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Noki or dassie-rat (*Petromus typicus*) feeding ecology and petrophily

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ABSTRACT. The noki or dassie-rat (*Petromus typicus*) is a rupicolous diurnal herbivore that is endemic to the southwestern arid biogeographical zone of Africa. It is the only representative of the hystricognath family Petromuridae. During our study of the social structure of nokis, we gathered data on their feeding behaviours during four periods totaling nearly seven months from 2000 through 2003.

Nokis fed on a wide variety of plants with a preference for fresh leaves and stems, fruits, and flowers when available. They also ate a wide variety of dry leaves and stems. Relatively few plants and plant parts were avoided. There was no indication that food was cached or stored. There was no evidence that nokis and rock hyraxes (*Procavia capensis*) competed for food resources, despite often feeding together. We speculate that a previously undescribed and unusual noki behaviour (the "tail-stand") is associated with coprophagy.

In hot and arid regions of Australia, some herbivorous mammals feed on the rich flora in rocky areas that is associated with unique water regimes often found in these habitats. A similar relationship may partially explain why nokis are endemic to rocky habitats in the southwestern arid zone of Africa. Other features contributing to the adaptive syndrome include their phylogeny and historical zoogeography, a need for dietary water, a low metabolic rate, a flexible and diverse diet, and an unusual suite of behaviours associated with digestion. The result is an obligate petrophile.

KEY WORDS : Diet, Dassie-rat, Feeding, Namibia, Noki, *Petromus*, Petrophily, Rupicolous

INTRODUCTION

The noki or dassie-rat (*Petromus typicus* A. Smith, 1831) belongs to the monospecific hystricognath family Petromuridae. We prefer the common name “noki” because it avoids the confusion by many people between dassie-rats and rock dassies (rock hyraxes in the mammalian order Hyrcoidea) and true rats (species in the rodent families Muridae and Cricetidae). Noki is derived from a Hottentot dialect (SHORTRIDGE, 1942) and was used by GEORGE & CROWTHER (1981).

Nokis are endemic to Africa in the southwest arid biogeographical region (MEESTER, 1965), where they are closely associated with rocky habitats, especially the Namibian escarpment zone with its numerous mountains, cliff faces, and inselbergs or kopjes (COETZEE, 2002). They occur from extreme southwestern Angola south through Namibia, and into northwestern Cape Province of South Africa. The aridity of the escarpment and closely related Namib Desert is at least 15 million years old (WARD & CORBETT, 1990) and the noki has had an ancient association with these biomes (MEESTER, 1965), as demonstrated by several morphological adaptations to living in rock crevices (GEORGE & CROWTHER, 1981; SKINNER & SMITHERS, 1990). These include a flattened cranium, flexible ribs, and dorso-lateral mammae.

Nokis superficially resemble ground squirrels, including their largely diurnal activity. Apart from general natural history observations (e.g., SKINNER & SMITHERS, 1990) and reports based largely on opportunistic observations (e.g., COETZEE, 1983), there are only two field studies of noki ecology (WITHERS, 1979; GEORGE & CROWTHER, 1981). Recently, reproduction and behaviour of captive nokis have been studied (MESS, 2002).

Because the noki has a limited distribution, there is considerable interest in this near-endemic Namibian family of rodents (GRIFFIN, 1998). In this paper we report information on noki feeding ecology that we gathered while studying the social structure and behaviours of free-ranging nokis in Namibia.

METHODS

Our study was near the Erongo Wilderness Lodge (21° 27.679 S, 15° 52.523 E) on Okapekaha Farm, about 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 dikes and domes that rise about 100 m above the surrounding peneplain and smaller 10-20 m high granite outcrops or kopjes (Fig. 1) surrounded by intruding fingers of the surrounding bushveld. The vegetation at the study site is composed of low trees and bushes interspersed with seasonally dense annual and perennial forbs and perennial bunch grasses. The dominant trees include *Combretum apiculatum*, *Sterculia africana*, *Terminalia prunoides*, and *Boscia albitrunca* and the more dominant bushes included several species of *Grewia*, *Croton gratissimus*, *Dichrostachys cineria*, and *Mundulea sericea*.

Annual mean rainfall at Omaruru Prison is 292.9 mm, with virtually all of this falling during the months of November through April (Fig. 2). Annual average minimum and maximum temperatures are 11.4 and 31.0° C, with May through August being the coolest as well as driest months (Fig. 2).

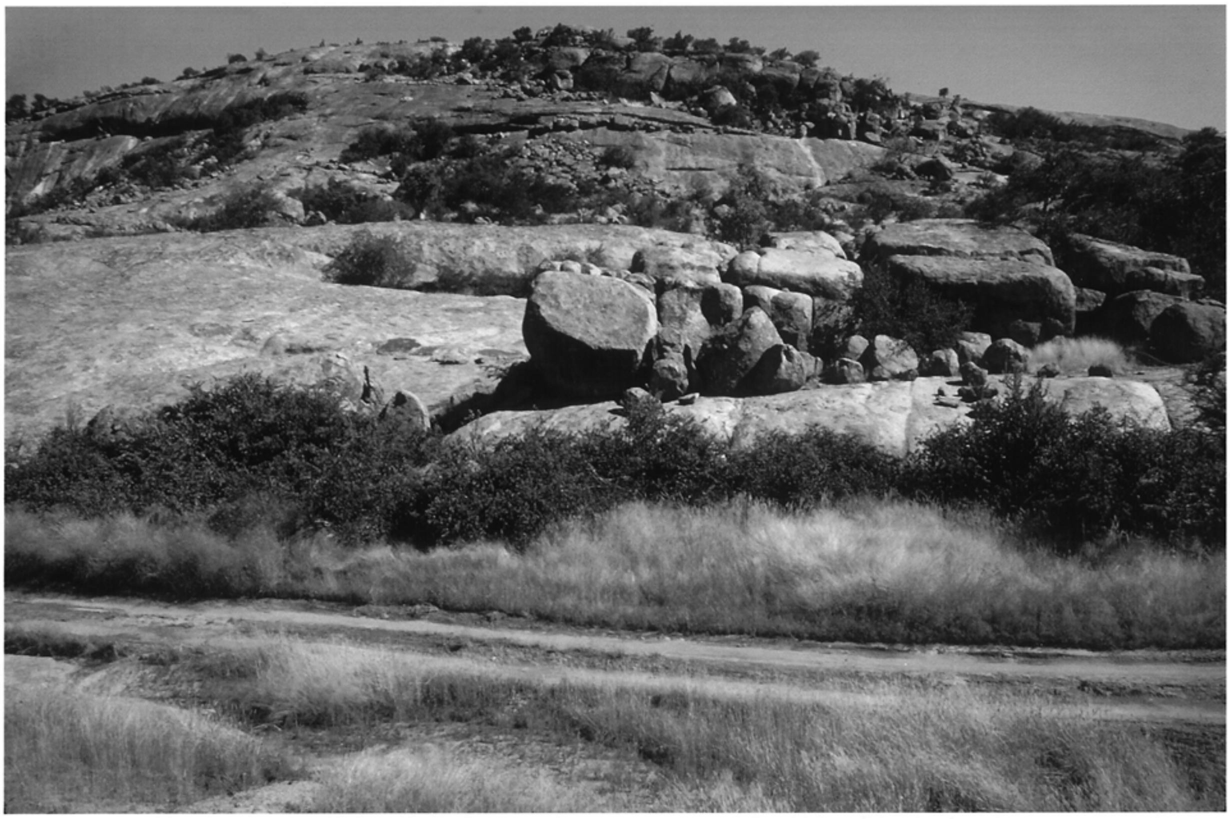

Fig. 1. – Single kopje (3-m-high cluster of boulders in foreground above road) at the Erongo Mountains, Namibia, study site where many of our observations occurred. Note the dense concentration of food plants (mostly *Grewia* spp. and bunch grasses) at the base of the granite rock.

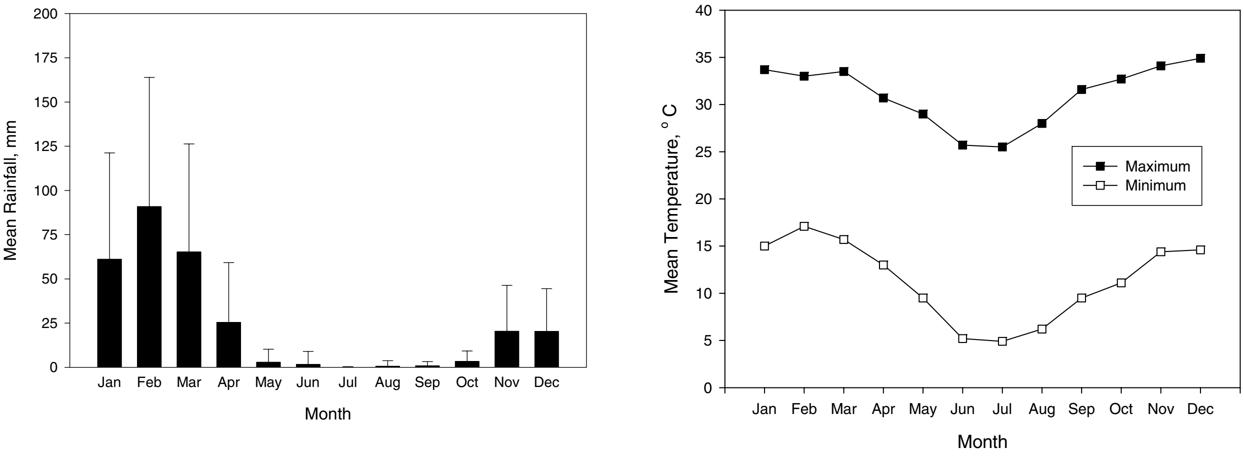

Fig. 2. – Left : Average (40 years) monthly rainfall at Omaruru Prison, located about 10 km from the noki study site. Right : Average (10 years) maximum and minimum monthly temperatures at Omaruru Prison.

It is particularly difficult to catagorise the phenology of arid-land plants because they respond very differently to the high year-to-year climatic variation (Hüser, 1976). For example, whether and when some perennial plants lose their leaves (generally those classified as "inconsistently deciduous" in Table 1) is closely tied to the occurrence of freezing temperatures and the quantity and timing of the seasonal rainfall. To draw some generalizations about noki feeding ecology, we have subjectively assigned some phenological traits to the common plants at out study site (Table 1), realizing that in some instances this is probably an oversimplification.

TABLE 1

Common plants found at our noki study site (alphabetical order by genus). Those that are especially associated with boulder habitats (e.g., noki habitat) in the Erongo area (personal observations and P. Carven, personal communication) are indicated by an asterisk (*) in the "Traits" column, while those without an asterisk also are commonly found in the surrounding bushveld. Plants not observed eaten by nokis during the 2000-2003 study period are indicated with a dash (--) in the "Parts Eaten" column. In the "Traits" column, we assigned one feature from each of the following groups (separated by commas): perennial (P) or annual (A), deciduous (D) or inconsistently deciduous (I), tree (T) or bush (B) or forb (F) or grass (G). We subjectively ranked each food plant in importance (most = 1 and least = 3) to noki diet based on our observations.

Scientific Name	**Parts Eaten**	**Traits**
Abutilon angulatum	Green leaves & stems	P, D, B, 3, *
Abutilon fruticosum	Green leaves & stems	P, D, B, 3, *
Abutilon ramosum	Green leaves & stems	P, D, B, 3, *
Acacia erubescens	Green leaves	P, D, T, 3
Adenolobus garipensis	Flowers	P, I, B, 3, *
Barleria lancifolia	--	P, D, B, *
Barleria sp.	--	P, D, B
Bidens biternata	Entire green plant, dry stems	A, D, F, 2
Blepharis obmitrata	Green leaves	P, D, B, 3
Boscia albitrunca	Flowers	P, I, T, 3
Cardiospermum pechuelii	--	P, D, B
Combretum apiculatum	Dry leaves	P, D, T, 1
Commiphora glaucescens	Dry leaves & stems	P, D, T, 3, *
Croton gratissimus	--	P, D, T, *
Cyphostemma omburense	Green & dry leaves	P, D, F, 1
Dichrostachys cinera	Green leaves	P, D, B, 3
Dombeya rotundifolia	--	P, D, B, *
Dyerophytum africanum	--	P, D, B, *
Enneapogon scoparius	Dry stems	P, D, G, 2
Erythrina decora	--	P, D, T, *
Ficus ilicina	--	P, I, T, *
Forsskaolea viridis	Entire green plant	A, D, F, 1
Grewia bicolor	Green & dry leaves & fruit	P, D, B, 1
Grewia flava	Fruit	P, D, B, 2
Grewia flavescens	Green leaves	P, D, B, 1
Grewia tenax	Green leaves	P, D, B, 1
Helinus integrifolius	Green leaves	P, D, B, 3, *
Hibiscus micranthus	Green leaves & stems	P, D, B, 3
Hibiscus castroi	--	P, D, B
Indigofera filipes	--	P, I, B
Jamesbrittenia pallida	--	P, D, B, *
Lycium basciifolium	Green leaves	P, I, B, 3
Montinia caryophyllacea	Dry leaves	P, D, B, 3 *
Mundulea sericea	--	P, D, B, *
Obetia carruthersiana	--	P, D, T, *
Portulaca sp.	Green leaves	A, D, F, 1
Schmidtia kalahariensis	Dry stems	P, D, G, 2
Solanum rigescentoides	Green leaves	P, D, B, 3, *
Steganotaenia araliacea	--	P, D, T, *
Sterculia africana	Dry leaves, flowers	P, D, T, 2, *
Stipagrostis uniplumis	Dry stems	P, D, G, 2
Talinum arnotii	Green leaves	A, D, F, 1
Terminalia prunioides	--	P, D, T

After determining the suitability of the study site in June 2000 we captured, tagged, and observed four to six nokis during each of four periods : 25 December 2000 through 5 January 2001, 5 September through 21 November 2001, 24 April through 7 July 2002, and 10 May through 26 July 2003. We caught animals with 4.5 x 4 x 15 inch folding aluminium or 16 x 5 x 5 inch single-door wire mesh live traps set during daylight hours and baited with pieces of raw carrots or apples. To prevent hyperthermia in captured animals we positioned traps in the shade or avoided trapping during mid-day.

We attached radio transmitters with collars made of antenna wire inside Tygon tubing (Holohil Systems Ltd., Carp, Ontario, Canada; model MD-2C, 2.2 g weight, 120-day battery life, 20-pound test 10-cm-long wire whip antenna). We radio-located each of the nokis several times a day between 0430 and 2230 hours. When air temperatures were below about 30º C we sat on top of granite boulders and with 8 x 40 binoculars watched tagged as well as untagged nokis. Even with the advantage of being able to always find the radio-tagged animals, observation often was difficult because of obstructing rock, the animals' wariness, and their use of narrow and deep rock crevices for shelter.

RESULTS

The nokis exhibited a catholic diet of plants and plant parts (Table 1), including dry fragments of unidentifiable leaves and stems when fresh plant matter was available. However, some plants appeared to be particularly important in the diet of nokis, perhaps because they were especially common, nutritious, or moist (importance category 1 in Table 1). For example, at the end of the dry season and prior to the rains (September and October, Fig. 2), when nearly 90% of the common plants at our study site were leafless (Table 1), several trees flowered. The nokis often foraged on the surfaces of boulders and the ground under *Sterculia africana* and *Boscia albitrunca* trees where they gleaned fallen flowers. After the main rains (April and May), they foraged on the green leaves, flowers, and fruits of bushes, especially several species of *Grewia* (Table 1). With the approach of the dry season (June and July) nokis focused on plants that still contained moisture, particularly the vine *Cyphostemma omburense* with its fleshy leaves, and annual forbs (e.g., *Forsskaolea viridis* and *Portulaca* sp.) that grew in the deep shade and moist soil at the base of granite boulders. At the height of the dry season (August and September) nokis fed mostly on dry leaf and stem detritus that accumulated at the bases of rock faces and in rock crevices. Although it was difficult to identify these dry plants, we suspect they were the same species that the nokis fed on during other parts of the year.

Another aspect of their habitat is that the plants were highly clumped and the clumps often were composed of different species (Fig. 1). Thus, nokis on one kopje had access to different food plants than nokis on a nearby kopje. For example, the kopje in Fig. 1 lacks several species, most notably the trees *Boscia albitrunca* and *Commiphora glaucescens* and the bushes *Adenolobus garipensis* and *Mundulea sericea*. This spatial variation in species composition made it difficult to determine which plants nokis avoided; we suspect that they actually fed on most plants, even if we only documented them eating 28 out of the 43 (65.1%) most common plants found associated with kopjes in our study area (Table 1). Some plants, however, were only eaten at specific stages in their phenology. For example, the leaves and stems of *Montinia caryophyllacea* were only eaten once they had dried in late July and August. Other plants seemed to be completely avoided, including *Croton gratissimus*, *Jamesbrittenia pallida* and *Indigofera filipes*. Indeed, unlike some of the other plants that we did not see nokis feed on (e.g., *Barleria lancifolia* and *Hibiscus castroi*,), the former three also showed no evidence of being browsed by the other rupicolous mammals on our study site, such as rock hyrax (*Procavia capensis* Pallas, 1780), klipspringer (*Oreotragus oreotragus* Zimmermann, 1783), and Jameson's Rock Rabbit (*Pronolagus randensis* Jameson, 1907). Although we often observed nokis feeding on dry grass stems (Table 1), which were abundant in some areas at the bases of the kopjes (Fig. 1), we did not see them eat or harvest grass seed-heads.

The upper portions of the kopjes that the nokis occupied were virtually devoid of growing plant matter, which required the animals to descend to the base of the rocks to find food (Fig. 1). They often carried single leafed twigs or grass stems (up to about 20 cm long) from the bases of the kopjes to favoured basking and resting spots higher in the rocks, where they fed on the material, including later in the day or on a subsequent day if it was not initially consumed. For example, in late June 2003 at 0655 hrs. one of the collared male nokis moved from the crevice where he spent the night to a crevice at the lower edge of the kopje and began to harvest the green leaves and stems from a *Grewia flaviscens* bush that was about 1.5 metres from his crevice. During the 35-minute feeding bout he made nine trips to the bush, each time bringing back to his crevice a leafed stem, which he ate in his crevice before returning for more. After the feeding bout, he started a session of basking in the sun, which lasted most of the morning. Even though nokis often harvested plants, we found no evidence that this material was actually cached or stored for later consumption.

We never observed or radio-tracked the animals further than about 10 m away from the base of kopjes and rock crevices, where they immediately retreated if disturbed. Although they often climbed into bushes and out onto tree limbs to forage, they usually remained within leaping distance (ca. 1 m) of rocks and safety. The high risk of predation while foraging was illustrated by three of the radio-tagged nokis being killed and eaten at favoured foraging sites. Even though these three different sites were only 2-3 m from the safety of rock crevices at the bases of kopjes, we suspect that the diurnal and solitary black mongooses (*Galerella nigrata* Thomas, 1928), which we often saw hunting in and around our kopjes, surprised and captured the foraging nokis before they could reach the safety of a rock crevice.

We tallied radio locations associated with nokis foraging or harvesting (we did not include instances of plants being ingested after they had been harvested and carried up into the kopje) by daylight quarters between 0600 and 1800 hours in 2001 and 2002. We used the proportion of our radio-tracking effort in each quarter and total feeding bouts to calculate the expected foraging bouts per quarter. These data, starting with 0600 to 0900 hrs., were 20 observed and 10 expected, 4 and 10.5, 4 and 11, and 22 and 18.5. The observed distribution is significantly different from the expected ($X^2 = 9.82$, df = 3, P=0.02), indicating that foraging was concentrated in early morning and late afternoon.

Three times we observed an unusual behaviour by adults that we call a "tail stand" (Fig. 3). These occurred on flat basking sites and entailed standing on the front feet and propping up the hindquarters with the downturned and stiffened tail while vigorously kneading or scratching the abdomen simultaneously with both rear feet. Each "tail stand" lasted about 10 seconds. We suspect this behaviour may be related to their feeding habits (see discussion).

Fig. 3. – Adult female noki performing a "tail stand." Drawing based on a photograph of a free-ranging female at a basking site.

Rock hyraxes and nokis often foraged simultaneously in the same *Grewia* bushes, sometimes within 10 cm of each other, but we never saw any agonistic behaviour between the two species. They also used the same basking spots and on 11 occasions we observed single rock hyraxes displace single nokis from these sites. In these cases the approaching rock hyrax either seemed oblivious to the presence of the noki, or it displaced the noki after slowly and cautiously approaching it in a posture that suggested curiosity. In several cases the approach even included an attempt to sniff the basking rodent. In all instances, the noki fled only when the rock hyrax approached very closely, often to within a few centimetres. Although we observed nokis responding to rock hyrax alarm calls by bolting for cover, they did not react to rock hyrax territorial cries. We never had an opportunity to determine whether rock hyraxes responded to the noki "cheeeeeee" alarm call.

DISCUSSION

The diet of nokis was quantified using faecal analyses in the Augrabies Falls National Park on the Orange River in South Africa (GEORGE, 1981) and at Tumasberg, an inselberg in the Namib Desert of Namibia (WITHERS, 1979), which are about 200 km and 950 km south of our Erongo study site. In general, the diet at these two sites was unremarkable; *Petromus* ate a wide variety of plants in rough proportion to their occurrence. However, the dominant plants and diet at the two sites and our study site were different with little overlap in species eaten, which demonstrates the catholic and flexible diet of nokis. Captive nokis also show a wide tolerance for different plant foods (MESS & ADE, this volume).

WITHERS (1979) found little seasonal variation in the diet of nokis, and like nokis at Augrabies Falls (GEORGE, 1981), they ate predominately the stems and leaves of grasses and dicotyledonous plants. Nokis at Erongo seasonally ate different species, as illustrated by their focus on forbs during the wet season (these plants disappeared during the dry season). Also, the diet of the Erongo nokis closely followed the phenology of most plants -- focusing on flowers, then fruits, and then leaves and stems according to the season. It is possible that seasonal differences were not found at Tumasberg with faecal analysis because some tissues (e.g., flowers and fruits) are difficult to detect and there is unlikely to be any significant difference between green and dry leaves of the same species after being digested.

The obvious avoidance by nokis of several plants at our study site (see Results section) is likely due to their containing secondary defence compounds, as evidenced by their strongly aromatic leaves. It is not clear, however, why nokis at all three study sites seemed to avoid grass seed-heads, with their presumed higher energy content compared to leaves and stems.

Nokis, unlike many desert rodents, are not able to rely only on metabolic water (WITHERS et al., 1980) and thus need free-standing water (personal observations; MESS & ADE, this volume) or moisture in plants. Indeed, the importance of water in their diet was shown at Augrabies Falls by their preference for the bases of grass stems, which have a higher water content than tops (GEORGE, 1981). Our study site was more mesic compared to Augrabies Falls and Tumasberg, which average about one half and one third the annual rainfall of our site. Because noki metabolic rate is about 25% lower than the predicted weight-specific rate (WITHERS et al., 1980), perhaps their diet at Erongo was influenced more by the nutritional quality of food plants than by moisture content.

The nokis at Tumasberg ingested a significant amount of insect material (WITHERS, 1979), whereas insectivory was not documented at Augrabies Falls (GEORGE, 1981). We did not observe nokis searching for or eating invertebrates, and captives do not eat insects or meat (MESS & ADE, this volume). It is not clear if insects were ingested inadvertently at Tumasberg, or if they were purposefully eaten in relation to optimal foraging or water needs. In any case, it further demonstrates the flexible diet of nokis.

WITHERS (1979), COETZEE (1983), and MESS & ADE (this volume) describe coprophagy in nokis, and Coetzee also describes captive nokis remasticating food after sitting up on their rear legs and bending their head sharply down to the abdomen and then jerking upright. This "jack knife" motion apparently induces regurgitation prior to remastication. We observed coprophagy and the jack knife action, but only a very few times and we were unable to clearly distinguish the two. Indeed, MESS & ADE (this volume) have not observed regurgitation and remastication in captives and believe that the jack knife action is actually related to male autogrooming of the genitals or possibly masterbation. In any case, if coprophagy and the jack knife behaviours had not been previously described (COETZEE, 1983) we probably would not have recognised them. It is possible that coprophagy occurred more frequently than our observations indicate, especially if it was performed mainly while animals were hidden from view in rock crevices. Another possibility is that coprophagy and remastication (if it indeed occurs) are related to increasing the efficiency of digesting plant material with a high fiber content (Coetzee, 1983), and are thus more common where coarser plants and plant parts dominate the diet, as may be the case at the more arid Augrabies Falls and Tumasberg study sites. Perhaps the "tail stand" is also related to digestive efficiency -- the aggressive kneading of the abdomen with the rear feet somehow aiding in coprophagy by manipulating or stimulating the digestive track.

At Augrabies Falls, rock hyraxes and nokis do not compete for shelters because they use different sites based on their dissimilar body sizes and the food plants they both use apparently are plentiful enough to avoid competition (George & Crowther, 1981). The lack of food caches by either species also suggests that this resource is not limited. During our study, we observed no agonistic behaviours between the two species at feeding or basking sites, which further supports the absence of competition between the two. Indeed, nokis responded to the alarm calls of rock hyraxes, suggesting that their close spatial and temporal association was mutually beneficial because of increased vigilance for predators.

In hot and dry regions of Australia, some herbivorous mammals are closely associated with rocky habitats because they feed on the particularly diverse and productive flora at these sites (Freeland et al., 1988). The rich flora is the result of the water concentrating and retaining characteristics of the rocky areas. A similar moisture-related explanation for the vegetative richness of riparian zones is more widely recognised. The bases of kopjes and rock faces at our study site also supported a relatively rich flora. Not only were plants denser at the bases of kopjes, but they seemed to grow taller and remain green longer than in the surrounding bushveld. In addition, there was some evidence of greater species diversity. For example, of the 43 common species found at our noki study site, 19 (44.2%) were especially associated with our kopje habitats (Table 1), while the remainder were more widespread in the surrounding bushveld. Similar patterns in plant communities have been found on other Namibian inselbergs (Burke, 2002, 2003). We believe the rich flora associated with the bases of kopjes is an important factor in providing an abundant, reliable, and seasonally rich source of food for nokis as well as other rupicolous herbivorous mammals.

CONCLUSIONS

Nokis exhibit a rupicolous adaptive syndrome characterised by several remarkable and inter-related features of their feeding ecology. They are restricted to harsh rocky habitats where their flexible and catholic herbivorous diet is well suited to the rich but clumped, variable, and highly seasonal vegetation. In addition, their low metabolic rate and need for non-metabolic water probably relates to their variable and flexible diet. The unusual behaviours associated with digestion enable them to feed efficiently on plant parts with a high fibre content, which is likely critical during the dry season when nearly all plants have lost their leaves. Nokis have several peculiar morphological adaptations to living in rock crevices that suggest a long association with rocky areas. All these features result in the noki being an obligate petrophile.

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