# Utilization of the termite *Hodotermes mossambicus* (Hagen) by gekkonid lizards near Keetmanshoop, South West Africa

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Five species of primarily nocturnal geckos (*Ptenopus garrulus maculatus, Chondrodactylus angulifer angulifer, Pachydactylus bibronii, P. mariquensis latirostris* and *P. punctatus)* collected near Keetmanshoop, South West Africa on the night of 3 October 1987 were found to contain large numbers of the harvester termite *Hodotermes mossambicus.* The mass of termites consumed ranged up to 61,1% of empty gecko body weight. Termite consumption of this magnitude and extensive above-ground foraging by large numbers of *Ptenopus* appear to be uncommon and probably reflect gecko usage of a large-scale *Hodotermes* foraging bout associated with the onset of the rainy season. The availability of such a concentrated food resource may be particularly important for vitellogenic female geckos.

Groot hoeveelhede van die grootgrasdraertermiet *Hodotermes mossambicus* het in die spysverteringskanaal van vyf spesies van hoofsaaklik naglewende geitjies (*Ptenopus garrulus maculatus, Chondrodactylus angulifer angulifer, Pachydactylus bibronii, P. mariquensis latirostris* en *P. punctatus*), wat gedurende die nag van 3 Oktober 1987 naby Keetmanshoop, Suidwes-Afrika versamel is, voorgekom. Die massa van die verorberde termiete het tot 61,1% van die ongevoede liggaamsmassa van die geitjie beslaan. Termietverbruik op hierdie skaal en die uitgebreide bogrondse soektog na voedsel deur groot getalle van *Ptenopus* is blykbaar buitengewoon en weerspieël moontlik die benutting deur die geitjies van 'n grootskaalse voedselsoektog van *H. mossambicus* met die aanvang van die reënseisoen. Die beskikbaarheid van so 'n benutbare voedselbron mag van besondere belang wees vir vitellogene wyfie-geitjies.

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Termites constitute an important component of the diets of a number of terrestrial and rupicolous gekkonid lizards in the arid and semi-arid regions of southern Africa (Fitzsimons 1943; Loveridge 1947; Pianka & Huey 1978; Pienaar, Haacke & Jacobsen 1983). Certain geckos, such as *Ptenopus garrulus, Chondrodactylus angulifer* and *Palmatogecko rangei* which inhabit South West Africa appear to feed chiefly on termites, at least at certain sites (Fitzsimons 1935; Haacke 1975). Although the diets of these and many other geckos have been established through the analysis of stomach contents, there has been little evidence bearing on the dynamics of feeding bouts, or the spatio-temporal significance of food availability to the foraging strategies of nocturnal gekkonids. Like other, primarily insectivorous vertebrates, geckos are capable of utilizing and perhaps 'predicting' (via environmental cues) localized outbreaks or concentrations of arthropod prey.

Among lizards, patchy resource utilization is most clearly demonstrated by those taxa that prey largely or exclusively on concentrations of social insects. A prime example of this is seen in the North American iguanid lizards of the genus *Phrynosoma* which feed on ants, often near nest sites (Pianka & Parker 1975). Termites are used in several capacities by lizards in general and geckos in particular. This may take the form of predation on alate reproductives as they swarm (Light 1929, 1934; Arora 1962; Frith 1981) or may even involve the part-time occupation of termitaria for the purposes of food gathering, shelter or egg incubation (Mitchell 1965; Goodland 1965; Branch & Erasmus 1982; Riley, Stimson & Winch 1985). Undoubtedly, the most frequent type of lizard/termite interaction is, as with *Phrynosoma*, predation by lizards on non-winged soldiers and workers. The nocturnal foraging patterns of both termites and geckos, however, have prevented a direct assessment of the dynamics of this type of predator-prey interaction. We herein provide an analysis of the utilization of a termite activity bout by the nocturnal gekkonid lizard community in the vicinity of Keetmanshoop, South West Africa.

## Materials and Methods

Reptiles were collected or observed along National Highways 1 and 4 from Keetmanshoop to approximately 20 km south-east and south-west, respectively. Animals were located in the headlights of a vehicle travelling 30-50 km/h from sunset until approximately 4 h after sunset. All animals seen on the road or on the verge of the road were collected by hand (or in some cases, examined and released). Comparable collecting techniques were employed throughout South West Africa and results so obtained form the basis of comparative statements in this

**Table 1** Geckos collected near Keetmanshoop, South West Africa on 3 October 1987

| Species | CAS specimen no. | | Sex | SVL(mm) | Weight(g) | Stomach contents: Items | Weight (g) | % Body weight |
|---|---|---|---|---|---|---|---|---|
| *Ptenopus garrulus maculatus* | Field | 8640[1] | F | 54,60 | 3,75 | 35 *Hodotermes mossambicus* | 1,31 | 34,9 |
| | Field | 8641[1] | F | 54,65 | 3,75 | 33 *H. mossambicus* | 1,83 | 48,8 |
| | | 167734 | F | 55,90 | 3,54 | 9 *H. mossambicus*, 1 ant | 0,29 | 8,2 |
| | | 167735 | F | 55,80 | 3,75 | 9+ *H. mossambicus* | 0,50 | 13,3 |
| | | 167738 | F | 48,50 | 2,16 | 38 *H. mossambicus* | 1,32 | 61,1 |
| | | 167739[2] | F | 58,50 | 4,71 | 12 *H. mossambicus* | 0,43 | 9,1 |
| | | 167740 | F | 54,05 | 3,66 | 16 *H. mossambicus* | 0,46 | 12,6 |
| | | 167741 | F | 49,20 | 2,65 | 42 *H. mossambicus* | 1,22 | 48,8 |
| | | 167742 | M | 54,35 | 3,23 | 24 *H. mossambicus* | 1,00 | 31,0 |
| | | 167744 | M juv. | 38,15 | 1,25 | 5+ *H. mossambicus* | 0,40 | 32,0 |
| | | 167746 | F | 54,05 | 3,66 | 16 *H. mossambicus* | 0,46 | 12,6 |
| | | 167747 | F | 54,90 | 3,89 | 7 Nasutitermitinae | 0,31 | 8,0 |
| *Chondrodactylus angulifer* | | 167723[3] | F | 89,95 | 14,07 | 12 *H. mossambicus* | 0,58 | 4,1 |
| | | 167721 | F | 102,00 | 20,61 | 6 *H. mossambicus*, 1 shed skin | 1,45 | 7,0 |
| | Field | 8644[1] | M | 103,00 | 21,00 | 20+ *H. mossambicus* | 1,24 | 5,9 |
| | | 167722 | F | 90,20 | 15,67 | 89 *H. mossambicus* | 3,29 | 21,0 |
| *Pachydactylus bibronii* | Field | 8639[1] | M | 59,20 | 6,00 | – | – | – |
| | | 167714 | F | 62,40 | 6,06 | 40 *H. mossambicus* | 1,69 | 27,9 |
| | | 167716 | M | 53,85 | 4,39 | 3 *H. mossambicus* | 0,20 | 4,6 |
| | | 167717[2] | M | 65,75 | 7,37 | – | – | – |
| *Pachydactylus mariquensis* | Field | 8642[1] | F | 50,55 | 2,80 | 2 *H. mossambicus* | 0,12 | 4,3 |
| *Pachydactylus punctatus* | | 167657 | F | 33,35 | 1,04 | 1 *H. mossambicus* | 0,03 | 2,9 |

[1]Cleared and stained specimen, body weight estimated based on conspecifics. [2]Specimen killed and fixed > 24 h after capture. [3]Dead on road, body severely damaged, stomach contents partial only.

paper. Specimens were injected intraperitoneally with T-61 euthanasia solution, fixed in 10% neutral buffered formalin and stored in 70% ethanol. Stomachs were removed and their contents identified, blotted and weighed. All specimen measurements were taken after preservation.

## Results

Twenty-two specimens of five species of terrestrial and rupicolous geckos were collected near Keetmanshoop on the night of 3 October, 1987 (see Table 1). In addition, two snake species were also captured — *Bitis caudalis* (four specimens) and *Telescopus semiannulatus* (one specimen). In addition to the animals collected, another approximately 20 *Ptenopus garrulus* and smaller *Pachydactylus* were observed on the road (including road-killed individuals). Geckos were found in unequal numbers along different areas of the transects (Figure 1). The most notable clumping of specimens was seen 13,0–17,0 km south-east of Keetmanshoop on Highway 1 and 13,5– 18,0 km south-west of the town on Highway 4.

*Ptenopus* were heard calling in huge numbers along the length of both transects and even in vacant lots in Keetmanshoop itself. Of those specimens collected that contained stomach contents, all contained termites, and

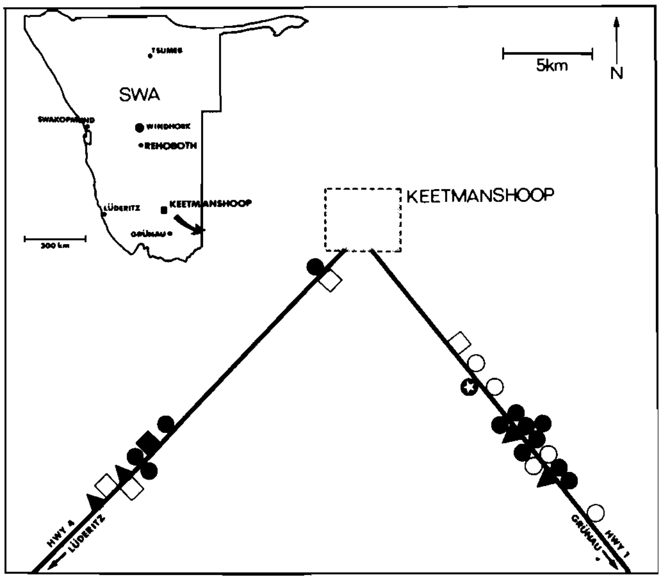


**Figure 1** Stylized map of the Keetmanshoop region indicating collecting sites of geckos on 3 October, 1987. Symbols: Closed circle = *Ptenopus garrulus maculatus;* open circles = *P. g. maculatus* (specimens not collected); open square = *Pachydactylus bibronii;* closed triangle = *Chondrodactylus angulifer;* closed square = *Pachydactylus mariquensis;* star = *Pachydactylus punctatus.*

all but one of these contained only the species *Hodotermes mossambicus*, a harvester termite of the family Hodotermitidae known to be the dominant food item of *Chondrodactylus* and *Pachydactylus bibronii* elsewhere in their ranges (Pianka & Huey 1978). No alates of this species were found. All specimens, as far as could be determined, represent the two types ('small and large') of foraging worker termites known in this species (Hegh 1922; Watson 1973). The larger workers, characterized by their enormous, flattened heads constituted approximately three fourths of the total of the *H. mossambicus* consumed. The only exception to the consumption of *H. mossambicus* was a single *Ptenopus garrulus maculatus* (CAS 167747) that contained the remains of seven soldier nasuti-termitine termites (family Termitidae). In addition one ant, a shed skin (Table 1), and small particles of plant material and sand were also recorded from gecko stomachs.

As many as 40 termites were found in *Pachydactylus bibronii*, 42 in *Ptenopus g. maculatus* and 89 in *Chondrodactylus angulifer*. This accounted for a range of 4,1–61,1% of empty body weight ($\bar{x}$ = 21,7% for specimens of these three taxa with at least one prey item). For *P. g. maculatus* alone this range was 8,0–61,1% ($\bar{x}$ = 26,7%). There was no obvious correlation between percentage body weight consumed and location along the transect. A return to the Keetmanshoop transect on 19 October, 1987 yielded 20 specimens of geckos (10 *Chondrodactylus*, 6 *Pachydactylus bibronii*, 3 *P. punctatus*, 1 *P. mariquensis*). No *Ptenopus* were seen, although animals were heard calling along the entire transect. Most of the animals collected on this date were returned alive to Canada so no stomach analysis was performed. Nonetheless, the animals were not distended as were the specimens collected 16 days earlier, and for two specimens for which it could be determined, prey weight as a percentage of body weight was 5,0% (*Chondrodactylus angulifer*) and 2,3% (*Pachydactylus mariquensis*). These two specimens and another three *P. bibronii* that contained only traces of prey were found to have ingested, in addition to *Hodotermes mossambicus*, coleopterans, acridids and unidentified, non-isopteran insect parts. Although *Ptenopus* were heard calling every night in South West Africa, only two additional specimens were seen and collected while night driving over a three-week period. These specimens (CAS 167748–9) were found 8,7 and 5,2 km south of Rehoboth on 4 October, 1987. Neither specimen contained termites; the former had eaten a single ant, the latter three ants, a cricket and a solifugid.

## Discussion

The consumption of *Hodotermes mossambicus* by *Chondrodactylus angulifer* and *Pachydactylus bibronii* is well established (Pianka & Huey 1978), although *Ptenopus garrulus* appears to prey more frequently on considerably smaller termites, at least in the Kalahari (Pianka & Huey 1978). The huge number of *H. mossambicus* consumed by geckos near Keetmanshoop on 3 October, 1987 appears to represent a capitalization by all of these lizards on a spatio-temporally limited resource. On this date lizards were able to accummulate food resources of up to 61,1% of their own (empty) body weight. Even for those taxa that feed on *H. mossambicus* regularly, this magnitude of consumption is abnormally high and must certainly be enough to satisfy the energy demands of many days or weeks of activity.

The cause of the termite activity bout can be surmised on the basis of several factors. The absence of alate reproductive *Hodotermes* from the stomach contents argues against localized premating swarming and no evidence of flying alates or detached wings was observed in the area. Further, *H. mossambicus* typically swarms somewhat later in the spring, some three to five days after the first major rains (Nel & Hewitt 1978). Sociotomy, or the mass movement of representatives of *all* castes in a colony in order to found a new colony (Grassé & Noroit 1951) can also be ruled out, both because it is unknown in the Hodotermitidae and because only workers were among the geckos' prey. It appears most likely that the geckos took advantage of a periodic major foraging expedition by the harvester termites. Soldiers are not known to accompany workers on such expeditions in the genus *Hodotermes* (Bouillon 1970). Furthermore, *H. mossambicus* is known to exhibit seasonal cycling in its behaviour which involves intensive diurnal winter foraging with a shift to more sporadic nocturnal surface activity at the beginning of the rainy season (Sands 1965; Nel 1968; Coaton & Sheasby 1975). There also occurs in the spring a shift from diurnal to nocturnal foraging patterns by *Hodotermes* (Coaton 1958), thus making these insects available to the primarily nocturnal gekkonids. While no rain fell during the night of 3 October 1987, localized showers were encountered the following day between Keetmanshoop and Windhoek and partially cloudy skies with periodic, localized showers had occurred the day before. The distribution of engorged geckos along the entire length of the transect (but not near Rehoboth, nor at Keetmanshoop later in the month) suggests that seasonal and climatic conditions affected termite activity at many nests in the region, but that this activity was not universal in space or time.

Unlike other termitophages, such as aardwolves, which also feed on nocturnally surface foraging termites (Kruuk & Sands 1972; Cooper & Skinner 1979), geckos, because of limitations of size and exposure to predators, cannot cover large distances in search of numerous nests. Nor, like ants or other arthropod predators can they invade nests directly. Thus, because only a small number of patchy resources (i.e. termite nests) may be within reach, geckos take advantage of the temporal variability of the patches and, as indicated by these data, may ingest huge amounts of food when it becomes available and then restrict their own foraging under less favourable conditions. Such a strategy would certainly be compatible with the observations that burrow excavation, rather than night driving, has traditionally been the more effective means of collecting *Ptenopus* (W.D. Haacke, pers. comm.). That *Ptenopus* activity patterns seem more greatly affected by termite activity may support the contention that *Ptenopus* is more a termite specialist than *Chondrodactylus* or *Pachydactylus* spp. The former, by virtue of its larger size, may be capable of taking larger prey such as arachnids, and is known to feed on other lizards (Loveridge 1947; Brain 1962). *Pachydactylus* spp., on the other hand, are capable of utilizing a wider variety of foraging sites, including stones and vegetation, than are the burrowing *Ptenopus*.

The preponderance of female *Ptenopus g. maculatus* collected and observed is somewhat puzzling. While there are data on male calling patterns (Haacke 1969, 1975), little is known about female behavioural patterns. All of the adult females collected possessed ovarian or unshelled oviductal eggs, in concordance with Haacke's (1975) report that hatchlings of this subspecies have been found from October to May and the statement of Pianka & Huey (1978) that Kalahari *Ptenopus* eggs yolk from late August through late January. The large number of females observed during the night of October 3 suggest that vitellogenesis may place particular demands on female resource acquisition.

The utilization of termites by *Ptenopus* and other geckos near Keetmanshoop illustrates the concept that has recently been promoted (e.g. Greene 1986) that rare large prey items (or in this case, rare or sporadic concentrations of prey items) may be vital, and often overlooked, components in the understanding of feeding ecology. In the case of nocturnal lizards and their prey, such relationships are particularly poorly known. Only through long-term studies of geckos at single localities will such patterns become clear and the significance of rare concentrations of prey arthropods be understood.

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## References

ARORA, G.L. 1962. Biological observations on some termites from Hoshiarpur, Punjab. In: Termites in the Humid Tropics, pp. 111–113. UNESCO, Winterthur.

BOUILLON, A. 1970. Termites of the Ethiopian region. In: Biology of Termites Vol. II, pp. 153–280, (eds.) Krishna, K. & Weesner, F.M. Academic Press, New York.

BRAIN, C.K. 1962. A review of the gecko genus *Ptenopus* with the description of a new species. *Cimbebasia* 1: 1–18.

BRANCH, W.R. & ERASMUS, H. 1982. Notes on reproduction in South African water monitors, *Varanus niloticus niloticus* (Sauria: Varanidae). *J. Herpetol. Assoc. Afr.* 28: 4–9.

COATON, W.G.H. 1958. The hodotermitid harvester termites of South Africa. *Dept. Agri. Sci. Bull., S. Afr., Entomol. Ser.* 375: 1–112.

COATON, W.G.H. & SHEASBY, J.L. 1975. National survey of the Isoptera of Southern Africa. 10. The genus *Hodotermes* Hagen (Hodotermitidae). *Cimbebasia,* Ser. A. Vol. 3: 105–138.

COOPER, R.L. & SKINNER, J.D. 1979. Importance of termites in the diet of the aardwolf *Proteles cristatus* in South Africa. *S. Afr. J. Zool.* 14: 5–8.

FITZSIMONS, V.F. 1935. Notes on a collection of reptiles and amphibians made in the southern Kalahari, Bushmanland and Great and Little Namaqualand. *Ann. Transvaal Mus.* 15: 519–550.

FITZSIMONS, V.F. 1943. The lizards of South Africa. *Mem. Transvaal Mus.* 1: 1–528 + 24 pls + 1 map.

FRITH, C.B. 1981. Utilization of a single brief termite eruption by predators. *Nat. Hist. Bull. Siam Soc.* 29: 173–174.

GOODLAND, R.J.A. 1965. On termitaria in a savanna ecosytem. *Can. J. Zool.* 43: 641–650.

GRASSÉ P.P. & NOIROT, J.C. 1951. La Sociotomie: migration et fragmentation de la termitière chez les *Anoplotermes* et les *Trinervitermes*. *Behaviour* 3: 146–166.

GREENE, H.W. 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana (Zoology),* N.S. 31: 1–12.

HAACKE, W.D. 1969. The call of the barking geckos (Gekkonidae: Reptilia). *Sci. Pap. Namib Desert Res. Sta.* 46: 83–93 + 1 pl.

HAACKE, W.D. 1975. The burrowing geckos of Southern Africa, 1 (Reptilia: Gekkonidae). *Ann. Transvaal Mus.* 29: 197–243 + 2 pls.

HEGH, E. 1922. Les Termites. Imprimerie Industrielle et Financiére, Bruxelles.

KRUUK, H. & SANDS, W.A. 1972. The aardwolf (*Proteles cristatus* Sparrman 1783) as a predator of termites. *E. Afr. Wildl. J.* 10: 211–227.

LIGHT, S.F. 1929. Notes on Philippine termites III. *Philip. J. Sci.* 40: 421–452 + 9 pls.

LIGHT, S.F. 1934. The constitution and development of the termite colony. In: Termites and Termite Control, pp. 22–41. (Ed.)Kofoid, C.A. University of California Press, Berkeley.

LOVERIDGE, A. 1947. Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool.* 98: 1–469 + 7 pls.

MITHCELL, F.J. 1965. Australian geckos assigned to the genus *Gehyra* Gray (Reptilia, Gekkonidae). *Senckenberg. Biol.* 46: 287–319.

NEL, J.J.C. 1968. Distribution of the foraging holes and soil temperatures of the harvester termite *Hodotermes mossambicus* (Hagen). *S. Afr. J. Agric. Sci.* 11: 173–182.

NEL, J.J.C. & HEWITT, P.H. 1978. Swarming in the harvester termite *Hodotermes mossambicus* (Hagen). *J. Entom. Soc. South Afr.* 41: 195–198.

PIANKA, E.R. & HUEY, R.B. 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia* 1978: 691–701.

PIANKA, E.R. & PARKER, W.S. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975: 141–162.

PIENAAR, U. de V., HAACKE, W.D. & JACOBSEN, N.H.G. 1983. The Reptiles of the Kruger National Park, revised edition. National Parks Board of South Africa, Pretoria.

RILEY, J., STIMSON, A.F., & WINCH, J.M. 1985. A review of Squamata ovipositing in ant and termite nests. *Herpetol. Rev.* 16: 38–43.

SANDS, W.A. 1965. Mound population movements and fluctuations in *Trinervitermes ebenerianus* Sjöst. (Isoptera, Termitidae, Nasutitermitinae). *Insects Sociaux* 12: 49–58.

WATSON, J.A.L. 1973. The worker caste of the hodotermitid harvester termites. *Insects Sociaux* 20: 1–20.