 f
76E f	*	0	1	1	1
141 m	2	*	0	0	0
627 f	4	0	*	0	0
865 f	0	0	0	*	4
206 f	0	0	0	10	*

sightings of basking by D4E/206, and on 11 occasions (13%) the two were basking within 3 m. Pair A51/864 was associated seven out of 36 sightings (19%). There was also a temporal component to these associations: All 11 cases of pair D4E/206 basking close together occurred during the first 28 days after their young was born and none in the next 28 days, although they had mostly congruent home ranges (see below).

Parental behaviours

The precocial neonate of D4E/206 was first sighted on 8 May, but based on parental behaviours, it was probably born 2 days earlier. The birth site and subsequent sightings at basking sites were different (Fig. 3C). The home ranges of both adults shrank markedly with the appearance of the neonate (Fig. 3A, B) and for the following week the male spent nearly as much time in close association with the young as the female. During this time, one or the other parent nearly always attended the neonate, but rarely simultaneously. At 1 week postpartum, the male spent less time with the young. At the end of our observations on 7 July, the male only visited the young briefly during the day, but he continued to shelter at night with his mate (and their young?). While with the young, a parent basked or napped between bouts of intense allogrooming, and the female nursed for 2–5 min several times a day. Bouts of allogrooming lasted for 5–40 s and focused on the young's face, head, and back of the neck, and the young climbed all over the parents and often licked their

mouths. After bouts of grooming or nursing, the young resumed basking and napping, often curled up on top of the extended front feet and legs (lap resting) or on top of the base of the extended bushy tail (tail resting) of a parent.

Both adults were exceptionally vigilant and protective while near the young. For example, three days after female 206 gave birth, we observed male D4E aggressively chase away an adult male Namibian rock agama lizard (*Agama planiceps*) that had inadvertently approached to within a meter of the basking pair.

We did not find changes in the home ranges of pair A51/864 (Fig. 1B) associated with their single young because we estimate that it was about 4 or 5 weeks old when we started our observations on 16 May 2002. At the end of our observations on 7 July 2002, the single young on both territories were still occasionally nursing – about 2 and 3.5 months postpartum.

Scent marking

Nokis dust bathed at sites near the bottom of kopjes where they loosened soil by scratching with their front feet and then rolled on alternate sides several times. These sites did not seem to function as scent-marking stations because they were rarely used or visited. The only evidence of direct scent marking was rubbing the chin on rock surfaces, which was especially intense by intruders that explored commonly used rest spots. Chin rubbing was not associated with home range boundaries, nor were the large

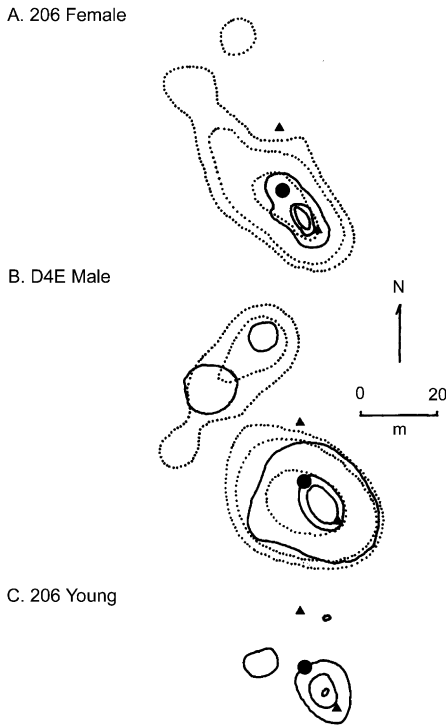


Fig. 3. Fixed kernel home ranges (50%, 75%, and 95% of fixes) for female 206 (A), male D4E (B), and young Y206 at the Erongo study site, Namibia. Parent home ranges are during 13 days before (dotted lines) and 13 days after (solid lines) the birth of young on about 6 May 2002. Home range of young, which was not radio-tagged, is based only on visual sightings for the entire study period (Tab. 1). Solid circle is birth site and two solid triangles represent the same paired locations for each individual. The scale is common to all three.

accumulations of faeces and urine-stained rock at heavily used rest sites.

Predation

Numerous nokis disappeared while we were absent from our study site each year (Tab. 1), and several died while we were present. There is no doubt that diurnal black mongooses were responsible for the deaths of some, and probably most, of our tagged animals. The importance of *G. nigrata* as a noki predator was corroborated by the reaction of nokis to their presence. For example, on 6 and 26

September 2001, several basking nokis sounded high-pitched “cheeeeeee” alarm calls before disappearing into rock crevices when a black mongoose hunted nearby. Although nokis responded to the alarm calls of nearby rock hyraxes (*Procavia capensis*) when large diurnal raptors flew low overhead, as well as to raptors by themselves, we found no evidence that raptors took any of our radio-tagged nokis.

Similarly, we found no evidence that any of our radio-tagged nokis were preyed upon by large reptiles that we observed, including the veld leguaan or monitor lizard (*Varanus albigularis*), southern African python (*Python natalensis*), western spitting cobra or zebra snake (*Naja nigricincta*), or puff adder (*Bitis arietans*).

Discussion

We initially expected that nokis would be relatively long-lived with a stable social structure, reflecting their small litters of 1–3 highly precocial young (Mess 2002) that are born during a restricted breeding season (Coetzee 2002). Previous ecological studies (Withers 1979, 1983; George 1981) also supported this expectation. Our spatial data, however, were complicated by the unexpected indirect human influence on the population. We started our study in the same year that the Erongo Wilderness Lodge opened, after a few years of construction in a remote area that had previously been uninhabited by people. Initially, we occasionally saw black mongooses hunting in the area, but we did not realize how common they were until an adult was accidentally captured in 2003 (Rathbun 2005). This male was radio-collared and subsequently several additional adults were radio-tagged (Cowley 2004). We discovered that some of these mongooses were surreptitiously feeding on discarded food from the lodge kitchen, staff was feeding them, and they occasionally visited a bird feeding station at the lodge. Unfortunately, we did not monitor the mongoose population until the end of our study, but we suspect that predation from their increasing numbers resulted in the collapse of the noki population at our study site.

Although the decline of *P. typicus* and our small sample sizes complicate the interpretation of our data, the changes in individuals provided insights that may have otherwise eluded us. We interpret our observations as follows:

In 2000, adult male 209 was presumably paired with the female that was killed by the mongoose in the trap, leaving the presumed father with a young-of-the-year (male 141). Female 76E was probably a young from the previous year, based on the restricted size of her home range compared to adult male 209. In 2001, male 209 was paired with adult female 865, based on home range overlap, and female 206 was their young-of-the-year, based on joint basking and sheltering behaviours as well as home range congruence and size. Male 209 maintained an exclusive home range from adult male 141 – his presumed son. Adult female 76E (presumed previous year's daughter of 209) remained loosely associated with her father (209) and his new mate (865) and young (206). Adult male 141 and subadult female 627 formed a pair, based on their similar home ranges that were exclusive of adjacent male 209.

With the death of male 209 in 2001, female 76E and neighbouring male 141 expanded their home ranges, while male 141's mate (female 627) expanded her range to encompass all other female ranges. Only minor aggression related to occupancy of favoured basking sites accompanied these changes.

In 2003, adult male D4E remained on his home range with possibly a new mate (adult 401), or more likely with his young from the previous year (Y206). The latter interpretation is more consistent with the small size of the female's home range and lack of pair-bond behaviours between the two. The latter interpretation is also supported by male D4E's subordination to the intruding male during aggressive encounters. The adjacent pair from the previous year disappeared and was replaced by a new pair (we were unable to capture the presumed male).

Based on our data and the above interpretation, intra-specific aggression was between males, whereas females tolerated intruding males, and females generally tolerated each

other. This sex-specific aggression resulted in exclusive male home ranges and at times overlapping female home ranges that included multiple generations of young or a male co-opting a neighbouring widow. We observed no behaviours associated with advertizing home range boundaries, nor do nokis concentrate prominent dung piles on home range boundaries or scent mark these areas. The aggression we observed, and our interpretation of noki use of space, suggests that pairs did not defend their home ranges, but rather males defended their mates against other males. This interpretation is also supported by the greater home range overlap of females by their mates, rather than vice versa. We conclude that social monogamy in nokis is mainly the result of mate guarding, where a male prevents reproductive access to a single female by other males. Although monogamous pairing was most intensive during periods of reproduction, spatial pairing persisted during other times.

Social monogamy includes several subcategories, including uni-parental versus bi-parental monogamy and facultative versus obligate monogamy (Komers 1996). Different life history traits, and varying reproductive benefits to the individuals involved, are responsible for the evolution of the different forms of social monogamy. Obligate monogamy in many mammals has traditionally been attributed to the necessity of paternal care, especially in those species with altricial young (Kleiman 1977; Wittenberger and Tilson 1980). More recently, male mate-guarding has been proposed as the principal adaptive factor in the evolution of all mammalian social monogamy, with paternal care of young (where it occurs – mostly in some rodents, carnivores, and primates) likely being secondarily derived (Brotherton and Komers 2003; but see Ribble 2003). The mate-guarding hypothesis was mainly developed based on studies of dik-diks (*Madoqua kirkii*), which are dwarf antelopes found in eastern and south-western Africa (Brotherton and Manser 1997; Brotherton and Rhodes 1996; Komers 1996), and further supported by other species such as sengis or elephant-shrews (Ribble and Perrin 2005; Rathbun and Rathbun 2006).

Dik-diks and sengis, which exhibit uni-parental monogamy, share many similar life history traits, including small litters of highly precocial young (Brotherton and Rhodes 1996; Rathbun 1979) that reduce opportunities for paternal care. In contrast, the monogamous California mouse (*Petromyscus californicus*) is bi-parental because paternal huddling and warming of altricial nestlings increases their survivorship (Ribble 2003). Even though noki young are highly precocial, like dik-diks and sengis, we observed evidence of bi-parental care, including highly coordinated use of space, allogrooming, and direct paternal protection of young. Remarkably, paternal warming of the precocial neonates may also have occurred.

Nokis have a low metabolic rate for their size (Withers et al. 1980), and this coupled with their diet of sometimes poor quality forage (Withers 1979; George 1981), makes the conservation of energy particularly adaptive. This is corroborated by prominent thermoregulatory behaviours, especially solar basking and exchanging heat by lying spread-eagled against rock faces (G. B. Rathbun and C. D. Rathbun, unpublished data). Noki young, having a smaller mass than adults, may face an even greater thermoregulatory challenge, which would explain their lap and tail resting. The near-freezing night temperatures of the south-western arid zone during the winter breeding season of *Petromus* (Coetzee 2002), the lack of nest material in night shelters (at least in the northern part of their range; G. B. Rathbun and C. D.

Rathbun unpublished data), and the high proportion of nights that males spent sheltering with their mates when young were presumably present all suggest that paternal warming of young at night contributed to their bi-parental monogamy, like the California mouse.

Acknowledgements

We are grateful for the logistical support and fellowship provided by our colleagues in Namibia, including Mike Griffin of the Ministry of Environment and Tourism, Tim and Laurel Osborne of Windpoort Farm, and Seth Eisab of the National Museum. We thank our friends at the Erongo Wilderness Lodge for enthusiastically hosting us, especially owner and builder Danie Holloway and his sons Sean and Justin, managers Roger and Romilly Fussell and Mike and Helene Warren, and the entire staff – especially Lindy van den Bosch. The Western Ecological Research Centre of the U.S. Geological Survey kindly loaned us radio-tracking equipment. Our work was completed under research permit No. 505 from the Ministry of Environment and Tourism. We are thankful to C. (Neels) Coetzee for encouraging us to study *Petromus*, and we benefited from his insightful comments and suggestions on an early version of this study, along with those of Andrea Mess and an anonymous reviewer. Paquita Hoeck kindly provided German translations.

Zusammenfassung

Soziale Monogamie der Felsenratte (*Petromus typicus*) in Namibia

Die Felsenratte (*Petromus typicus*, auch Noki genannt) ist ein bisher wenig untersuchtes, tagaktives Nagetier (Unterordnung Hystricognatha), das nur in felsigen Gebieten und Felsspalten im südwestlichen Afrika vorkommt. In den Jahren 2000 bis 2004 wurde eine zeitweilige Untersuchung von elf mit Radiosendern versehenen Individuen in Namibia durchgeführt. Die Tiere wurden während über 250 Stunden direkt beobachtet, um deren natürliche Lebensweise und Sozialstruktur zu dokumentieren. Die Studie wurde abgebrochen, als die Anzahl Felsenratten kollabierte. Grund dafür war wahrscheinlich die Bejagung durch eine wachsende Population von schwarzen Mangusten (*Galerella nigra*), die unbeabsichtigt in einer nahegelegenen Touristenlodge gefüttert wurden. Adulte Felsenrattenmännchen und -weibchen hielten als monogame Paare Territorien inne, die in Grösse und Form ähnlich waren. Die starke Paarbindung war durch viele koordinierte

Verhaltensabläufe geprägt. Die Fortpflanzung war jahreszeitlich bedingt und bestand aus einem einzigen nestflüchtenden Jungen. Mehrere Generationen blieben im elterlichen Territorium ohne massgeblich Aggressionen zu zeigen. Die meisten Aggressionen traten zwischen erwachsenen Männchen auf, während ausgewachsene Weibchen Toleranz gegenüber anderen Weibchen und eindringenden Männchen zeigten. Obwohl die soziale Monogamie der Felsenratten wahrscheinlich das Resultat von Partnerverteidigung durch die Männchen ist, wurde beachtliche väterliche Fürsorge beobachtet, wie beispielsweise Allogrooming und Wachsamkeit gegenüber Feinden. Nokis haben eine relativ geringe metabolische Rate und zahlreiche thermoregulatorische Verhaltensweisen lassen vermuten, dass das nächtliche Zusammenkuscheln von Männchen und deren Paarungspartnern und Jungen ein wichtiger Faktor in der Evolution ihrer sozialen Monogamie sein könnte.

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Authors' address:

Galen B. Rathbun and Carolyn D. Rathbun, P.O. Box 202, Cambria, California 93428, USA
(e-mail: grathbun@calacademy.org)