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Feeding ecology of the common slit-faced bat (*Nycteris thebaica*) in KwaZulu-Natal, South Africa

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Monthly samples of arthropod remains ($n = 1,190$ culled parts) collected over a year from under a *Nycteris thebaica* night roost in the Kenneth Stainbank Nature Reserve (South Africa) show that prey eaten by bats vary significantly by order but not by season. Nevertheless, there was a significant interaction between the prey category and season, suggesting that these two factors are not independent from each other. Coleoptera (49.6% in the culled parts, calculated as percent composition) dominated in spring (September–November), Orthoptera (38.8%) in summer (December–February), Hemiptera (42.8%) in autumn (March–May), and Lepidoptera (36.3%) in winter (June–August). The diet also included a frog and a small fish ($n = 2$ parts).

Key words: *Nycteris thebaica*, Nycteridae, culled parts, diet, South Africa

INTRODUCTION

Common slit-faced bats (*Nycteris thebaica*; family Nycteridae) are widespread, savanna and semi-desert animals common throughout much of Africa and in the Middle East (Grey *et al.*, 1999). These slow-flying, highly manoeuvrable animal-eaters can hover (Fenton and Thomas, 1980; Fenton *et al.*, 1983; Aldridge and Rautenbach, 1987; Aldridge *et al.*, 1990), allowing them to forage close to surfaces and take prey from the ground and vegetation (LaVal and LaVal, 1980). They also can forage close to the tops of trees and around buildings, hawking insects from around lights (Fenton *et al.*, 1980, 1983). Their echolocation calls are of high frequency and low intensity and their wings are broad with low wing loading (6.3 N/m^2) and low aspect ratio (5.5; Aldridge *et*

al., 1987) — features that should equate with short commuting distances from roosts to foraging sites, and the use of passive cues to find prey (Fenton *et al.*, 1983).

Published accounts indicate that *N. thebaica* eats a range of prey and its diet is influenced by time of the year, geographic area, insect abundance and condition of the bat (Grey *et al.*, 1999), suggesting a generalist-opportunist feeding strategy. However, no published research has examined the diet of these bats at a single locality, over a complete year. Most studies have been observational (Felton, 1956; Makin, 1979; McLellan, 1986), providing snapshots in time (e.g., Chapman, 1958; Fenton, 1975; Whitaker and Black, 1976; Fenton *et al.*, 1977; Fenton and Thomas, 1980; Bowie *et al.*, 1999; Feldman *et al.*, 2000), but LaVal and LaVal (1980) examined

the diet of *N. thebaica* over a six-month period.

To test the suggestion that *N. thebaica* is a generalist-opportunist feeder, one of us (ECJS) collected and identified culled parts monthly over a year (May 1996–April 1997), from under a night roost of *N. thebaica* in South Africa. This allowed us to document periodic variation in the diet of *N. thebaica* and to compare the data with those reported elsewhere.

MATERIALS AND METHODS

The present study was conducted on a colony of *N. thebaica* that roosted under Brykenden house, within the 214 ha Kenneth Stainbank Nature Reserve (29°52'S, 30°53'E). This site is located along the kloofs and gorge of the Little Umhlatuzana River, 14 km from Durban, KwaZulu-Natal, South Africa. It is 70 km north of LaVal's and LaVal's (1980) study area at Umdoni Park. The reserve is a typical coastal-belt forest — “more or less open thornveld with numerous and extensive patches of forest” (Acocks, 1988).

Nycteris thebaica roosted in groups of 5–100 individuals, hanging from the wooden and corrugated iron floor joints under the sprung floor of the brick house. These bats used this roost both daily and nightly. Culled parts and faeces were collected from May 1996 to April 1997, from the five sites within the roost, where large volumes of culled parts and droppings were found. Containers (200 × 140 × 80 mm), lined with plastic freezer bags (420 × 330 mm) and dug partly into the sand for stability, were positioned under each site. The container contents were cleaned once a month; the faeces and culled parts were subsequently frozen to kill any organisms (e.g., Diptera and Psychidae) that might be living in the guano. Sorting into faeces and culled parts was done 48 hours after freezing.

The minimum number of individuals per order was calculated monthly from culled parts for each of the five sites, following LaVal and LaVal (1980), Whitaker (1988), and McDonald *et al.* (1990). The results from individual sites were added together providing the minimum number of prey specimens per order for the month. To estimate the importance of each order in the diet, we calculated percent composition, whereby items of a specific order were divided by the totalled number of specimens in all orders in that month, and multiplied by 100 (Whitaker and Black, 1976; Whitaker, 1988; McAney *et al.*,

1991). To make comparison with previous studies more meaningful and to follow seasonal trends, we analysed the above data in four seasonal groups: spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). The statistical package Statistica for Windows (StatSoft Inc., 2000) was used to perform parametric two-way (by prey order and season) ANOVA and the Kruskal-Wallis ANOVA by ranks test. Nevertheless, the results of both tests were similar and only those derived from parametric ANOVA are here reported.

RESULTS

The 1,192 culled parts were collected, with their number ranging from 16 to 396 monthly ($\bar{x} = 99.3$). The parts contained 10 orders of arthropods, dominated by Coleoptera, Lepidoptera, Orthoptera, and Hemiptera, but also including Blattoidea, Amblypygi (whip scorpions: *Damen* spp.), Araneae, Mantidea, Isoptera, and Hymenoptera, which represented 22.5% of the yearly diet (Table 1). In winter (July) and in early spring (September) culled parts also included a frog's leg and a small 4-mm fish, respectively.

The composition of bats' prey varied significantly by order ($F_{11, 96} = 5.98$, $P < 0.001$) but not by season ($F_{3, 96} = 2.43$, $P = 0.07$). Nevertheless, there was a significant interaction between the prey order and season ($F_{33, 96} = 1.93$, $P < 0.01$), suggesting that these two factors are not independent from each other, and the seasonal effect cannot be discarded. Coleoptera were most abundant in the diet in spring (October–November) and at the beginning of summer (December) but were represented throughout the year (Fig. 1), making up 29.8% of annual prey. Orthoptera (38.8%) dominated in the 2nd half of summer (January–February), whereas Hemiptera (42.8%) and Lepidoptera (36.3%) were most often eaten in autumn (March–May) and winter (June–August), respectively. Of special note is a regular appearance of termites (Isoptera) in November (Table 1).

TABLE 1. A monthly breakdown of prey orders consumed by *N. thebaica* from May 1996 until April 1997, presented by the minimum number eaten and the number of subsamples the order was found (in parentheses). Sample size refers to the number of culled parts collected

| Prey category | Year 1996 | | | | | | | | Year 1997 | | | |
|------------------|-----------|--------|-------|-------|-------|--------|--------|-------|-----------|--------|-------|--------|
| | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr |
| Arachnida | | | | | | | | | | | | |
| Amblypygi | 1 (1) | — | 3 (2) | 1 (1) | — | 1 (1) | 3 (2) | 1 (1) | 2 (2) | 2 (2) | 1 (1) | 1 (1) |
| Araneae | — | 2 (1) | — | 1 (1) | — | — | 2 (2) | — | — | — | — | — |
| Insecta | | | | | | | | | | | | |
| Orthoptera | 1 (1) | 2 (1) | 5 (2) | 5 (1) | 5 (2) | 14 (3) | 7 (4) | 5 (2) | 19 (4) | 11 (5) | 2 (2) | 19 (4) |
| Mantidea | 1 (1) | — | 2 (2) | 2 (1) | — | 2 (1) | — | — | — | 3 (2) | — | — |
| Blattodea | — | 1 (1) | — | 1 (1) | 1 (1) | 5 (1) | 4 (3) | 1 (1) | 1 (1) | 2 (2) | — | 1 (1) |
| Isoptera | — | — | — | — | — | 1 (1) | 3 (3) | — | 1 (1) | — | — | — |
| Hemiptera | — | — | — | — | — | 2 (1) | 3 (2) | 2 (2) | — | 9 (3) | 4 (2) | 23 (2) |
| Coleoptera | 1 (1) | 2 (2) | 3 (2) | 2 (1) | 4 (2) | 46 (3) | 21 (5) | 6 (3) | 10 (3) | 3 (2) | 2 (2) | 1 (1) |
| Lepidoptera | 2 (2) | 10 (3) | 7 (2) | 3 (1) | 6 (1) | 7 (3) | 3 (2) | 2 (2) | 4 (2) | 4 (3) | — | 3 (3) |
| Hymenoptera | — | — | 2 (2) | — | — | 2 (2) | — | — | 1 (1) | 1 (1) | 1 (1) | — |
| Amphibia | — | — | 1 (1) | — | — | — | — | — | — | — | — | — |
| Pisces | — | — | — | — | 1 (1) | — | — | — | — | — | — | — |
| Sample size | 27 | 41 | 56 | 57 | 58 | 396 | 175 | 50 | 190 | 36 | 16 | 90 |

DISCUSSION

Comparisons with other dietary studies of *N. thebaica* for wet and dry seasons revealed differences and similarities in the prey items and percent composition (Table 2), generally supporting the prediction that the bat is an opportunistic generalist.

Discrepancies between the studies may reflect some combination of differences in methodology and study area. Our data are most similar to those of LaVal and LaVal (1980) reflecting the use of similar protocols and geographic proximity. In spite of 18 years between studies, the variation in the diets of *N. thebaica* at sites 70 km apart

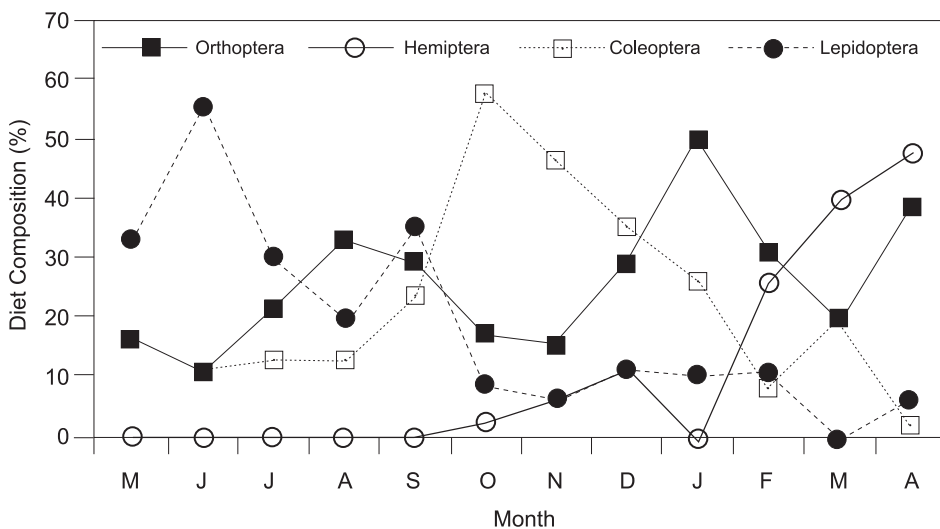


FIG. 1. Monthly trends of four prey orders in the diet of *N. thebaica* (based on 1,192 culled parts)

TABLE 2. Comparative percent composition of the diet of *N. thebaica* during summer (wet season) and winter (dry season). Analyses based on: R: remains found under a roost; S - stomach contents; F - faecal pellets

| Prey category | Summer | | | | | Winter | | | | |
|---------------|----------------|----------------------------|------------------|------------------------------|---------------------------------|----------------|----------------------------|--------------------------------|------------------------------|--|
| | This study (R) | La Val and LaVal, 1980 (R) | Fenton, 1975 (R) | Whitaker and Black, 1976 (S) | Fenton <i>et al.</i> , 1977 (F) | This study (R) | La Val and LaVal, 1980 (R) | Bowie <i>et al.</i> , 1999 (F) | Whitaker and Black, 1976 (S) | |
| Arachnida | | | | | | | | | | |
| Amblypygi | 5.0 | — | — | — | — | 7.2 | — | — | — | |
| Araneae | — | 0.3 | — | — | — | 5.4 | 2.5 | 35.9 | 9.6 | |
| Insecta | | | | | | | | | | |
| Orthoptera | 47.0 | 49.1 | 54.5 | 31.6 | — | 21.8 | 46.6 | 43.6 | 13.3 | |
| Mantodea | 2.5 | 3.9 | — | — | — | 7.2 | — | — | — | |
| Blattodea | 3.4 | 1.8 | — | — | — | 3.6 | 5.3 | 5.7 | — | |
| Isoptera | 0.8 | 10.9 | — | — | — | — | 1.1 | — | — | |
| Hemiptera | 12.6 | 6.6 | — | — | — | — | 2.8 | — | — | |
| Coleoptera | 17.6 | 9.3 | — | 45.2 | 5.0 | 12.7 | 9.2 | 8.0 | 18.5 | |
| larvae | — | — | — | — | — | — | — | — | 8.0 | |
| Neuroptera | — | 3.9 | — | — | — | — | 0.6 | — | — | |
| Lepidoptera | 8.4 | 12.8 | 45.5 | 12.5 | 83.0 | 36.3 | 30.8 | 2.7 | 7.1 | |
| larvae | — | — | — | 4.8 | — | — | — | — | 31.7 | |
| Hymenoptera | 2.5 | 1.3 | — | — | — | 3.6 | 0.1 | — | — | |
| Diptera | — | 0.1 | — | 2.1 | 13.0 | — | — | — | 1.3 | |
| Trichoptera | — | — | — | — | — | — | — | 1.3 | — | |
| Chilopoda | — | — | — | — | — | — | — | — | 3.9 | |
| Vertebrata | — | — | — | — | — | — | — | — | — | |
| Amphibia | — | — | — | — | — | 1.8 | — | — | — | |
| Unidentified | — | — | — | 3.8 | — | — | — | — | 6.7 | |

is strikingly similar although the peaks of the dominant orders are one month apart.

Chapman (1958), Fenton (1975), and LaVal and LaVal (1980) found that *N. thebaica* consumes mainly Orthoptera, followed by Lepidoptera. The bats we studied ate Coleoptera, Orthoptera, and Lepidoptera then Hemiptera in descending order of abundance. While there are no data on the seasonal abundance of insects at Stainbank Nature Reserve, LaVal and LaVal (1980) showed that moth abundance decreased during dry winter and rose during wet summer. They suggested that low abundance of moths is directly related to low abundance in other orders, which are always less numerous than moths. If so, comparing our results with those of LaVal and LaVal (1980), indicates that *N. thebaica* preys on Lepidoptera when other orders are low in number. Indeed, in both studies moths did not contribute greatly to the diet in summer when their abundance is high, perhaps suggesting a preference for harder bodied prey.

It remains to be determined if interspecific competition influences bats' diet. At Mkuzi Game Reserve (ca. 275 km N Stainbank) Bowie *et al.* (1999) compared the diets of sympatric *N. thebaica* and *Hipposideros caffer*. Their and our results showed that *N. thebaica* eats the same five of seven insect orders as *H. caffer*, with Orthoptera dominating. But while we found Lepidoptera to be the second most often consumed type of insects, they were second lowest in Bowie's *et al.*'s (1999) study although they dominated the diet of *H. caffer*.

Consumption of vertebrate prey (mainly frogs and fish) by nycterids has been associated with larger (ca. 30–40 g) species, namely *N. grandis* (Fenton *et al.*, 1987). Although *N. thebaica* will take geckoes from a wall (B. Porter, pers. comm.), published data have not identified it as a consumer of vertebrates. We suggest that size of prey combined with bats' generalism

influences the diet of *N. thebaica*, probably explaining the occurrence of geckoes, frogs and fish.

While we occasionally found vegetation in faeces of *N. thebaica* during winter we did not at other times of the year. Vegetation has been observed in droppings of several other South African microchiropterans, including *Scotophilus viridis* (Fenton *et al.*, 1985), *Neoromicia capensis*, *N. zuluensis* and *Nycticeinops schlieffeni* (S. Ellis, pers. comm.). B. Lovegrove (pers. comm.) suggested that vegetation may be a source of additional unsaturated fatty acids, which are important in the seasonal acclimation of heterothermic mammals (Geiser *et al.*, 1992). In marsupials dietary changes appear to allow the acquisition of sufficient unsaturated fatty acids in winter (Bozinovic and Mendez, 1997) but it remains to be determined if this is the case in Microchiroptera.

Our results confirm the suggestion that *N. thebaica* is a generalist species, taking a wide range of prey items although it may prefer hard-bodied over soft-bodied prey. Dietary flexibility combined with versatile flight behaviour has allowed this species to inhabit a variety of habitats over a wide geographic range.

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