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Variation in foraging behaviour, habitat use, and diet of Large slit-faced bats (*Nycteris grandis*)

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Abstract

Examined the diet of *Nycteris grandis*, a 30–35 g African nycterid which varied significantly from year to year, season to season and roost to roost, suggesting flexible foraging behaviour and opportunism. Frogs, insects, and bats formed the bulk of the bats' diet. Although five species of frogs were consumed, two dominated the diet. Insect prey were mainly larger Lepidoptera and Orthoptera with occasional consumption of smaller species (< 10 g) of bats. Diurnal insects (butterflies – Lepidoptera; dragon flies – Odonata) and small (≤ 10 g) birds also were eaten. Over 14 nights in June 1990, prey taken by *N. grandis* did not reflect the availability of frogs, bats or insects. Radio-tagged *N. grandis* showed significant variation in approach to foraging, including the use of woodland or river habitat, and two foraging techniques, namely hunting from continuous flight or from a perch.

Introduction

Variability in prey arises in several circumstances. For example, animals make decisions about factors such as where and when to forage, and what and how much to eat (CANGIALOSKI 1991; LUCAS and WALTER 1991; MENZEL 1991; VALONE 1991) which can produce variation in the approach to foraging, patterns of habitat use, and prey selection. Variation in individuals' behaviour and learning also affect foraging (KAMIL et al. 1987) contributing to overall patterns of behaviour and habitat use (e.g., KIEFFER and COLGAN 1991) which often affect diet. Also contributing to varied diets are prey availability (e.g., SCHALLER 1972; KRUK 1972) and/or the use of different approaches to hunting sometimes adjusted according to the prey being hunted (e.g., HENRY 1986; MILLS 1990). Flexibility in hunting behaviour can translate into variation in diet and improved chances of survival, particularly under marginal conditions.

Since most species of animal-eating bats are insectivorous, their prey is much smaller than them. Insectivorous species that hunt from continuous flight and use echolocation to detect and track prey, usually eat airborne insects (FENTON 1990). Variability in the diets of such aerial insectivores appears to reflect prey availability. For example, both the bird, *Chordeiles minor* (common nighthawks), and the bat, *Eptesicus fuscus* (big brown bats) forage from continuous flight and vary their diets according to prey availability (BRIGHAM 1990, 1991). In some bat communities, species-specific approaches to foraging translate into different patterns of habitat use, prey selection and life history (BARCLAY 1991).

But there are animal-eating bats that use more than one approach to foraging, alternating between foraging from continuous flight or from a perch (FENTON 1990). Among these species, larger bats (e.g., *Nycteris grandis* – FENTON et al. 1990; *Megaderma lyra* – AUDET et al. 1991) consume larger prey, including small vertebrates. Bats using more than one approach to foraging and eating a variety of prey represent an opportunity to

assess interactions between variation in approach to foraging and variation in the prey taken.

Nycteris grandis (Nycteridae) weighs 30–35 g and occurs widely in Africa in rain forest and savannah woodlands (SMITHERS 1983). Along the Zambezi River in Zimbabwe, *N. grandis* eats large arthropods, fish, frogs, birds and bats, and tagged individuals consistently use the same day and night roosts (e.g., FENTON et al. 1990). Previous dietary analyses over 14 months suggested distinct seasonal variation, for example with bats constituting most of the prey biomass in the “winter” (June and July) diet. Radio-tagged bats adjusted their approaches to hunting according to prevailing conditions, sometimes foraging from continuous flight, other times from perches, differences that coincided with variation in habitat use and in prey consumed (FENTON et al. 1990).

This study had three goals: 1. to assess variation in prey over a longer period of time and to explore the prevalence of previously identified seasonal trends; 2. to use a more intensive behavioural study to consider how variation in prey related to prey availability, approach to foraging, and patterns of activity and habitat use; and 3. to determine the circumstances in which other species of bats are prey.

Material and methods

The study area was in Mana Pools National Park in Zimbabwe (15° 44' S; 29° 21' E) where prey selection data cover the period from April 1988 to June 1990, the more intensive study was conducted from 15 to 30 June 1990.

Prey selection was determined from remains gathered from beneath two feeding perches, a disused watertower (8 m by 8 m by 20 m) and the verandah outside the park office headquarters. Discarded pieces of prey were collected approximately once a month (April 1988 to 14 June 1990) or every day (15 to 30 June 1990) at feeding perches and the remains were sorted according to number of prey and identified as accurately as possible.

During the period 15 to 30 June 1990, we used radio tracking to monitor habitat use, activity patterns, and foraging behaviour of individual *N. grandis*. We captured five *N. grandis* (three males and two females) in their day roosts and attached 0.9 g Holohil BD-1 transmitters to their mid-backs using Skinbond[†] adhesive. Radio-tagged bats were tracked using AVM LA12 receivers with collapsible five element Yagi antennae. Pairs of observers on foot or single observers in vehicles, in touch by walkie-talkie, tracked tagged bats from 17:45 h (approximately 15 min before dark) to 06:00 h about 30 min after dawn. Most data, however, come from one individual followed throughout 7 nights. Within one day, one female shed her transmitter, and we occasionally followed three other bats. Data about the bat's movements and behaviour were recorded on hand-held cassette recorders, from which we obtained minute-by-minute details about behaviour.

Using a Javelin night vision scope, we observed *N. grandis* roosting in the water tower at night. These observations permitted us to assess the bats' behaviour within the roost, including eating, grooming, and general activity. On four occasions when the large *Nycteris* were roosting in the water tower, we released smaller bats (six *Nycticeius schlieffeni*, one *Eptesicus capensis*) into the water tower. This was done once with one bat during the day, and twice at night with pairs of bats. Behavioural observations were recorded on a cassette tape recorder.

To assess prey availability, we sampled the flying insects and bats. Flying insects were sampled using a Malaise trap set in woodland approximately 20 m from the south bank of the Zambezi River. The trap was checked daily at dawn and at dusk, and the numbers and identities of insects over one cm long were recorded. We looked and listened for frogs as we moved through the study area radio-tracking bats. Bats were sampled using two techniques. On seven nights at 15 min intervals we simultaneously monitored bat activity for one minute periods. Using Mini-2 Bat Detectors (Ultra Sound Advice, 23 Aberdeen Road, London N5 2UG, England) observers scanned from 20 to 80 kHz, counting trains of echolocation calls as bat passes. On 8 nights we set two 6 m high by 30 m long mist nets (RAUTENBACH 1985) from 18:00 to 20:00 to sample bats active over or near the Zambezi or Mana Rivers, in woodland within 50 m of the Zambezi, in woodland ca 1 km from the Zambezi and at a pan located in mopane woodland (3 km from the Zambezi). Except for the latter site, the dominant species in the woodland was *Acacia albida* with occasional *Trichelia emetica*.

Results

Variation in diet

Between April 1988 and the end of June 1990, we obtained 45 samples of prey consumed by the *N. grandis*, 37 from the water tower (Fig. 1) and 8 from the office. The identities of 1335 prey were determined as precisely as possible and represented 1 unidentifiable fish, 832 frogs (6 species), 14 bats (at least 4 species), 292 Lepidoptera (46 species) and 197 other arthropods (Orthoptera: Acrididae, Tettigoniidae, 5 genera; Mantodea 2 genera; Coleoptera; Homoptera: Cicadidae; Odonata 1 genus; Coleoptera; Neuroptera; and Solpugida).

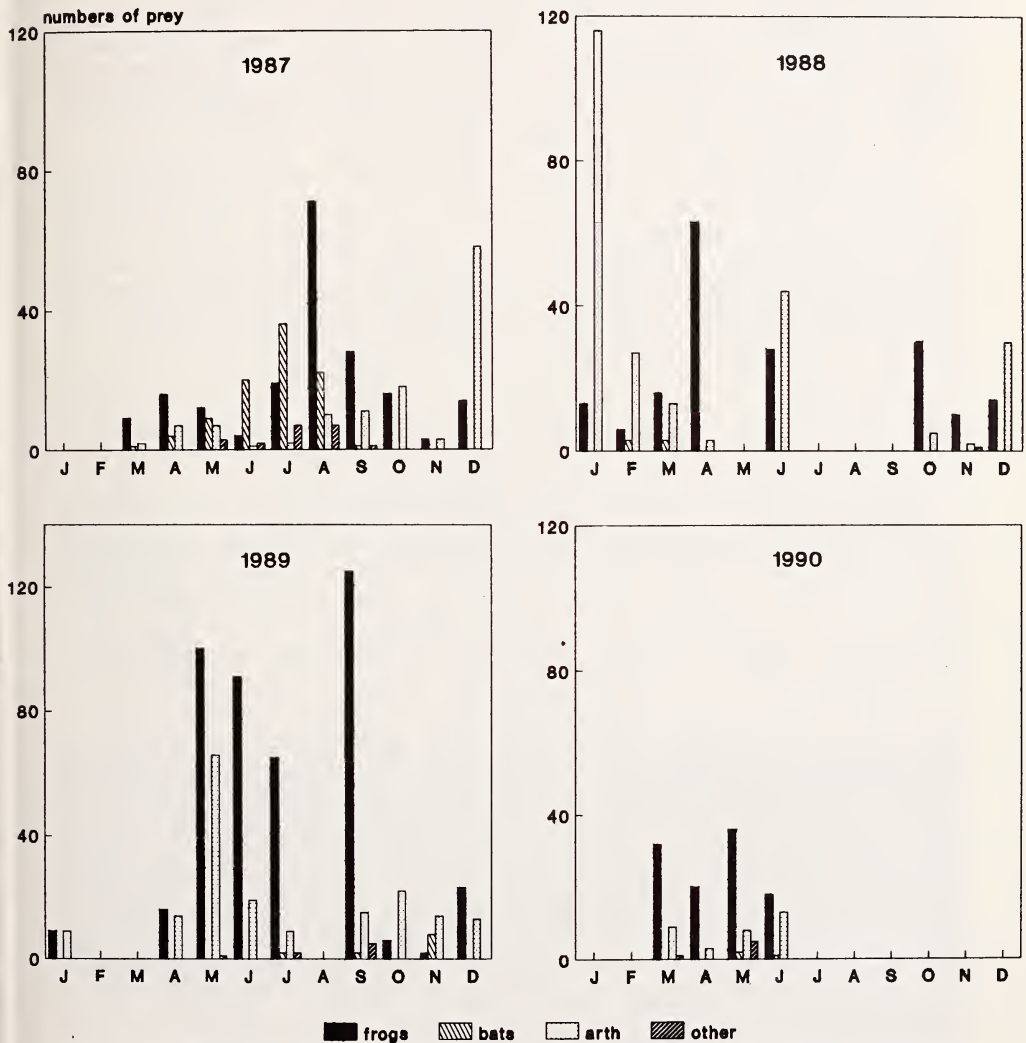


Fig. 1. Four histograms compare the incidence of frogs, bats, arthropods and other prey (fish and birds) in the diet of *Nycteris grandis* using the water tower as a feeding perch in 1987, 1988, 1989 and 1990. The numbers of frogs were determined by counts of legs, bats and birds by counts of wings, fish by counts of tails and arthropods by counts of legs, wings or head capsules. Letters on the horizontal axis indicate months of the year

Nine of 14 bat remains included enough skull material to identify the items as 8 vespertilionids (*Pipistrellus* or *Eptesicus*) and one rhinolophid (probably *Rhinolophus darlingi*). The other five bat remains consisted of wings. Forearms of bat prey ranged from 28–31 mm long (vespertilionids) whereas that of the rhinolophid was 48 mm. These correspond to bat weights of 3–5 g for the vespertilionids and 8–10 g for the rhinolophid (*R. darlingi*; SMITHERS 1983).

Of 832 frogs captured by the bats, 16% (133) were unidentifiable and 81.2% (676) were in the genus *Ptychadena* (255 *P. anchietae* and 421 *P. mascariensis*). The bats also had taken 13 *Chiromantis xerampelina*, 7 *Hemisis* (probably *H. marmoratus*, the only species known from the area), 2 *Xenopus muelleri*, and 1 *Tomopterna cryptotis*.

Among the arthropods, moths dominated the diets, although 17 butterflies (14 hesperiids, 2 nymphalids, 1 pierid) also were taken. The moths were mainly sphingids and noctuids with some pyralids, geometrids, lymantriids, and saturniids. The distribution of sphingids and noctuids by size (by forewing length) reveals a tendency to take larger species (forewings > 50 mm long), and larger sphingids form a significantly ($\chi^2 = 133$, d.f. = 5, $P \ll 0.001$) larger part of the diet than do large noctuids.

Where possible, we have compared these prey with those reported for 1987 and the earlier part of 1988 (FENTON et al. 1990). Considerable month to month and year to year variation characterizes the diets (Fig. 1). Seasonal trends identified in the 1987 sample (FENTON et al. 1990) are not predictable patterns. This point is demonstrated by statistical comparisons: the incidence of frogs, bats, arthropods, and other prey taken in October, November and December (1987, 1988, and 1989) shows significant variation in the quantities taken among years ($\chi^2 = 108.3$, d.f. = 14, $P < 0.001$); as did the prey taken in April, May and June of 1989 and 1990 ($\chi^2 = 42.27$, d.f. = 12, $P < 0.001$). The incidence of two species of frogs, *Ptychadena anchietae* and *P. mascariensis*, in the March to end of December 1988 samples from the office (46 and 24, respectively) and the water tower (164 and 19, respectively) shows that *N. grandis* using the water tower took significantly more *P. mascariensis* ($\chi^2 = 20.0$, d.f. = 1, $P \ll 0.001$) than those at the office.

Between 15 and 30 June 1990 we could compare prey availability and diet for bats using the water tower as a feeding roost. *N. grandis* consumed 23 prey (4 frogs, one bat and 18 insects). Fifteen of the insects were large (forewing > 50 mm) sphingid moths (*Daphnis nerii* and *Euchloron megaera*). One smaller (wing length 3 cm) sphingid (*Nephele communa*) and two gryllids also were captured. The bats usually brought frogs to their feeding perches during the first hour after dark, while the bat and the sphingids were normally taken between 23:00 and 01:00 h. On 7 consecutive nights starting on 15–16 June 1990, the malaise trap caught 39 insects ≥ 1 cm long (26 moths, 5 mantids, 4 Orthoptera, one Neuroptera, one Trichoptera and two unidentified), but no sphingids. In June 1990, we heard no frogs calling along the river and observed none in 13 nights of walking in the woodland and along the edge of the river. Monitoring the echolocation calls of bats revealed that about 50% of the activity of species using high intensity echolocation call occurred within the first hour after dark, 80% in the first three hours. Mist net samples revealed that smaller bats (≤ 10 grams) were abundant and diverse in woodland within 50 m of the river, although the most were encountered at the site farthest from the river (Table 1). The bat captured and eaten by a *N. grandis* during our study and brought to the watertower around midnight, was a rhinolophid or hipposiderid with forearms 48 mm long. Hunting *N. grandis* took prey, insects, frogs and bats that we did not encounter in our sampling.

Variation in behaviour

The male *N. grandis* we followed for 7 entire nights either hunted from a perch or from continuous flight, behaviour reflected by long and short flight times, respectively (Tab. 2). The bat alternated its foraging between the area within 50 m of the river banks and

Table 1. Captures of bats in mist nets between 18:00 and 20:00 h in different habitats relative to the rivers

Number of nights	Mass in g	Over/near water Zambezi 2	Pan 1	Woodland < 50 m from River 3	Woodland > 500 m from 2	Total 8
<i>Epomphorus crypturus</i>	70	0	1	0	1	2
<i>Nycteris thebaica</i>	10	0	0	2	0	2
<i>Rhinolophus hildebrandti</i>	28	0	0	1	0	1
<i>Pipistrellus rueppellii</i>	8	0	0	1	0	1
<i>Eptesicus capensis</i>	5	1	2	0	1	4
<i>Eptesicus zuluensis</i>	4	0	0	1	0	1
<i>Eptesicus cf. melckorum</i>	6	1	2	0	0	3
<i>Eptesicus rendallii</i>	7	1	0	0	1	2
<i>Nycticeius schlieffeni</i>	5	0	37	14	5	56
<i>Scotophilus borbonicus</i>	18	13	28	6	5	52
<i>Chalinolobus variegatus</i>	8	1	0	4	1	6
<i>Miniopterus schreibersii</i>	7	0	0	1	0	1
<i>Tadarida pumila</i>	10	0	0	3	0	3
Totals		17	70	33	14	134

Table 2. The numbers of flights of different durations made by radio-tagged male *Nycteris grandis* within 50 m of the Zambezi River (R) or in woodland (W) on different dates in June
The dates indicate the day at the beginning of the night

Flight	19 June		21 June		23 June		24 June		25 June		26 June		27 June	
	R	W	R	W	R	W	R	W	R	W	R	W	R	W
≤ 2 min	0	4	4	22	4	1	2	7	13	2	2	0	2	0
3–5 min	1	7	1	3	0	4	0	3	2	4	1	2	2	0
6–10 min	1	3	1	2	0	3	0	2	2	2	2	0	3	0
> 10 min	1	2	0	1	0	0	0	3	2	1	1	0	3	0
Lost contact														
Time in min		5		8		9		40		65		5		7
Average flight														
Time in min	7.3	5.6	2.7	2.5	1.8	6.3	0.8	5.0	3.5	5.2	6.2	4.5	8.5	0

woodland up to 2 km south of the river. Analysis of the numbers of flights of different duration by this male revealed significant night-to-night variation in flight behaviour ($\chi^2 = 37.2$, d.f. = 18, $P < 0.001$) and habitat use (river versus woodland; $\chi^2 = 51.5$, d.f. = 39, $P < 0.001$). On most nights the bat began foraging along the river flying there from a disused military bunker less than 50 m from the river or from a 2 km distant hollow *Acacia albida*. Each night it visited the river at least briefly, but on some nights never hunted in the woodland away from the river (Tab. 2). In both habitats the bat used both approaches to hunting. There was no evidence that roost location (*Acacia* versus bunker) affected the bat's choice of foraging areas.

The radio-tagged *N. grandis* showed a peak in flight activity in the hour following dark and, on 5 of 7 nights, another peak between 23:00 and 01:00 (Fig. 2). Over five nights we were in contact with a second radio-tagged male *N. grandis* for a total of 20 h, and this individual showed the same general patterns of flight behaviour and habitat use as the individual we studied intensively.

Radio signals suggested that *N. grandis* roosted motionless in night roosts for long periods of time, an impression supported by 12 h of direct observation of these bats

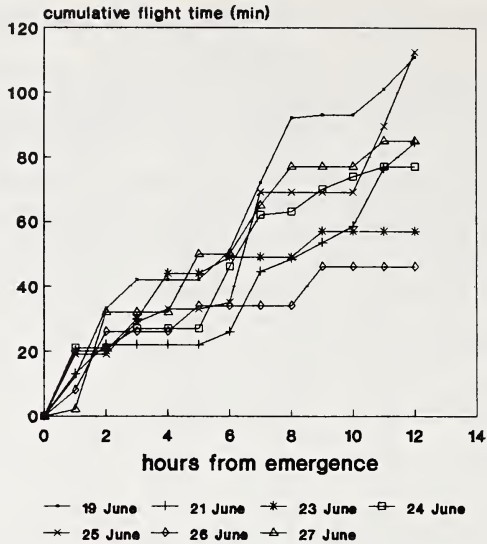


Fig. 2. The differences in patterns of flight times reflect foraging and are illustrated by variation in cumulative flight times (in minutes) for a single bat over 7 nights in June 1990. The dates are identified as follows: 19th = night of 19–20 June, 21st = night of 21–22 June, etc

roosting in the watertower on three nights. After feeding, bats usually groomed themselves and, about once an hour, shifted position within the roost, by either flexing its wings and rotating on the perch, or by flying about 1 m to a different perch. When a *N. grandis* arrived in the watertower, it typically landed away from any others already there. On three occasions (3, 5 and 7 min after arriving) a new bat flew a short distance and roosted about 10 cm from one already in the watertower. Twice, we observed bats arriving with food: they ate their prey and groomed before approaching other *N. grandis*.

Bats as prey

In June 1990, small vespertilionid bats were common in the vicinity of the watertower during our intensive study, but we found no evidence of their being captured by the *N. grandis* (unlike the situation in this exact location in 1987). One explanation for this difference is that they take only bats that fly into their night roost. This explanation is possible in that we twice saw smaller bats fly into the watertower when *N. grandis* was roosting there.

To test this possibility, we released small vespertilionids into the watertower when at least one *N. grandis* was present. During each release, both doors to the water tower were open so small bats could escape. Our single daytime release of a *Nycticeius schlieffeni* elicited no response from the single roosting *N. grandis*, although the small bat flew about the water tower and was conspicuous by its wing flapping and echolocation calls. In contrast, every time we released a small bat into the water tower at night, the roosting *N. grandis* attacked it. In preparation for an attack, a roosting *Nycteris* would partly open its wings and dive towards the flying or roosting bat. The *N. grandis* appeared to vocalize before it left its perch to pursue a bat. During attacks, the smaller bats typically also produced calls audible to human observers in addition to their echolocation calls. The intensity of the attacks ranged from a few passes at the smaller bat, to repeated and

persistent attacks for over 30 min. Small bats that had landed and were motionless on the tower wall never were attacked.

The typical attack rate was 1 every 2 minutes with each attack lasting about 30 sec. One prolonged attack lasted about one minute. The *N. grandis* returned to its perch between attacks and when two *Nycteris* simultaneously were in the tower, one bat usually made several attacks before the other one joined in. None of the ca. 75 attacks we witnessed was successful, and the smaller bats flew out through an open door. The *N. grandis* never pursued the small bats out of the watertower. Bat-eating by *N. grandis* does not appear to be an accidental occurrence generated by other bats straying into roosts occupied by the larger bats.

Discussion

Our results illustrate annual, seasonal and locational variation in prey taken by *N. grandis*, as well as variation in habitat use and approach to foraging. The general patterns of variation in diet are consistent with the general trends previously published for this bat (FENTON et al. 1987), but not with the seasonal diet portrayed by FENTON et al. (1990). The variations in foraging behaviour and habitat use we documented by radio-tracking resemble those reported elsewhere (FENTON et al. 1987; FENTON et al. 1990). Taken together, the patterns of variation indicate that *N. grandis* is opportunistic in its use of prey, habitats and approach to foraging. The combination of behavioural flexibility and access to the large Zambezi River which flows throughout the year may account for the occurrence of *N. grandis* in Zimbabwe, the southern edge of its range (SMITHERS 1983).

Comparison of the short term information about prey availability and prey captured suggests that *N. grandis* rely on some mechanism(s) to locate preferred targets. For example, although the bats take large noctuids and sphingids, other large moths such as saturniids or lasiocampids are conspicuously absent from the diet. Similarly, the *N. grandis* capture some 5–10 g bats that are common (*Eptesicus* or *Pipistrellus*) but not others (e.g., *Nycticeius schlieffeni*). Also absent from the diet are less common species with diagnostic wing patterns (e.g., the white-winged *Eptesicus rendalli*, the variegated winged *Chalinolobus variegatus*). Absent from the 1989 and 1990 samples were other species in the genus *Nycteris*, which had been a regular prey item in 1987 and early 1988 (recognizable by the distinctive t-shaped tail cartilage).

The frogs the bats ate also suggest a variety of approaches to hunting (PASSMORE and CARRUTHERS 1979; D. G. BROADLEY, pers. comm.). The two *Ptychadena* species show different patterns of escape behaviour, moving towards the water (*P. mascariensis*) or away from it (*P. anchietae*) in the face of danger. *Hemisus* is non-aquatic, living in burrows in the litter by day, while *Chiromantis* is arboreal and cryptic. *Tomopterna* only visits the water to breed and *Xenopus* is virtually entirely aquatic.

The bats could have achieved their selection of prey by using particular foraging flight paths or hunting perches in certain areas. This pattern also could reflect habitat selection by the prey. The radio-tracking data from this and other studies (e.g., FENTON et al. 1987; FENTON et al. 1990) demonstrate that individuals consistently hunt in the same areas, varying their pattern of use of woodland versus the areas along and over the river. In other predators, different approaches to foraging often produce different prey. For example, HENRY (1986) found that using different approaches to foraging in the same areas resulted in the capture of different prey by red foxes, and KRUUK (1972) had previously demonstrated this for spotted hyaenas.

Nycteris grandis sometimes use prey-generated sounds to find their targets, whether insects, frogs or other bats, but unlike the Neotropical *Trachops cirrhosus* (TUTTLE and RYAN 1981), *N. grandis* shows no sign of locating frogs by listening to their calls (FENTON et al. 1983). *Nycteris grandis* behaves like *Cardioderma cor* from east Africa (RYAN and

TUTTLE 1981), using sounds associated with movement to locate its prey. The bats eaten by *N. grandis* include both high (*Eptesicus*, *Pipistrellus*, and *Rhinolophus*) and low intensity echolocators (*Nycteris*) but the available data do not indicate whether or not *N. grandis* uses the echolocation calls of its bat prey to find these victims.

Some of the prey suggests that *N. grandis* occasionally exploit animals that have been flushed or disturbed. Specifically, butterflies and dragon flies typically stop flying before *N. grandis* emerges, and do not begin flying until after *N. grandis* have returned to their roosts for the day. Exploiting flushed or disturbed prey also could explain the diurnal birds eaten by the bats (FENTON et al. 1981, 1990). The consistent low incidence of diurnal prey suggests that its use is more opportunistic than the result of an active foraging technique. This explanation does not appear to apply to the bats eaten by *N. grandis*.

The importance of prey availability in determining the actual *N. grandis* diet may be suggested by several aspects of the data. First, the significant variation in the prey remains between feeding perches (this study or FENTON et al. 1990) illustrates that parallel samples from nearby sites differ significantly. These differences are important because telemetry data indicate that individuals consistently use the same feeding perches and foraging areas, but the same individual radio-tagged bats did not use the two feeding perches in 1987 or 1990. Variation in prey availability and individual differences also could explain the differences in diet between roosts and between years. Observational learning which has been reported from other bats (GAUDET and FENTON 1984) and associations between mothers and their young (VAUGHAN 1976; VAUGHAN and VAUGHAN 1987) could account for individual differences in hunting technique and prey selection.

In its approaches to foraging, habitat use and prey selection, *Nycteris grandis* resembles other large animal-eating bats in the families Megadermatidae (AUDET et al. 1991; VAUGHAN and VAUGHAN 1986; RYAN and TUTTLE 1987; VAUGHAN 1976) and Phyllostomidae (Phyllostomidae – BROOKE 1989; MEDELLIN 1988; BELWOOD 1988; TUTTLE and RYAN 1981; VEHRENCAMP et al. 1977). These bats differ from others (e.g., some Vespertilionidae and Molossidae) that show less flexibility in foraging behaviour (AUDET 1990; HICKEY and FENTON 1990; BARCLAY 1989; BRIGHAM 1991; FENTON and RAUTENBACH 1986; KRONWITTER 1988; RYDELL 1986; RACEY and SWIFT 1985) or flexible foraging behaviour and a smaller range of prey (JONES 1990; JONES and RAYNER 1989; NEUWEILER et al. 1987; BELWOOD 1988; FENTON and RAUTENBACH 1986). Large animal-eating bats with flexible behaviour are the ones typically referred to as “carnivorous”, although the label may be inappropriate because invertebrates may comprise a large part of the diet (NORDBERG and FENTON 1988).

Nycteris grandis regularly feeds on larger prey items and shows patterns of variation in approaches to hunting and diet comparable to those of other predators. These variations appear to reflect individual decisions probably based on experience and local conditions.

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Zusammenfassung

Flexibilität in Jagdverhalten, Gebietsanspruch und Ernährung bei der Großen Schlitznasen-Fledermaus, *Nycteris grandis*

Das Beutespektrum von *Nycteris grandis*, einer 30–35 g schweren Fledermaus der afrikanischen Familie Nycteridae, variierte signifikant zwischen verschiedenen Jahren sowie in Abhängigkeit von der Jahreszeit und der Kolonie. Dies läßt auf ein flexibles, opportunistisches Jagdverhalten schließen. Der Hauptteil der Beute bestand aus Fröschen, Insekten und Fledermäusen. Von fünf gefressenen Froscharten überwogen zwei in der Nahrung, Nachtfalter (Lepidoptera) und Heuschrecken (Orthoptera) dominierten das Spektrum der verzehrten Insekten. Gelegentlich wurden kleinere Fledermäuse (< 10 g) konsumiert. Tagaktive Schmetterlinge (Lepidoptera), Libellen (Odonata) und kleine Vögel (≤ 10 g) fanden sich ebenfalls in der Nahrung. In 14 Beobachtungsnächten im Juni 1990 ergab sich kein Zusammenhang zwischen der von *N. grandis* eroberten Beute und dem verfügbaren Nahrungsangebot. Telemetrierte Tiere zeigten signifikante Unterschiede in der Art der Nahrungssuche. Die Jagdgebiete lagen in bewaldeten Gebieten sowie in Flußlandschaften. Im Jagdverhalten wechselten die Tiere zwischen der Jagd aus andauerndem Flug und der Ansitzjagd.

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