Fluctuations in Availability of Arthropods Correlated with Microchiropteran and Avian Predator Activities

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Aerial arthropods were sampled by driving a standard transect along the riparian forest of the Luvuvhu River, South Africa, to assess hourly and seasonal variations in available biomass. Sampling, with an air-plankton net mounted on a vehicle, was conducted hourly over 48-hour periods during the fullest phase of the moon for each of eight months during 1986/87. Seasonal variation in availability of terrestrial arthropods was assessed by means of six pitfall traps set in the riparian forest. On a daily basis, the available biomass of aerial arthropods was found to increase markedly at and during the two hours following sunset, with a slight peak at or in the two hours preceding dawn. Highest monthly availability was found to correspond with the warm summer rainy season, with a marked increase after the first rains. The peak for terrestrial arthropods was found to occur later in the summer than for aerial arthropods. These patterns of arthropod availability correlate well with the daily activity rhythms and seasonal reproduction of microchiropteran bats and their avian predators.

Key words: Arthropods, biomass, insectivorous, bats, raptors, variation, activity rhythms, breeding strategies.

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Introduction

It is widely acknowledged that temporal patterns in availability of food will influence the timing of activities of consumers. However, there is little documentation of these patterns for arthropods in southern Africa, nor of attempts to correlate these patterns with activities of their consumers. This study indicates that patterns of rainfall, temperature and relative humidity, through their effects on arthropod availability, affect the activity and breeding patterns of primary consumers, such as bats, as well as of secondary consumers, such as raptorial birds.

Environmental factors such as temperature, rainfall, plant and arthropod phenology, daylight-length, and latitude have all been examined as factors influencing the seasonal and daily periodicity of bats (Erkert 1982). However, behaviour, physiology and the importance of differential food availability, although recognised, appear to have been under-stressed.

Bats exhibit a strictly nocturnal and volant life style, which in effect constrains them to a specialised niche. Microchiropteran bats have, for instance, developed echolocation abilities sensitive enough to allow navigation as well as location and catching of flying prey on the wing with no reliance on light. Probably their most extreme adaptation is manifested in their reproductive strategies. They entail tactics to delay embryonic development between mating during autumn (when animals are in prime physical condition) and parturition during mid-summer (when arthropod availability is at a peak), thus allowing females to meet the increased energy demands of advanced pregnancy or lactation (Racey 1982). In temperate regions these clearly relate to enforced hibernation to avoid the deprivations of severe winters, particularly with regard to nourishment.

This study was conducted in a tropical environment along the Luvuvhu River in the northern regions of the Kruger National Park (KNP), South Africa. This is an area of summer rainfall that supports deciduous woodland dominated by mopane, except along the Luvuvhu and Limpopo rivers where the riparian forest acts as a corridor to allow tropical elements from the coastal forests of Moçambique into an otherwise semi-arid region (see Gertenbach 1983 for details of the vegetation, rainfall and climate of the study area).

Thirty-eight of the 41 species of bats recorded from the KNP (Pienaar, Joubert, Hall-Martin, De Graaff & Rautenbach 1987) occur along the Luvuvhu River. Three species belong to the Megachiroptera, whereas 35 are insectivorous Microchiroptera. This is the area with the highest recorded diversity of bat species in the Republic of South Africa, offering excellent opportunities to study a variety of aspects of bat biology in a tropical environment.

A number of raptorial birds, which are known or suspected to include bats in their diet (Steyn 1982; Kemp 1987), also hunt in or over the riparian forest. These include both diurnal Falconiformes (*Hieraaetus spilogaster, Accipiter tachiro, A. minullus, Polyboroides typus, Falco peregrinus, Macheirhamphus alcinys*) and nocturnal Strigiformes (*Strix woodfordii, Glaucidium capense, Bubo lacteus*), species from both orders also hunting crepuscularly.

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Methods

The height at which bats were caught in macronets (Rautenbach 1985) was recorded previously, and it was established that the majority was active at a height of between 1–3 m. Assuming that most bats forage at this level in response to a higher density of prey, a conical air-plankton net supported by a metal frame of 112 cm × 65 cm was mounted 1,75 m off the ground on the cab of a light delivery truck. A standard 8 km transect was repeated along the southern edge of the riparian forest of the Luvuvhu River, down Nyala Drive and back, in the northern KNP (22°25′S; 31°13′E). The transect was driven at a speed of 15–20 km/hour, starting each hour on the hour, over a period of 48 hours. It was conducted during the fullest phase of the moon, to control for any influence of the lunar cycle on arthropod availability, and was repeated during each of the eight months that the study area was visited. Flying arthropods caught in the net were funnelled, through a metal throat at the apex of the net, into a small bag made of fine-gauge material tied at the outer end of the throat. The inner surface of the net and bag were sprayed with a contact insecticide to ensure that arthropods did not escape after contact with the net. The holding bag was removed at the end of each drive, the net cleared of any remaining arthropods, the contents killed in an atmosphere of technical ether, and all arthropods stored in marked plastic vials.

Terrestrial arthropods were sampled by means of a line of six white plastic buckets of 63 cm circumference (20 cm diameter), sunk into the ground 20 m apart. The line of pitfall traps was at right angles to the riverbed, with the first trap on the riverbank at the normal high-water level, the next four in the riparian forest, and the last in the ecotone with the deciduous woodland. The traps were operated for an average period of ten days over the fullest phase of the moon. Trapped arthropods were killed and preserved by ethylene glycol in the bottom of each bucket.

Sampling of aerial arthropods was conducted during the months of July, October, November and December of 1986, and January, February, April and June of 1987. Terrestrial arthropods were sampled for between nine to 11 days, during June and October of 1986, and January, April and July of 1987.

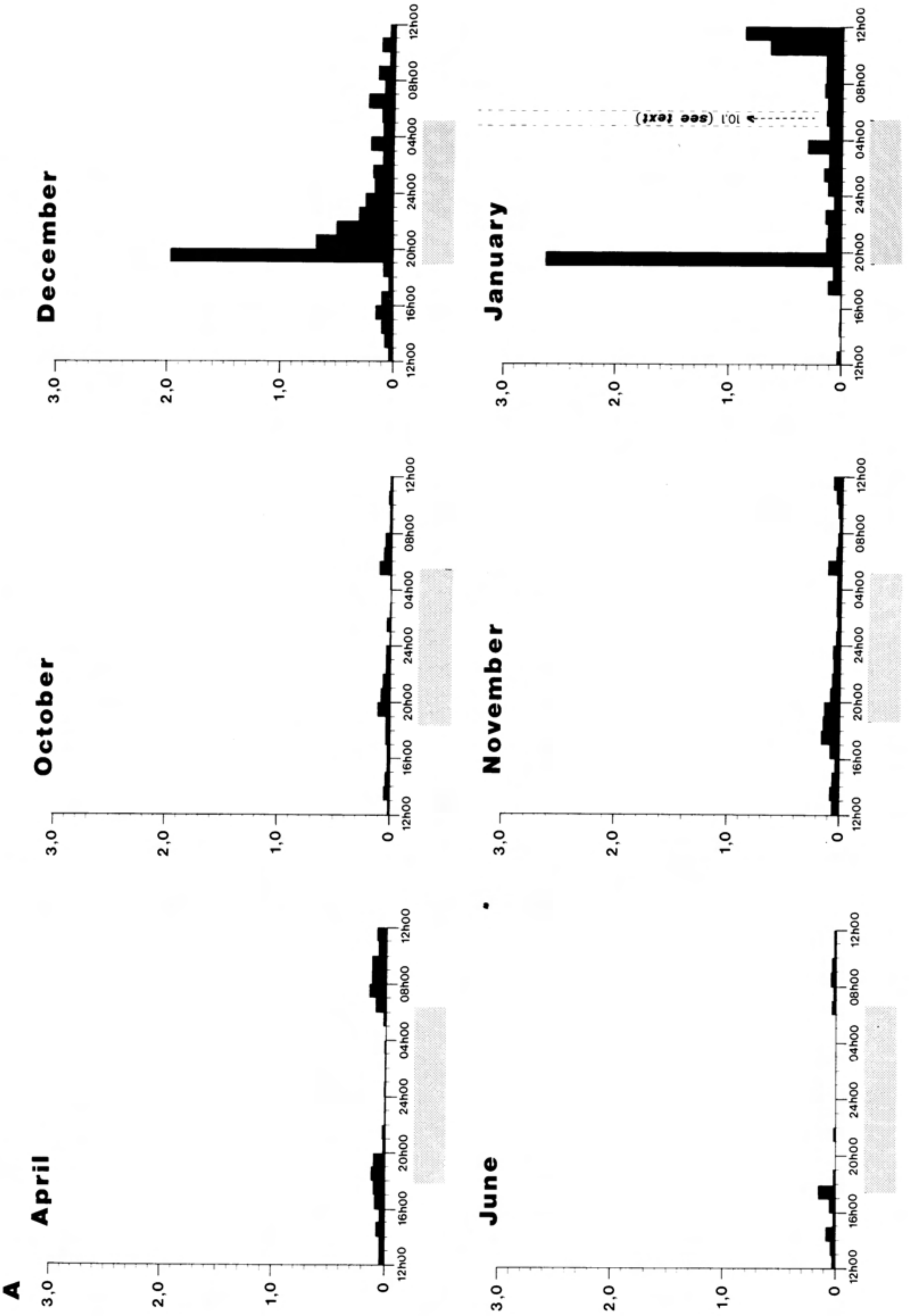
In the laboratory, the pitfall samples were washed with water and air dried. All arthropod samples were dried for 72 hours in an oven at 40 °C, whereafter samples were weighed on an electronic balance to the nearest 0,1 mg. An hourly index of available biomass of aerial arthropods was calculated as the average for the two corresponding periods of the 48-hour sampling session. A monthly index of availability was calculated by summing the mass of all arthropods collected during each 48-hour sampling session. Since the terrestrial arthropods were sampled over periods varying between nine and 11 days, the mass collected in all six traps for each sample period was expressed in mass caught per day.

Temperature and relative humidity were recorded by means of a thermo-hygrograph during the period 15–22 July 1986.

Results

An index of the arthropod biomass available in the air for each hour of the day during the fullest phase of the moon is presented for each of the eight months that the area was sampled during 1986 and 1987 (Table 1, Fig. 1A). The arthropod biomass increased markedly, often dramatically, in the hours of, and just after sunset, and this was consistently the time of highest arthropod availability during any day. During the dry winter and early summer months of April to November, the dusk increase was only some 5X the availability during the preceding afternoon hours. However, during the mid-summer months, after the rains had begun, the increase was much higher; for December an increase of 20X was recorded, for January 26X, declining to 8X for February. Arthropod availability declined sharply later at night throughout the year and was generally equivalent to the hours of full daylight, except for a virtual absence of any aerial arthropods at night in the cool months of April, June and July.

A minor peak was also evident during the hours around dawn. In this respect arthropods collected during the sampling period started at 05h00 on the second morning of the January sample warrant further comment. Light showers fell during the previous day and night. The following dawn flying termites took to the air in great numbers, yielding 10,1 g of termites during this period as opposed to only 0,08 g of arthropods recorded the preceding morning. This was obviously a special event and unusual emergences of other arthropods after the rain may have caused the peaks recorded during the 10h00 and 11h00 sampling periods.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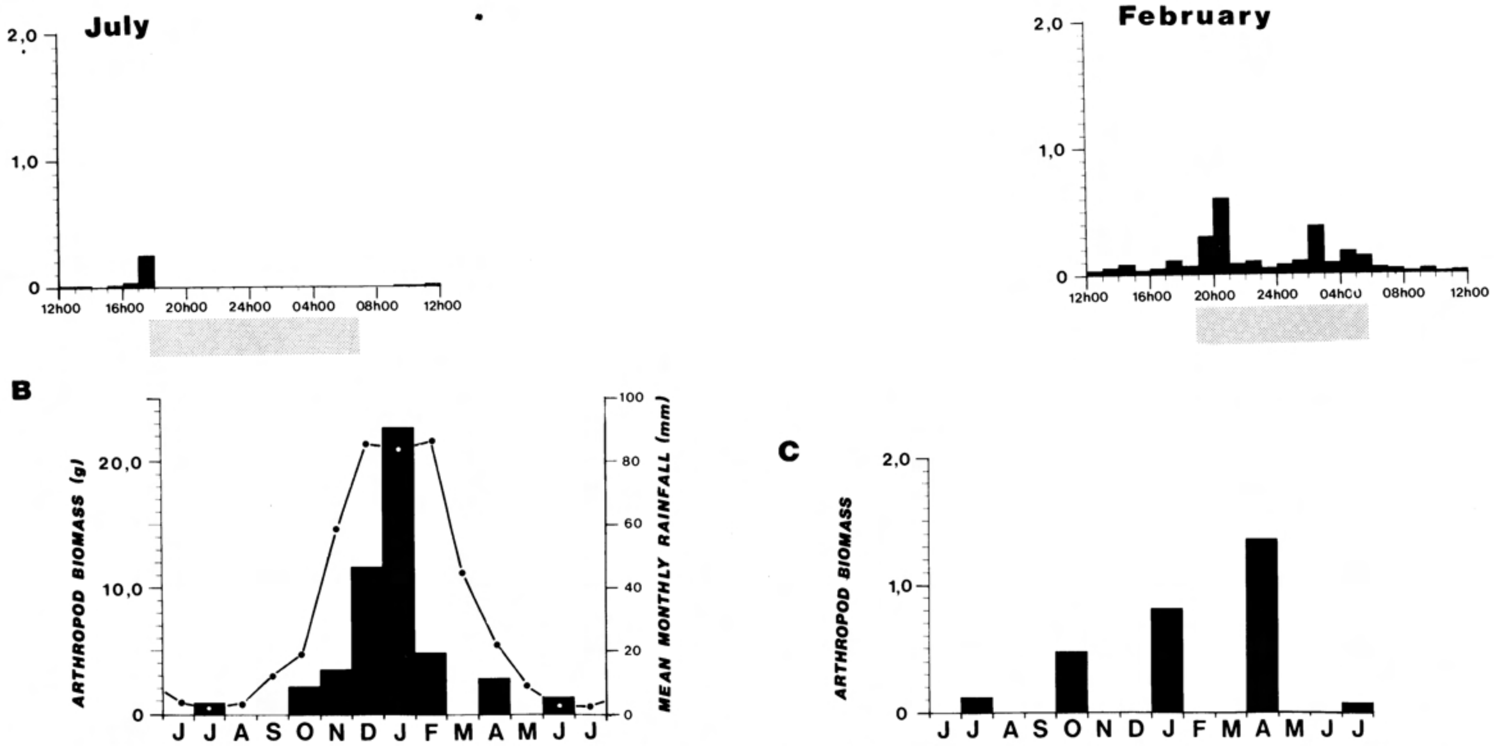

Fig. 1A. Average hourly biomass of aerial arthropods recorded over a 48-hour period by means of a vehicle-borne airplankton net driven over a set 8 km transect during the fullest phase of the moon for the months of 1985/86 as indicated. Shaded blocks denote hours of darkness during respective sample months. Fig. 1B. The cumulative total of aerial arthropod biomasses (grams) recorded during the eight monthly sampling sessions, and the mean monthly rainfall (48-year average measured at Pafuri) indicated by the broken line. Fig. 1C. Total biomasses (grams) of arthropods collected in all six pitfall traps set for 9–11 days over five fullest phases of the moon as indicated, expressed as an average accrued per day.

Table 1

Total arthropod biomass collected along an 8 km transect within the riparian forest of the Luvuvhu River, KNP, South Africa, using a vehicle-mounted air-plankton net at hourly intervals over 48 hours in the months of April–December 1986 and January–February 1987

	April	June	July	Oct.	Nov.	Dec.	Jan.	Febr.
12h00–13h00	00,031	00,036	00,007	00,018	00,080	00,021	00,058	00,044
	00,060	00,035	00,024	00,009	00,052	00,044	00,014	00,032
13h00–14h00	00,053	00,064	00,013	00,072	00,131	00,119	00,000	00,042
	00,041	00,034	00,019	00,047	00,038	00,026	00,018	00,078
14h00–15h00	00,044	00,121	00,013	00,068	00,077	00,029	00,000	00,016
	00,084	00,046	00,012	00,029	00,060	00,181	00,038	00,127
15h00–16h00	00,052	00,022	00,025	00,052	00,048	00,074	00,000	00,015
	00,029	00,032	00,014	00,017	00,049	00,241	00,035	00,056
16h00–17h00	00,060	00,052	00,038	00,025	00,053	00,044	00,000	00,031
	00,093	00,066	00,027	00,036	00,112	00,157	00,022	00,056
17h00–18h00	00,078	00,105	00,226	00,031	00,048	00,032	00,234	00,146
	00,110	00,208	00,276	00,061	00,286	00,048	00,024	00,082
18h00–19h00	00,177	00,027	00,002	00,053	00,144	00,055	00,081	00,062
	00,079	00,024	00,008	00,039	00,159	00,118	00,066	00,061
19h00–20h00	00,127	00,012	00,010	00,179	00,161	00,727	05,132	00,403
	00,069	00,011	00,002	00,055	00,136	03,252	00,143	00,205
20h00–21h00	00,014	00,010	00,000	00,113	00,096	00,859	00,163	00,140
	00,029	00,007	00,000	00,058	00,079	00,514	00,106	01,061
21h00–22h00	00,025	00,007	00,000	00,098	00,038	00,657	00,134	00,095
	00,034	00,039	00,010	00,036	00,118	00,344	00,106	00,076
22h00–23h00	00,012	00,002	00,000	00,052	00,057	00,426	00,221	00,145
	00,026	00,003	00,000	00,036	00,065	00,192	00,072	00,071
23h00–24h00	00,020	00,002	00,000	00,044	00,097	00,128	00,040	00,061
	00,019	00,001	00,000	00,037	00,058	00,364	00,091	00,052
00h00–01h00	00,012	00,002	00,000	00,023	00,045	00,025	00,208	00,063
	00,010	00,001	00,000	00,011	00,047	00,304	00,036	00,080
01h00–02h00	00,003	00,008	00,000	00,045	00,051	00,140	00,244	00,100
	00,013	00,009	00,000	00,022	00,027	00,220	00,063	00,121
02h00–03h00	00,004	00,018	00,005	00,018	00,051	00,125	00,161	00,052
	00,010	00,001	00,000	00,015	00,044	00,059	00,066	00,026
03h00–04h00	00,019	00,002	00,000	00,006	00,021	00,137	00,541	00,103
	00,008	00,010	00,000	00,011	00,060	00,281	00,071	00,058
04h00–05h00	00,002	00,012	00,000	00,013	00,044	00,114	00,060	00,062
	00,014	00,002	00,000	00,011	00,045	00,085	00,173	00,299
05h00–06h00	00,032	00,004	00,000	00,084	00,149	00,112	10,092	00,126
	00,015	00,002	00,000	00,128	00,097	00,107	00,080	00,171
06h00–07h00	00,101	00,013	00,002	00,077	00,053	00,204	00,228	00,036
	00,068	00,050	00,001	00,062	00,047	00,258	00,043	00,068
07h00–08h00	00,146	00,154	00,002	00,046	00,031	00,078	00,291	00,055
	00,143	00,033	00,001	00,055	00,049	00,096	00,013	00,030
08h00–09h00	00,182	00,011	00,009	00,019	00,026	00,085	00,249	00,028
	00,060	00,077	00,008	00,037	00,031	00,209	00,048	00,026
09h00–10h00	00,064	00,013	00,018	00,029	00,021	00,046	00,258	00,055
	00,182	00,054	00,019	00,029	00,046	00,044	00,026	00,027
10h00–11h00	00,052	00,009	00,029	00,049	00,053	00,043	01,264	00,156
	00,079	00,045	00,010	00,023	00,063	00,199	00,013	00,031
11h00–12h00	00,094	00,013	00,025	00,013	00,103	00,044	01,715	00,028
	00,046	00,034	00,015	00,046	00,060	00,040	00,014	00,048

The daily temperatures and relative humidities, as recorded over 7 days during July 1986, are presented in Fig. 2. Whereas daily temperatures increased steadily from sunrise to reach a maximum at about 14h00 and thereafter declined steadily until about 06h00 (sunrise), relative humidity reached a nadir at 14h00 and, as daytime temperature decreased, relative humidity increased until sunset (*c.* 18h00), whereafter it stabilised (normally between 80–90%) for the rest of the night. Although it will require further investigation, it would appear that a combination of highest daily relative humidity and the highest night-time temperature, immediately after sunset, create conditions most favourable for arthropod flight activity, resulting in the brief peak of availability of aerial arthropods. Sudden changes in temperature, with their reciprocal effect on relative humidity, may account for some of the fluctuations and anomalies in the record of arthropod activity.

The total biomass of aerial arthropods collected during each month is presented in Fig. 1B. The availability of flying arthropods was seasonal, with maximum availability during December and January, whereafter availability indices dropped sharply to a minimum during the cold and dry months of the year, particularly from April to July and presumably also August and September.

This seasonal trend was not mirrored by the terrestrial arthropods sampled by means of pitfall traps (Table 2, Fig. 1C). Biomass increased from a low during July 1986 to a maximum as late as April 1987, followed by a return to a low level in July 1987.

Table 2

Total biomass of arthropods caught in six 20 cm diameter pit traps set within riparian forest of the Luvuvhu River, KNP, South Africa, for periods of July (9,5 days) and October (9,0 days) of 1986 and January (11,0 days), April (11,0 days), and July (9,0 days) of 1987

	July	October	January	July	April
TRAP 1	06,275	16,286	13,354	02,657	12,198
TRAP 2	01,690	07,669	14,032	01,400	18,871
TRAP 3	00,574	02,925	06,434	01,017	33,950
TRAP 4	00,242	05,263	10,115	01,036	39,944
TRAP 5	00,258	04,625	20,460	00,349	24,167
TRAP 6	02,639	03,418	17,790	00,514	07,771
Total	11,678	40,186	82,186	06,973	136,900

Discussion

We accept that no unbiased method exists to census arthropod availability and particularly composition, but point out that our primary objective was to obtain a general index of arthropod availability, both in the air and on the ground, as nourishment for bats and other insectivores. We assume that our results reflect the general patterns of differential hourly and seasonal availability of arthropods.

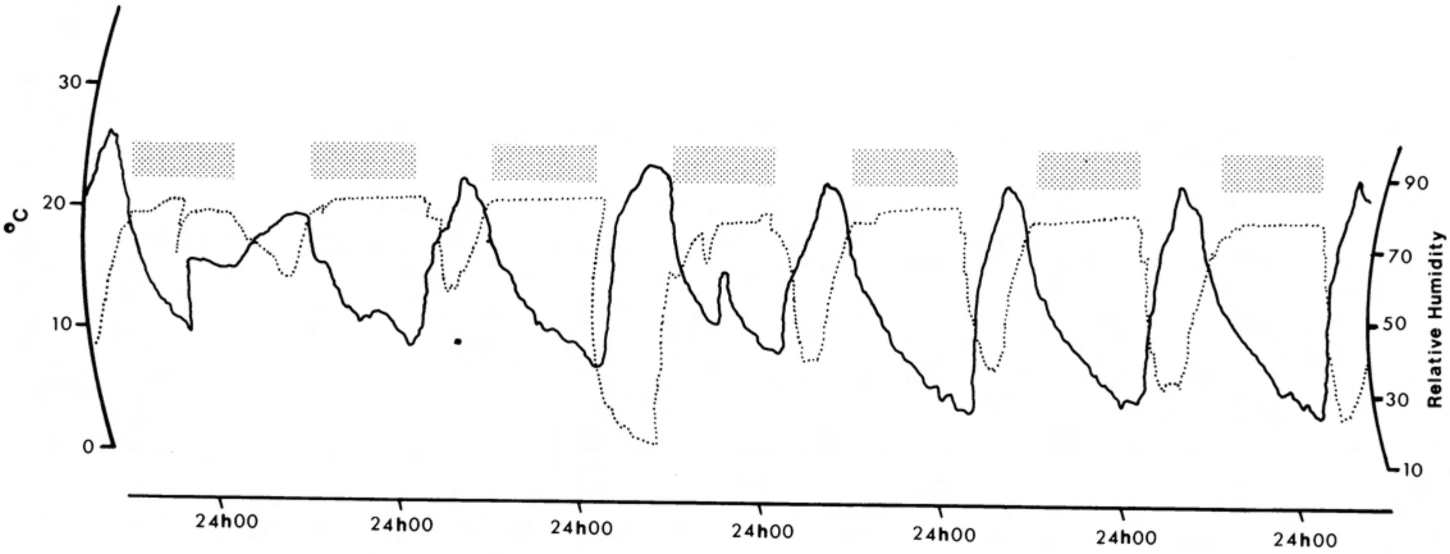

Fig. 2. Graph representing the daily temperatures and relative humidities recorded at ground level in riparian forest along the Luvuvhu River during the period 15–22 July 1986. Shaded blocks denote hours of darkness.

The pattern of high arthropod availability during the wet season is obvious subjectively and has been documented repeatedly here and elsewhere in Africa, despite focussing on different arthropod communities and using a variety of sampling methods (Transvaal bushveld, Kemp 1976; Transvaal thornveld, Bearder & Martin 1980; Tanzanian grassland, Sinclair 1978; Kenyan grassland, Dingle & Khamala 1972; Kenyan bushveld, Lack 1986; and references therein). Lack (1986) also examined hourly variations in availability, only during daylight hours, but this also demonstrated a marked rise at dusk, equivalent to the notable and consistent dusk peak recorded in this study.

The extent to which peak arthropod availability during a wet season exceeded background levels during a dry season varied between studies. It ranged from 2–3X for terrestrial arthropods in Kenya (Lack 1986) versus 15X in this study, 4–5X for arthropods in East African grassland (Dingle & Khamala 1972; Sinclair 1978; Lack 1986), 15X in the grass layer of Transvaal bushveld (Kemp 1976), 7–14X for flying insects in wooded savanna (Sinclair 1978; Bearder & Martin 1980; this study), to 17–60X for woody vegetation in Senegal (Morel 1968, *in* Lack 1986).

The 1986/87 rainfall season along the Luvuvhu River was well below average (44% of 48 year average of 432 mm) but was preceded by an above average rainfall season (112%). The precipation during the months that these samples were collected was both late and consistently below average (Fig. 1B, October 49%, November 30%, December 45%, January 40%, February 85%, March 30%, April 6% and May 40% of average). This may have affected arthropod availability detrimentally but we have no reason to suspect that the seasonal trend illustrated in Fig. 1B is not representative of any year, irrespective of actual rainfall. Clearly, however, seasonal arthropod availability is closely correlated to seasonal rainfall (Fig. 1B; Sinclair 1978) and presumably at least to some extent to other seasonally fluctuating environmental factors such as ambient temperatures and nutrient availability. It is predicted that these factors will influence the amplitude of seasonal changes but not the basic pattern.

Studies on *Miniopterus schreibersii* (Van der Merwe 1973a, 1973b, 1975, 1979, 1980, 1986, 1987; Richardson 1977), *Miniopterus fraterculus* (Bernard 1980), *Myotis tricolor* (Bernard 1981), *Rhinolophus clivosus* (Bernard 1983), *Rhinolophus capensis* (Bernard 1985), *Nycteris thebaica* (Bernard 1982) and *Hipposideros caffer* (Bernard & Meester 1982) show that all these highland, cave-dwelling microchiropteran species follow the typical temperate-region pattern of obligate hibernation during winter together with migratory habits and various physiological and behavioural strategies to delay embryonic development between copulation in autumn and parturition in mid-summer. Racey (1982) points out that the greatest causal factor for these adaptations is the necessity to overcome the winter period of food deprivation.

A study on the reproductive strategies of bats along the Luvuvhu River was initiated during 1983. The rhinolophid, nycterid and hipposiderid species, as well as *Miniopterus schreibersii* and *Myotis tricolor* all displayed the typical reproductive patterns of their highland counterparts and females typically produce single offspring during mid-summer (unpublished data). Several species of insectivorous bats restricted primarily to the wooded savannas of the eastern Transvaal lowveld, the northern Transvaal and regions further to the north and east were selected for detailed study of their reproductive strategies. This was to determine, *inter alia*, whether their easterly distribution in more equable conditions, as found along the riparian forests of the Levuvhu River, allow reproductive strategies different from highveld species. None of these species were cave dwellers, obligatory hibernators, or seasonal migrants. *Scotophilus dinganii* (unpublished data), *S. borbonicus* (Van der Merwe & Rautenbach, *in press* a & b; Van der Merwe, Rautenbach & Penzhorn, *in press*), *Eptesicus capensis* (unpublished data), *E. cf. melckorum* (unpublished data), *E. zuluensis* (unpublished data), *Nycticeius schlieffenii* (Van der Merwe & Rautenbach 1986, 1987; Van der Merwe 1987), *Pipistrellus rusticus* (unpublished data), *Tadarida pumila* (Van der Merwe, Rautenbach & Van der Colf 1986; Van der Merwe Giddings & Rautenbach 1987; Van der Merwe 1987) and *T. condylura* (unpublished data) all display seasonal reproductive patterns, either by sperm storage or delaying embryonic development during winter (the Vespertilionidae), or by abstinence from any reproductive activity during winter (the Molossidae).

It would appear that those species along the Luvuvhu River, for which reproductive data are available, all display the reproductive strategies typical of bats of temperate regions, despite existing in a more equable climate. We consider that the single most important factor enforcing this overwintering strategy in reproduction is insufficient food to sustain winter activities.

Erkert (1982), in reviewing aspects of daily activity rhythms of bats, concluded that bimodal activity patterns under normal environmental conditions are characteristic of most microchiropteran bats studied to date. The main peak of activity coincides with the few hours following sunset, with a considerably smaller peak usually found shortly before sunrise. Isolated studies on the daily activity patterns of southern African bats show similar bimodal activity peaks (Aldridge & Rautenbach 1987; Barclay 1985; Bell & Fenton 1984; Fenton 1975; Fenton, Boyle, Harrison & Oxley 1977; Fenton, Bell & Thomas 1980; Fenton & Thomas 1980; Fenton, Thomas & Sassen 1981; Fenton, Brigham, Mills & Rautenbach 1985; Fenton & Rautenbach 1986; Fenton, Cumming, Hutton & Swanepoel 1987; O'Shea & Vaughan 1980; Vaughan 1976, 1977; and personal unpublished data). It would appear, from mistnetting results, that all insectivorous bats along the Luvuvhu River display high activity peaks shortly after sunset, although considerable variation is obvious for the rest of the night. Vespertilionid bats appear to hunt on the wing and to return to their daytime roosts once satiated, but may to a lesser extent become active again prior to sunrise. Molossid bats appear to remain active throughout the night, whereas the Rhinolophidae, Hipposideridae and Nycteridae seek night roosts after an initial bout of continuous feeding on the wing soon after dark. Short feeding bouts may be undertaken from these night roosts or hunting may continue in the flycatcher mode from a perch.

The Rhinolophidae, Hipposideridae and Nycteridae were found to be cave-dwellers on the central highlands of South Africa, where they have a tendency to migrate and appear to be obligate hibernators. Information on the species belonging to these families along the Luvuvhu River is scant, but unpublished data suggest that there the same general patterns hold true. However, many vespertilionid and particularly molossid species along the Luvuvhu River remain active throughout the winter, albeit at a much reduced level. From Fig.

1A it is evident that there may not be sufficient nourishment during winter to sustain a continually active metabolism. More often than not activity is restricted to exploratory flights on clear evenings lasting only a few minutes. Such activities are invariably restricted to the brief period following sunset, when at least some feeding may be possible.

Irrespective of seasonal, intraspecific or interspecific variation in activity rhythms of bats along the Luvuvhu River, the highest incidence of bat activity coincides with the highest incidence of aerial arthropods. If these dusk and dawn peaks of arthropod activity prove to be widespread, they may present an important feature in understanding how bats evolved to exploit this nocturnal availability. They may also be important in understanding crepuscular foraging by diurnal birds, as well as diurnal aerial foraging by such birds as swallows and swifts and nocturnal foraging by nightjars.

The potential predators of bats along the Luvuvhu River can only be expected to take bats opportunistically, as each consumes a wide range of other prey types (Steyn 1982). It should be borne in mind that the dusk and dawn availability of arthropods is likely to produce activity in a wide range of insectivores other than bats, such as shrews and birds, and that the relatively high dusk temperatures should also encourage emergence of poikilothermic nocturnal insectivores, such as lower vertebrates and invertebrates. Many of these primary predators of arthropods are themselves likely prey for raptors and it is notable that a post-dusk and pre-dawn peak of delivery of prey to nests is mentioned for several owl species (Kemp 1987).

The extent to which raptors consume bats along the Luvuvhu River remains to be determined, but *Strix woodfordii* is known to be the most common owl species (Kemp & Kemp *in press*) and the most likely nocturnal predator. Of the other raptors, the accipiters *A. tachiro* and *A. minullus* are considered the most likely predators of active bats in the riverine forest, both occurring commonly and having been recorded taking insectivorous bats late into the dusk, the former showing specific bat-hunting behaviour at this time (Kemp & Rautenbach 1987). The only avian predator that specialises on bats, *Macheirhamphus alcinus*, is rare and possibly only a winter visitor along the Luvuvhu River. It is also notable that all the avian predators known to take insectivores regularly and to be resident along the Luvuvhu River breed in spring and fledge their young in mid-summer (Steyn 1982; Tarboton, Kemp & Kemp 1987). Even the two largest species (*Hieraaetus spilogaster* and *Bubo lacteus*) lay in winter but their young become independent in the following summer, when arthropods are most available.

Our data suggest that the strictly seasonal rainfall pattern along the Luvuvhu River is responsible for alternating periods of seasonal arthropod availability and scarcity, and that on a daily basis a combination of high humidity and highest night-time temperature create favourable conditions for peak arthropod activity at dusk. Bats appear to have adapted their reproduction to cope with seasonal periods of food scarcity, and their daily activities to utilise highest densities of aerial arthropod prey at dusk. These correlations may extend to other insectivores, which in turn may influence the timing of hunting and breeding of secondary predators, such as raptorial birds.

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