Mammalia (2006): 269–275 © 2006 by Walter de Gruyter • Berlin • New York. DOI 10.1515/MAMM.2006.038

Sheltering, basking, and petrophily in the noki or dassie-rat (*Petromus typicus*) in Namibia

Abritement, réchauffement, et pétrophilie chez le Noki ou Dassie-rat (*Petromus typicus*)

Galen B. Rathbun* and Carolyn D. Rathbun

Department of Ornithology and Mammalogy, California Academy of Sciences (San Francisco), c/o P.O. Box 202, Cambria, CA 93428, USA,
e-mail: grathbun@calacademy.org

*Corresponding author

Abstract

The rupicolous noki or dassie-rat (*Petromus typicus*) is endemic to the south-west arid biogeographical region of Africa. Nokis are diurnal and, compared to nocturnal small mammals, are relatively easy to observe, yet few field studies have been completed. Using radio-tracking and direct observation, a population of nokis in Namibia was intermittently studied over 3 years to document their basic natural history. Temperature loggers and temperature-sensitive radio tags were used to determine that nokis do not have a labile body temperature and do not go into daily torpor. They spend nights deep in rock crevices, but seemingly do not build or use nests. During the cool winter months they bask in the sun at sunrise, and during the heat of the day they shelter in cool rock crevices. During the warm part of the year they bask less frequently. Because nokis have a low relative metabolic rate and a diet of seasonally poor-quality forage, their frequent use of solar basking and passive heat gain and loss from the massive rocks in their habitat is probably related to conservation of energy.

Keywords: basking; noki; *Petromus*; sheltering; thermoregulation.

Résumé

Le rat rupicole Noki ou rat-daman (*Petromus typicus*) est une espèce endémique de la région biogéographique du Sud-Ouest Africain aride. Les nokis sont diurnes et comparés à leurs homologues nocturnes sont de ce fait faciles à observer, bien qu'ils n'aient fait l'objet que de peu de travaux de terrain. A l'aide de radio-pistages et d'observations directes, une population de nokis de Namibie a été étudiée par intermittence pendant trois années afin d'obtenir des données de base sur leur histoire naturelle. Des thermomètres et des colliers radio sensitif à la température ont permis de vérifier que ces rongeurs n'ont pas une température corporelle labile et ne tombent pas en torpeur dans la journée. Ils passent la nuit au fond des crevasses de rochers mais ne construisent pas ou n'utilisent pas apparemment de terriers. En hiver, ils se réchauffent au lever du soleil et lorsqu'il fait chaud dans la journée, ils s'abritent dans les crevasses rocheuses fraîches. Pendant les mois chauds, ils s'exposent rarement au soleil. Parce que les nokis ont un métabolisme relativement bas et un régime alimentaire parfois pauvre, leur utilisation fréquente du rayonnement solaire et le gain ou la perte passive de chaleur par les rochers où ils s'abritent leur permet probablement une conservation d'énergie.

Mots cles: abritement; chauffage; noki; *Petromus*; thermorégulation.

Introduction

THE noki or dassie-rat (*Petromus typicus* A. Smith, 1831) belongs to the monospecific hystricognath rodent family Petromuridae, which is endemic to the south-west arid biogeographical region of Africa (Meester 1965). Within this area, nokis are restricted to rocky or boulder-strewn habitats, especially along the Namibian escarpment zone that is characterised by 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, Scott 1995) and *Petromus* apparently has had an ancient association with these biomes (Meester 1965, Sénégas 2004).

Nokis physically resemble ground squirrels, but in nearly all other respects, especially their rupicolous habits, they are unusual. They exhibit several morphological adaptations to living in narrow rock crevices, including a flattened cranium, flexible ribs, and dorso-lateral mammae (George and Crowther 1981, Skinner and Smithers 1990). In addition, their metabolism (Withers et al. 1980), diet (Withers 1979, George 1981, Mess and Ade in press), feeding ecology (Rathbun and Rathbun 2005), and bi-parental social monogamy (Rathbun and Rathbun 2006) are closely tied to petrophily. Because of the limited information available on *Petromus*, we undertook a study of their natural history in Namibia during 2000–2003. In this paper, we present data on their sheltering and basking behaviours and relate these to temperature regimes in their rocky habitat.

Materials and methods

Study site

Our study was carried out near the Erongo Wilderness Lodge (21° 27.679′ S, 15° 52.523′ E) on Okapekaha

Farm, approximately 10 km west of Omaruru town in the foothills of the Erongo Mountains. The site is 1240 m above sea level and is characterised by huge rounded granite domes and faces that rise up to 100 m above the surrounding peneplain and smaller granite outcrops or kopjes of 10–20 m in height sitting on granite with small intruding fingers of the surrounding bushveld (Figure 1). The vegetation at the study site is composed of widely spaced low trees and bushes, mostly in gullies or dongas, interspersed with seasonally dense annual and perennial forbs and bunch grasses (Rathbun and Rathbun 2005).

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

After determining the suitability of the study site in June 2000, we radio-tracked and observed nokis during three subsequent periods that covered the seasonal climatic extremes: 5 September through 21 November 2001 (hot-dry), 24 April through 7 July 2002 (cool-wet), and 11 May through 23 July 2003 (cold-dry).

Trapping, tagging, and visual observations

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.

We marked nokis for subsequent individual visual identification within a study season by bleaching their 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 after about 5 min, but due to the very fragile nature of their skin we did not attempt to dry the pelage. We permanently marked nokis with passive integrated transponder chips (Destron-Fearing, South Saint Paul, MN, USA) and used the last three digits from these tags (e.g., male D4E) for naming animals (Rathbun and Rathbun 2006).

We attached radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada; model MD-2C, 2.2 g in weight, 120-day battery life, 20-pound-test and 10-cm-long fishing leader wire whip antenna) with 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 to reduce interfix autocorrelation. During daylight, we sat on top of granite boulders and, using 8×40 binoculars, observed the 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 accumulated approximately 250 h of noki observations during the three study visits, which does not include our radio-tracking effort (n=2842 radio and visual fixes). In 2003, our transmitters included a temperature circuit that allowed us to determine the temperature of the transmitter unit by measuring the time interval between pulsed signals.

Temperature loggers

In 2003, during the cool and dry winter, we deployed 17 temperature data loggers at the study site, but some of these were replicates or backups and some malfunctioned. Two different types of logger were used: iButton (Dallas Semiconductor, part DS1921F, accuracy ±1°C) loggers were programmed to record every hour and were secured to rock surfaces with duct tape, while TidbiT (Onset, part TBI32-05+37, accuracy ±1°C) loggers recorded every 10 min and these were placed within a 3-cm-diameter wire-mesh cage attached to the end of a 1-m-long bamboo pole, which we inserted deep into crevices next to where nokis sheltered.

We chose six temperature profiles that represent a variety of locations on two adjacent kopjes among the granite domes at the study site (Figure 1). We placed a

Figure 1 Adult female noki (#206) basking near the top of a kopje at the Erongo study site, Namibia, on 20 June 2002. The arrow is at her chin and her radio collar is visible. The dominance of granite slabs and kopjes are evident in background.

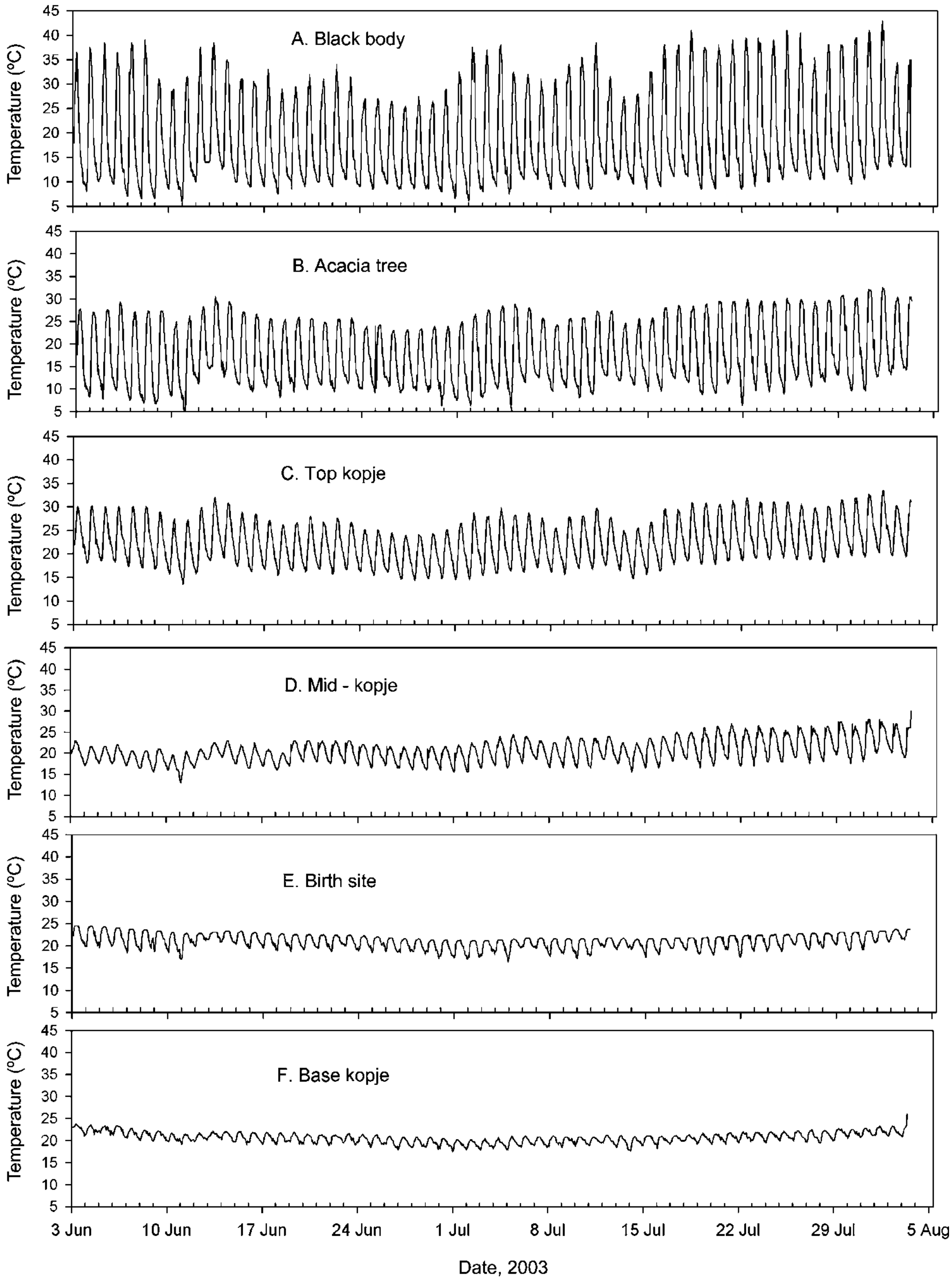

Figure 2 Hourly winter temperature profiles from 3 July through 3 August 2003 at the Erongo study site, Namibia. See the text for location (A–F) descriptions, which are arranged along an elevation gradient from top to bottom. See Figure 3 for summary statistics.

TidbiT logger 2 m above the ground in the shade of an acacia tree in a finger of bushveld located approximately 15 m from the two kopjes (Figure 2B). This site served as a comparison with the loggers located on the two kopjes. An iButton logger was placed in a small black metal box and positioned on the very top of a kopje (Figure 2A), completely exposed to the sun from dawn to dusk, to determine black-body (Mzilikazi et al. 2002) temperatures. The remaining four loggers were at sites actually used by nokis. We taped an iButton logger inside a shallow (shaded) rock crevice next to a favoured basking site on top of a 6-m-high kopje (Figure 2C, near the black body). We put an iButton logger mid-way down the same kopje in a vertical crevice often used by nokis as a day shelter (Figure 2D). A TidbiT logger was inserted 1 m down a horizontal crevice 1 m from the base of the same kopje, where a pair of nokis gave birth in 2002 and sheltered at night (Figure 2E; Rathbun and Rathbun 2006). A TidbiT logger was positioned 1 m into a crevice formed by a huge boulder sitting on basement rock at the bottom of a 12-m-high kopje where nokis sheltered at night (Figure 2F). The units were synchronised so that they all logged at 6 min (±10 min) before each hour.

Results

Habitat temperatures

Temperature profiles at 1-h intervals from 3 June through 3 August 2003 (Figure 2) illustrate the remarkable variation among six locations at the study site. The amplitude of the daily temperature extremes was increasingly buffered as the rock mass increased towards the bottom of

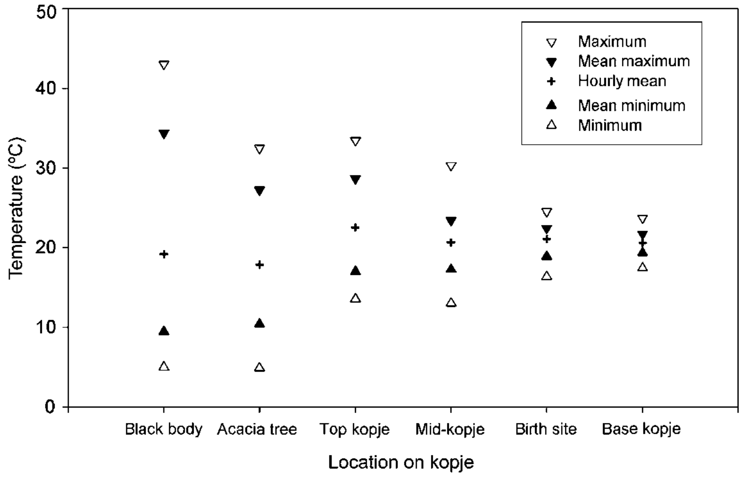

Figure 3 Summary statistics for six temperature profiles illustrated in Figure 2.

a kopje (Figures 2 and 3). For example, sheltered sites (Figure 2C–F) had average hourly temperatures above 20°C (20.6–22.5°C; Figure 3), but the daily maxima and minima withdrew towards the mean temperature the lower the site was on the kopje (Figure 3). The two fully exposed sites (Figure 2A,B) had mean temperatures that were below 20°C (19.2°C and 17.9°C), with the widest minima and maxima (Figure 3). The minimum temperatures for the black body (Figure 2A) and tree site (Figure 2B) were similar, but the maxima were quite different, illustrating the influence of full sun exposure on the black body (Figure 3). Another characteristic of the more exposed sites (Figure 2A–C), compared to those more sheltered by rock (Figure 2D–F) was the extended duration of the minima and maxima.

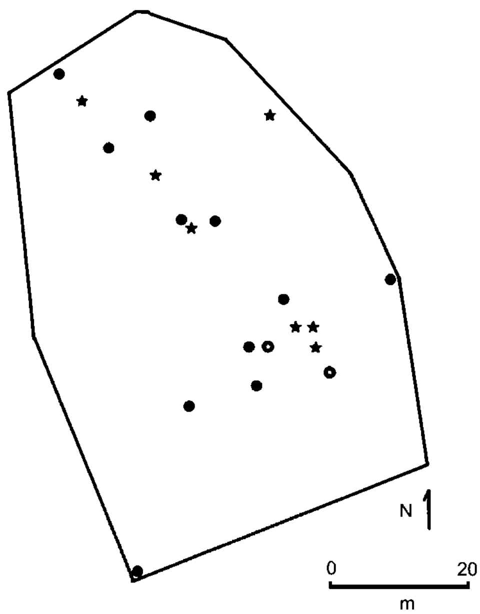

Figure 4 Minimum convex polygon area (0.36 ha, 852 locations) used by five nokis (see Figure 5) at the Erongo study site, Namibia, in 2001. The three most frequently used basking sites (stars, n=9) and night shelters (solid circles, n=13) of all five nokis are plotted. Two of the basking sites and night shelters (star within solid circle) appear at the same location, but were at different levels on the kopje. The scale bar represents 20 m.

Basking

During the winter, nokis basked in the sun on narrow ledges on rock faces and on top of boulders (Figure 1). Basking sites were widely distributed over home ranges (Figure 4) and each site was always within 1 m of an escape crevice. Basking sites were located anywhere from the top to the bottom of kopjes, but they were always exposed to full sunlight. Based on the distribution of our observational efforts in 3-h periods between 06:00 and 18:00 h and instances of basking that we observed, nokis spent significantly (χ^2=123.5, d.f.=3, $p<0.0001$) more time basking in early morning than late afternoon (Table 1). Nokis normally used several basking sites, but tended to use one or two most frequently (Figure 5A). It was difficult to assess the amount of time spent basking, because not all sites were visible at once and disruptions by potential predators and intermittent cloud cover resulted in fragmented bouts of basking. In 2003, when the temperature loggers were deployed and three nokis had temperature-sensing radio collars, we scan-sampled for basking every 10 min starting at dawn (06:00), through sunrise (06:30), until 08:30 or when basking terminated, whichever occurred last. We gathered data on 31 days from 12 May through 22 June and on some days we gathered data from more than one noki. Excluding the 14 sessions when we observed no basking nokis, the average duration of basking bouts (n=25) was 45 min, with a range of 10–110 min. Basking was initiated on average at 07:25 h and terminated at 08:06 h, with corresponding average black-body temperatures of 21.5°C and 25.8°C. There was no significant difference (one-tailed t-test, d.f.=29, p=0.24) between the mean black-body temperature at dawn (06:00 h) on mornings when nokis basked (13.8°C) and did not bask (14.5°C).

During our summer observations in 2001, nokis were more difficult to observe because they spent less time basking and more time in shaded rock crevices, often spread-eagled against a cool rock surface and sometimes panting. These summer behaviours were not observed during the winter study periods in 2002 and 2003, although on a few occasions we observed nokis after sunset flat against rock faces (not basking sites) that had been exposed to the sun all day.

Table 1 Noki solar basking in 2001 and 2002 at the Erongo study site, Namibia.

	06:00–08:59 h	09:00–11:59 h	12:00–14:59 h	15:00–17:59 h	Total
Effort (%)	29	18	20	33	100
Expected	61	38	42	69	210
Observed	147	53	7	3	210

Expected data are based on the proportion of time (=effort) spent observing nokis at the study site in each quarter. Observed data are based on radio-located animals.

Night shelters

While radio tracking at night, we nearly always found nokis deep in rock crevices, and nearly 80% of these sites (n=18) were low on or at the base of kopjes. Night shelters were distributed widely on home ranges (Figure 4), depending on the availability of deep crevices. Although nokis were rarely active at night when we radio-located them, they often changed shelters at some point during the night. For example, 47% of our total observations (n=192) of 12 individuals during our 2001–2003 study periods changed locations at night between evening (21:00–23:30 h) and morning (04:30–06:00 h). If we separate these data into a warm season (2001) and cool or cold season (2002 and 2003), however, the mean proportion that changed location was 66% (5 individuals and 82 observations) compared to 33% (7 individuals and 110 observations), respectively. We found considerable variation in how far animals moved during the night between shelters. For example, on 11 nights during 2001 when noki male 141 moved, the average straight-line distance between shelters was 36.4 m with a range of 16.6–70.1 m, while noki female 627 moved an average of 13.6 m with a range of 6.1–25.1 m.

During each study period, nokis used multiple night shelters (but usually alone) with little preference for one over another (Figure 5B). When there were young present, however, fewer night shelters were used, one site was used more frequently than the others, and the family group used the same shelter at the same time (Rathbun

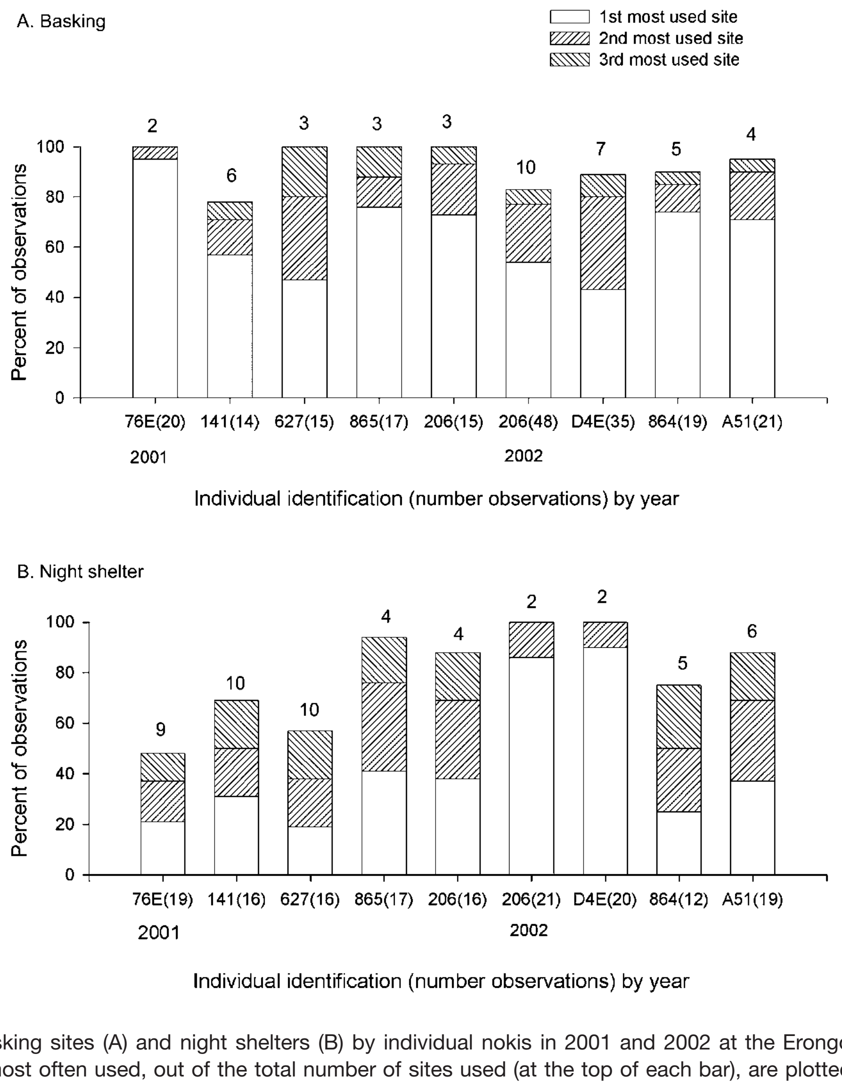

Figure 5 Use of basking sites (A) and night shelters (B) by individual nokis in 2001 and 2002 at the Erongo study site, Namibia. Only the three sites most often used, out of the total number of sites used (at the top of each bar), are plotted.

and Rathbun 2006; pair 206 and D4E in 2002, Figure 5B). The distance between the two night shelters used by the family group in 2002 was 13.4 m.

We examined 18 crevices used as night shelters by radio-collared nokis, including one where a young was born (see above), with a mirror attached to the end of a pole and a small light. Only two of these crevices had nesting material. One side of a wide horizontal crevice was stuffed full of harvested dry grass and twigs, as well as a few bleached rock hyrax (*Procavia capensis*) bones and land snail shells. When we radio-located the nokis in this crevice, however, they appeared to be using a very narrow portion adjacent to the nest. In the second case, we could not accurately determine the relationship between radio-tagged nokis that used a rock crevice with protruding nest material. We never saw any evidence of nokis collecting grass or twigs for nest building, including intensive observations associated with the pair that gave birth in 2002 (Rathbun and Rathbun 2006). There were two additional rock crevices in our study area with protruding nest material, but none of our radio-tagged nokis used them. On the peneplain adjacent to the study site, we found a grass and twig nest in a small isolated kopje, which was not occupied by nokis. When we trapped the site we captured several rock mice (*Aethomys namaquensis*) and when we dismantled the nest it was full of their faeces. Rock mice were also common on the kopjes at the study site, where we sometimes captured them in noki traps at night.

Noki temperatures

In 2003, we calculated the temperature of the radio transmitters each time we located the three collared nokis. When they were inactive in a night shelter, their average temperature was 34.8°C (n=114) with a range of 29.2–38.4°C. When basking in the sun, the average was 34.9°C (n=141) with a range of 27.8–42.2°C. When inactive during the day (not including visual observations of basking) the mean was 35.0°C (n=273) with a range of 22.3–47.0°C. When active during the day, the average was 33.3°C (n=210) and the range was 25.8–38.2°C. These means are statistically different (ANOVA, $p<0.001$).

Discussion

Temperature-sensitive radio collars have been shown to track the body temperature of mammals (Audet and Thomas 1996). The variability of our noki radio transmitters during major classes of activity (e.g., basking, foraging, social interaction, etc.) suggests that external air temperatures influenced the collars, but not greatly. For example, the body temperature of captive nokis is 34.9°C (Withers et al. 1980) and the slightly lower average transmitter temperature while active during the day (33.3°C) was probably caused by nokis foraging in deeply shaded and cool areas at the base of kopjes, where favoured food plants grew (Rathbun and Rathbun 2005). The average temperature while basking (34.9°C) was identical to that expected, but the range was wide because of the very cool temperatures encountered at sunrise and the warming effect of direct solar radiation during basking. Indeed, brief temperature spikes in excess of 45°C occurred when transmitters were in direct sun. The average temperature while sheltering at night (34.8°C), with its low variability, was probably the result of the buffering effect of the surrounding rock mass. Although these mean temperatures are statistically different, the 0.1°C difference is probably small enough to be biologically insignificant.

Solar basking, lying flat against rock surfaces, and sheltering at night in the warmest areas of kopjes, suggest that passive heating and cooling and avoidance of extreme external temperatures is important to nokis. The metabolic rate of captive animals is at least 25% lower than their predicted weight-specific value (Withers et al. 1980) and they feed on plants of poor caloric quality during the extended desert dry season (Withers 1979, George 1981), which suggests that their thermoregulatory behaviours are related to conserving energy. If this is indeed the case, we initially predicted that nokis might also have a labile body temperature and go into torpor. Behaviourally, their frequent early morning basking was very similar to eastern rock sengis (*Elephantulus myurus*), which enter torpor overnight and then passively raise their body temperature by basking in the morning sun (Mzilikazi et al. 2002). The use of different rock crevices at different times of the day and season by *Petromus*, depending on sun exposure and ambient air temperatures, was consistent with the sengi model of daily torpor. In addition, some bats similarly use passive heat from rocks to come out of torpor (Chruszcz and Barclay 2002). *Petromus*, however, did not become torpid based on our data. For example, the average temperature of their radio transmitters was 34.3°C, which is nearly identical to the 34.9°C body temperature of captive animals (Withers et al. 1980), and there was no evidence that their transmitter collars (and thus body temperatures) consistently dropped below ~34°C at night. In addition, Withers et al. (1980) were unable to induce torpor in captive *Petromus*.

If the conservation of energy is important to *Petromus*, why do they not use daily torpor, such as some bats and sengis? We suspect it is due to their vulnerability to predation and their need to remain responsive. Rupicolous mammal-eating snakes (e.g., spitting cobras, *Naja nigricincta*) have probably had a strong influence on noki behaviour and morphology. For example, in addition to a flat skull, flexible ribs, and lateral mammae, the *Petromus* that we handled had extremely fragile skin and fur that tore away from the body with disconcerting ease (and precluded us from using implanted radio transmitters or data loggers). This explains why an estimated 10% of noki study skins in museums are missing their tails (C. Coetzee personal communication). Skin autotomy probably prevents hunting snakes (and mammals, see below) from successfully biting or grabbing nokis after they have retreated into deep and very narrow rock crevices.

Although *Petromus* is thought to occupy nests of dry grass and twigs in rock crevices (Scott 1995, Coetzee 2002), nests at the study site apparently were not built or used. It is not clear, however, why *Petromus* did not use nests, especially in the context of their apparent need to conserve energy by using other thermoregulatory behaviours. It is possible that nokis at the study site, which is relatively mesic and botanically rich compared to more arid areas in southwestern Namibia (Rathbun and Rathbun 2006), had a higher-quality diet and thus lower need for energy conservation. Similarly, winter temperatures at Erongo are not as low as in more arid areas to the south-west or at higher elevations (Mendelsohn et al. 2002), perhaps resulting in nests not being used. Predation may also be a factor. If nokis used nests, which would require wider crevices to accommodate nesting material, not only would they compete for space with the larger rock hyraxes (George and Crowther 1981), but, more importantly, they might also be more vulnerable to mammalian predators. In the Erongo area, the black mongoose (*Galerella nigrata*) is a known predator (Rathbun and Rathbun 2006) that is specialised for hunting in rupicolous habitats (Rathbun 2004). Indeed, *G. nigrata* is found only as far south as the Erongo Mountains (Rathbun et al. 2005) and there may not be an ecological equivalent further south, where nokis appear to build nests.

Conclusion

Petromus is an obligate petrophile because of several inter-related aspects of its behavioural ecology. These factors include an ability to use poor-quality forage, specialised morphological and behavioural adaptations to avoid predation, physiological adaptations to arid habitats, and thermoregulatory behaviours that include solar basking, exchanging heat passively with massive rock surfaces, and using night shelters that are buffered from temperature extremes. Further studies of the temperature physiology of captive and free-ranging noki, however, are needed to fully understand the role of thermoregulation in their petrophily.

Acknowledgements

We are grateful for the logistic 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 Fussell, Mike and Helene Warren, and Lindy van den Bosch. Don Canestro and David Ribble kindly loaned us temperature loggers, while the Western Ecological Research Center of the US Geological Survey loaned us radio-tracking equipment. Our work was completed under research permit No. 505 from the Ministry of Environment and Tourism. We benefited greatly from the insightful comments and suggestions made by C. (Neels) Coetzee, Andrea Mess, and an anonymous reviewer on early versions of this paper.

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