Bats in riverine forests and woodlands: a latitudinal transect in southern Africa

I.L. Rautenbach, M.B. Fenton, and M.J. Whiting

Abstract: Using captures in mist nets and monitoring echolocation calls, we quantified bat distribution and activity and measured insect abundance as numbers of insects attracted to black lights at 15-min intervals. These data were collected simultaneously at pairs of sites in riverine and dry woodland savannah along a transect of ca. 350 km from north to south in the Kruger National Park, South Africa. The sites were situated in the north, central, and south of the park and data were collected in January 1993. Our study involved 18 sites, three pairs each in the areas of the Luvuvhu, Letaba, and Sabie rivers. Half of the sites were in riverine woodland, the others in dry woodland. No statistical association exists between bat captures and either bat activity or insect abundance. Bat activity, however, was related significantly to insect abundance. Although bats were significantly more abundant (captures) in riverine habitats than in dry woodland savannah, comparisons of bat diversity and evenness (rarefaction curves, species abundance curves, and Whittaker plots) showed no differences between these habitats. The data neither demonstrate a decline in bat diversity away from the equator nor suggest specific bat communities associated with riverine habitats. The data do demonstrate the important influence of insects on the activity patterns of insectivorous bats.

Résumé : Nous avons utilisé des données sur la capture dans des filets japonais et des enregistrements de cris d'écholocation pour quantifer la répartition des chauves-souris et leurs activités et nous avons également mesuré l'abondance des insectes capturés dans des pièges aux ultra-violets à 15 min d'intervalle. Les données ont été recueillies simultanément à des paires de sites, dans un habitat riverain et une savane boisée sèche, le long d'un transect nord-sud d'environ 350 km dans le parc national de Kruger en Afrique du Sud. Les sites étaient situés dans les parties nord, centre et sud du parc et les données ont été recueillies en janvier 1993. Nous avons choisi 18 sites, trois paires à chaque endroit, soit dans les bassins des rivières Luvuvhu, Letaba et Sabie. La moitié des sites se trouvaient dans des milieux riverains boisés, l'autre moitié dans des milieux secs boisés. Aucune relation statistique n'a été trouvée entre le nombre de chauves-souris capturées et leur activité ou l'abondance des insectes. L'activité des chauves-souris était cependant en corrélation significative avec l'abondance des insectes. Les chauves-souris étaient significativement plus abondantes dans les captures effectuées en milieu riverain qu'en milieu sec, mais la comparaison entre la diversité des chauves-souris aux deux endroits et leur régularité (courbes de raréfaction, courbes d'abondance des espèces et diagrammes de Whittaker) n'a révélé aucune différence entre ces deux types d'habitats. Les données n'indiquent pas de diminution de la diversité des chauves-souris à mesure qu'on s'éloigne de l'équateur et ne signalent pas non plus l'existence de communautés de chauves-souris spécifiques des habitats riverains. Les données soulignent cependant l'influence importante des insectes sur l'activité des chauves-souris insectivores.
[Traduit par la Rédaction]

Introduction

As mobile, long-lived, but sometimes sedentary animals that fill a variety of trophic roles (Wilson 1973; Fenton 1992; Findley 1993), bats offer challenges and opportunities to biologists interested in the factors affecting patterns of distribution and diversity. In these matters, bats are similar to and yet different from birds, as shown, for example, by work in the West Indies (Fleming 1982) and studies of altitudinal distributions in Peru (Graham 1990). The differences between bats and birds may involve both trophic diversity and physiological features (Graham 1990).

Received November 28, 1994. Accepted September 21, 1995.

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The diversity of bats increases dramatically with proximity to the equator (Wilson 1973; Wilson 1974; Findley 1993), making subtropical areas potentially important places to study the diversity of bats because small changes in latitude coincide with major changes in bat faunas. The patterns of change in bat diversity with latitude are affected by land area and water barriers. A clear indication of these effects is provided by the sharp decline in bat diversity that occurs from Trinidad through the West Indies, from 10°N at the southern end of Trinidad to about 23°N at the northern edge of Cuba (Fleming 1982). The changes in bat diversity have been variously ascribed to patterns of temperature, habitat complexity, and food availability (e.g., Graham 1983).

In North America, bats show a marked increase in species diversity between about 18° and 25° of latitude, coinciding with their exploitation of a greater variety of food (Wilson 1974). To see if this is a more general continental pattern, we documented the latitudinal pattern of bat diversity between about 22° and 25°S in Africa. In this area, there is no marked change in the trophic roles played by bats as insecti-

vores and frugivores occur to the south and north (Smithers 1983). We worked in the Kruger National Park in South Africa (Fig. 1). This comprises about 20 000 km^2 of deciduous woodland savannah and has a long and narrow north–south axis of about 3° of latitude or >350 km. The climate in the park is increasingly temperate towards the south end, and changes in temperature and rainfall are reflected by the species composition and physiognomy of the vegetation (Gertenbach 1983).

Three species of fruit bats and 38 species of insectivorous bats are known from the park (Pienaar et al. 1987), the greatest numbers of species occurring in the more tropical regions of the extreme northeastern districts (Pienaar et al. 1987), the area of most survey work. The north–south pattern is complicated by eight major rivers and their tributaries that drain from west to east and provide corridors of relatively moist tropical conditions and vegetation to the coastal forests of Mozambique (Gertenbach 1983).

At least three factors may affect the distribution of bats in and around the park, and they are not mutually exclusive. First, the decline in species richness with increasing distance from the equator evident in the Transvaal (Rautenbach 1978*a*, 1978*b*) may parallel the situation elsewhere (e.g., Wilson 1974) and reflect overall climatic conditions. Second, by their structural diversity (cf. Cody 1975; Humphrey 1975), the riparian woodlands associated with the major rivers may provide suitable conditions for some tropical species that cannot survive in drier woodlands. Third, because a close relationship exists between the seasonal and nightly abundance of insects and the seasonal breeding and daily activities of insectivorous bats (Rautenbach et al. 1988), reduced food availability with increasing latitude may be reflected by bat diversity.

Our study was designed to (*i*) test the prediction that a north to south reduction in bat diversity exists in the park; (*ii*) compare bat communities in woodland and riverine forest and test the prediction that some species are restricted to the riverine habitat (= higher structural complexity); and (*iii*) explore the impact of food availability by examining the relationships between bat captures and activity and insect availability. We examined these topics by sampling bats and insects along a north–south transect through the park (Fig. 1), comparing sites (Appendix) in riverine (50–100 m from the rivers) and dry woodland (≥3 km from the rivers) from 14 to 23 January 1993. We chose sites along three of the park's major rivers, the Luvuvhu, the Letaba, and the Sabie (Fig. 1).

Methods

We sampled 18 sites, 9 in riverine habitats along the Luvuvhu (3), Letaba (3), and Sabie (3) rivers and 9 in adjacent dry woodland (Fig. 1). We chose pairs of representative sites in riparian and adjacent woodlands and sampled them simultaneously from 18:45 to 00:00 (sunset at Skukuza 18:47 local time on 19 January 1993). Our study took place during the rainy season or summer, approximately 2 months after most female bats had borne young (Pienaar et al. 1987).

Gertenbach's (1983) classification of landscapes of the park describes the sampling sites. In the Sabie River region, our sites (landscape 4) are characterized by dense woody associations of *Acacia nigrescens* and *Combretum apiculatum*, with trees <4 m contributing 7.4% of crown cover. The localities in the Letaba region (landscape 22) are open shrub savannah dominated by *Colophospermum mopane* and *Combretum apiculatum*. Those sampled in the Luvuvhu region are characterized by tall stands of *Colophospermum mopane* and *Adansonia digitata* (landscape 25).

Two macro mist nets, 30 m long × 6 m high (Rautenbach 1985), were deployed per site and attended continuously by at least four people. Nets were erected across likely flight paths, perpendicular to the river in riparian forest. Once caught, bats were immediately removed from the nets and therefore we recorded species, sex, date, and time of capture. Captured bats were held in cages for the duration of netting sessions and then released. At each netting site, we monitored bat activity for 4 min every 15 min by recording the number of bat passes (sensu Fenton 1970) detected by narrowband bat detectors (Ultrasound Advice Mini 2) tuned progressively from 20 to 60 kHz (1 min each at 20, 30, 40, and 60 kHz).

We used two 12-V black lights, one at each site, to assess insect abundance per 15-min interval at all but one of the sites. Every 10 min the light was switched on and 4 min later a sample of insects was captured in 60 s using 10 figure-eight sweeps of a 30 cm internal diameter insect net. Captured insects were counted, measured, and recorded in 0–5, 6–10, 11–15, 16–20, 21–25, and >25 mm body length classes. When more than 100 insects were taken, a value of 99 was assigned and, in analysis, treated as an actual value. Although this may reduce the statistical power of tests, 99 was used as a surrogate value in only 1.5% of our samples.

The data were analyzed using STATISTIX 4.0 (Analytical Software 1992) following procedures of Sokal and Rohlf (1981). All data were checked for normality (rankit method) and homogeneity of variance (Bartlett's test with 0.05 as lower bounds of significance) prior to use of parametric statistics. An approximation of the *t* test (t'_s) was used when the data were slightly heteroscedastic (t'_s assumes heterogeneous variances); otherwise, pairwise comparisons were made using the Mann–Whitney test, where the normal approximation with continuity correction was applied. Data on insect abundance were $\log_e$ transformed prior to ANOVA and post hoc Scheffé's pairwise comparisons. Product–moment correlation coefficients (*r*) were used to determine the overall relationship between insect and bat abundance and between insect abundance and bat activity for each 15-min period summed. Correlations between the above variables were also sought for both riverine and woodland habitats. For comparisons of bat activity, bat captures and insect abundance in sites within an area were combined, or where habitats were combined, the level of significance was adjusted for non-orthogonal comparisons to monitor the experimentwise error rate at 0.05 (Dunn–Šidák method). Where adjustments occurred, the new critical values are indicated next to the test statistic. All pairwise comparisons were two-tailed and means are reported ± 1 SE. Significance was established at $p \leq 0.05$.

We used rarefaction and relative abundance curves for independent examination of species richness and evenness (Krebs 1989). This approach avoided the problems associated with information theoretic indices of species richness, evenness, and diversity (e.g., Hurlbert 1971; Southwood 1978; James and Rathburn 1981; Krebs 1989). Rarefaction is a statistical method for estimating the expected number of species in a random sample. Given a sample of *n* individuals of each species, the rarefaction method predicts the expected number of species ($E(S_n)$) in progressively smaller samples using the formula

$$E(S_n) = \sum_{i=1}^{s} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

where *S* is the total number of species and N_i the total number of

Fig. 1. Map of the Kruger National Park, showing the distribution of study sites (1–18).

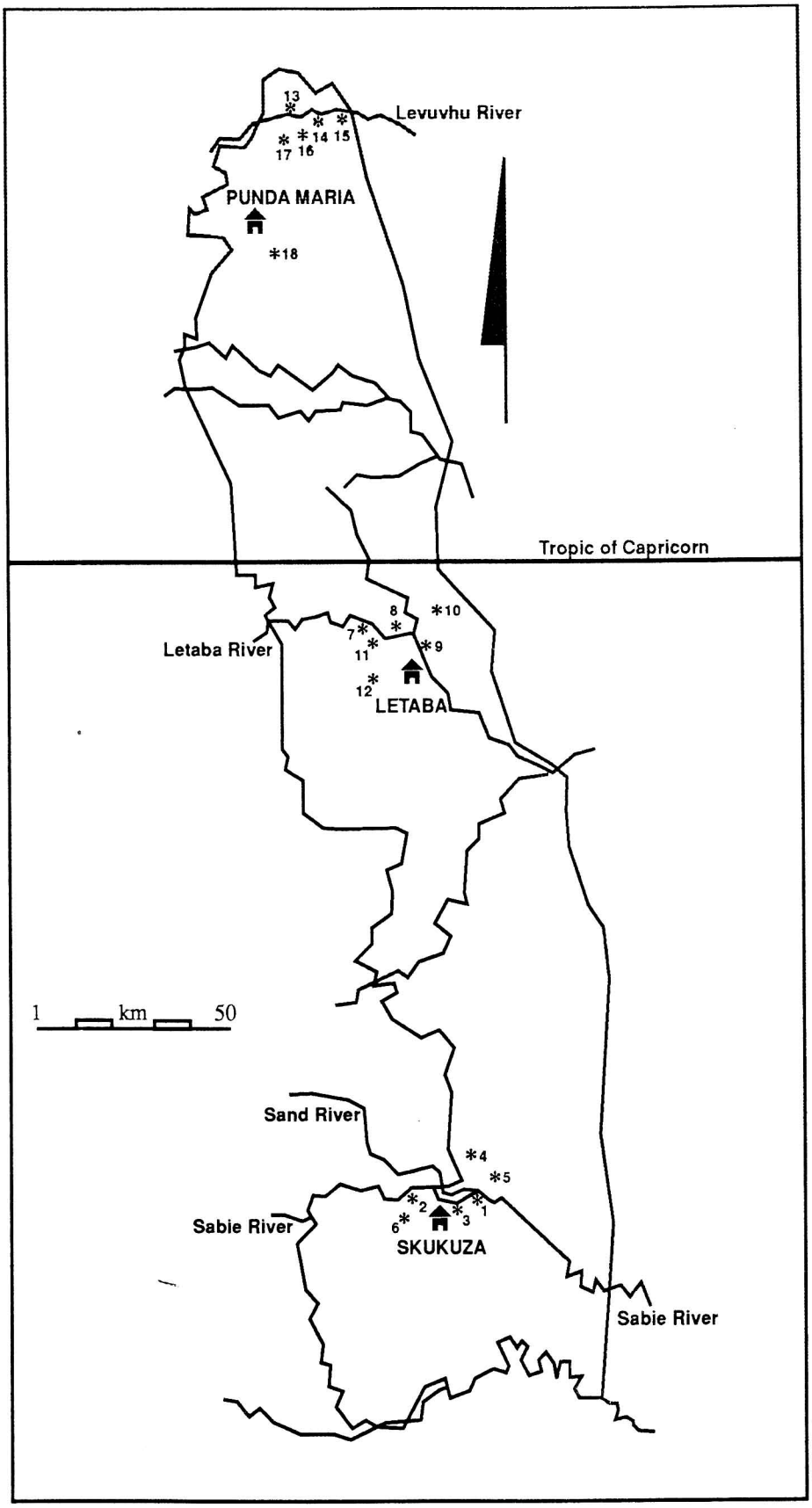


Table 1. Bats captured at the study sites in Kruger National Park, including riverine (RIV) and dry woodland (DRY) sites along or near the Sabie, Lebata, and Luvuvhu rivers.

	Sabie		Letaba		Luvuvhu		
	RIV	DRY	RIV	DRY	RIV	DRY	Total
Rousettus aegyptiacus	0	0	0	0	1	0	1
Epomophorus wahlbergi	0	0	2	0	0	0	2
Epomophorus crypturus	6	0	1	4	0	0	11
Taphozous mauritianus	2	0	1	1	5	2	11
Nycteris thebaica	0	0	0	5	0	1	6
Rhinolophus swinnyi	0	0	0	0	1	1	2
Rhinolophus darlingi	0	0	0	0	2	0	2
Rhinolophus fumigatus	0	0	0	0	7	1	8
Rhinolophus simulator	1	0	0	0	0	0	1
Myotis tricolor	1	0	0	0	0	0	1
Eptesicus capensis	13	22	5	2	4	4	50
Eptesicus hottentotus	0	0	0	0	3	0	3
Eptesicus zuluensis	0	1	0	0	2	0	3
Eptesicus cf. *melckorum*	1	0	0	1	0	0	2
Pipistrellus nanus	3	0	4	0	22	1	30
Pipistrellus rusticus	1	0	9	0	1	0	11
Pipistrellus kuhlii	1	0	1	2	0	0	4
Pipistrellus anchietae	1	1	0	0	0	0	2
Scotophilus borbonicus	55	18	19	12	8	20	132
Scotophilus dingani	6	5	5	23	22	10	71
Nycticeius schlieffeni	8	8	16	10	13	8	63
Tadarida aegyptiaca	0	0	0	1	0	0	1
Tadarida pumila	3	1	8	6	4	2	24
Tadarida condylura	7	2	103	10	0	3	125
Tadarida midas	0	0	0	2	0	0	2
Total individuals	109	58	174	79	95	53	568
Total species	15	8	10	11	14	11	25

individuals in species i (Krebs 1989). Rarefaction values were calculated using the program RAREFACT (Krebs 1989). Differences in species richness were calculated using nonparametric Kruskal–Wallis ANOVA.

In addition to species richness, at the community level it is necessary to provide a measure of relative distribution (evenness). Although rarefaction curves are a function of relative abundance, actual relative abundance (James and Rathburn 1981) is a more direct approach. A community with equal numbers of each species would be represented by a horizontal line, so relative abundance can be examined for departure from an even community. Relative abundance curves are presented by site and habitat and compared with expected logarithmic series (Whittaker) plots (equations in May 1975). The program LOGSERIE (Krebs 1989) was used to calculate expected Whittaker plots (May 1975). Because our data fitted a logarithmic series, LOGSERIE was used to calculate an index of diversity ($\propto$; Fisher et al. 1943) based on two variables, the number of species (S) in the sample and the number of individuals (N), using the formula

$$S = \propto \log_e(1 + N/\propto)$$

We also calculated sample variance using LOGSERIE from Anscombe (1950, cited in Krebs 1989) and used a two-way ANOVA to test for the influence of habitat (categorical variable) and latitude (independent variable) on species diversity ($\propto$; dependent variable).

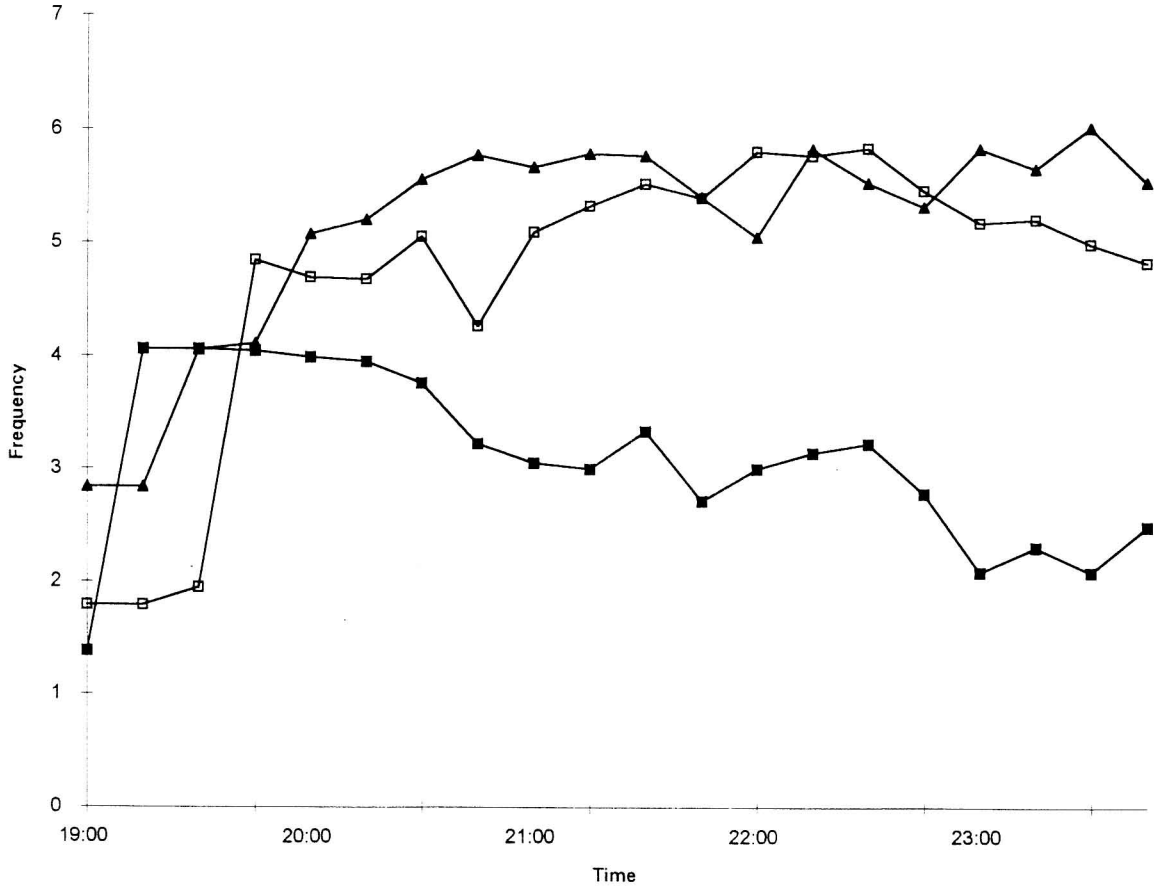
Results

A total of 568 individuals representing 25 species was netted, including the 3 frugivorous and 22 of the 38 insectivorous species known from the park (Table 1). The total numbers of bats netted per 15-min interval for all sites combined (Fig. 2) show a peak in activity just after dusk, with a steady decline thereafter until 00:00. This trend is evident in the subtotals for both riverine and dry woodland sites along each of the three rivers.

The mean numbers of bats of all species netted at riparian sites were significantly higher than (double) those taken in nearby woodland ($t'_{s0.01} = 3.63$, df = 93.9, $p < 0.001$; Table 1). Significantly more bats were caught in riparian forest than in woodland in the Letaba area ($Z = 2.48$, $p = 0.01$), but not near the Luvuvhu ($Z = 0.87$; $p = 0.39$) or the Sabie (Mann–Whitney $Z = 2.22$, $p = 0.03$) river. The greatest number of bats were caught in the Letaba area ($n = 242$), but a comparison of total bat captures in the different areas shows no significant differences (ANOVA, $F_{0.01[2,117]} = 2.96$, $p = 0.054$).

Species richness, shown as the rarefaction curves (Fig. 3), falls into two groups of sites (Figs. 3*a*, 4*a*), Sabie woodland sites and Letaba riverine sites forming the two lowest curves,

Fig. 2. Distribution of the logarithms (base e) of bat captures (■), bat activity (□; from bat passes), and insect captures (▲) over time, presenting data from all study sites.



and Luvuvhu riparian sites the highest curves, closest to those from the remaining sites. Species richness was highest at all riverine sites combined (Fig. 3*b*), but the differences between riverine and woodland sites were not significant ($H = 4.86$, $p = 0.677$). Species evenness, and its counterpart, dominance, are shown by the relative abundance curves, which do not split into two groups (Fig. 4). The greatest abundance of bats (Fig. 4; Whittaker plots, Fig. 5) occurred where bat communities were less even, dominated by a few species. Of particular note were Sabie and Letaba riverine sites dominated by a few species (Fig. 5*a*, Table 1).

Bat species diversity (Table 2) was variable, particularly in the Letaba area. The coefficient of variation for the Letaba sites combined was double that for the Luvuvhu sites and about 35% greater than that for the Sabie sites (Table 2). One Letaba woodland site had the highest diversity (16 individuals, 9 species), but there was no correlation between species diversity and latitude, regardless of habitat ($F_{0.01[1,16]} = 0.001$, $p = 0.971$). At most sampling locations, a few common species dominated the bat communities (Table 1).

Monitoring echolocation calls shows that bats were significantly more active in dry woodland than in riparian forest along the Sabie River ($t'_{s0.01} = -4.01$, df = 80.9, $p < 0.001$). The opposite occurred in the Letaba area ($t'_{s0.01} = 4.17$, df = 78.7, $p = 0.001$), and we found no significant differences in the Luvuvhu area ($t'_{s0.01} = 1.29$, df = 93.4, $p = 0.2$). There was no correlation between bat captures and bat activity ($r = -0.373$, $p > 0.05$; $n = 21$), indicating that echolocation calls provided a different picture of bat activity than did captures in mist nets. The echolocation calls steadily increased from dusk to 22:15 and declined thereafter (Fig. 2). Echolocation calls and captures show more bats in riverine than in dry woodland near the Letaba River; the reverse trends emerged near the Sabie and Luvuvhu rivers.

There was no overall significant difference in insect abundance among sites (ANOVA, $F_{0.01[2,369]} = 3.68$, $p = 0.02$), nor did overall insect abundance differ significantly between dry woodland and riverine forest ($t'_{s0.01} = 0.37$, df = 353, $p = 0.71$). Near Letaba, insects were significantly more abundant in riverine than in dry forest ($t'_{s0.01} = 3.25$, df = 68.5, $p = 0.002$). There were no significant differences in insect abundance at the Sabie ($t'_{s0.01} = -1.76$, df = 104.3, $p = 0.08$) or Luvuvhu ($t'_{s0.01} = -2.21$, df = 115.8, $p = 0.03$) sites.

Overall, there was no significant relationship between bat captures and insect abundance ($r = -0.174$, $p > 0.05$; $n = 21$) in either riverine ($r = 0.191$, $p > 0.05$; $n = 21$) or dry woodlands ($r = -0.409$, $p > 0.05$; $n = 21$). Bat activity, however, was significantly correlated with insect abundance ($r = 0.590$, $p < 0.01$; $n = 21$). Bat activity was positively correlated with insect abundance in dry woodland ($r = 0.518$, $p > 0.05$; $n = 21$) but not in riparian woodland ($r = 0.251$, $p > 0.05$; $n = 21$).

Discussion

Our data do not demonstrate a north–south trend in bat diversity or species richness along the length of the Kruger

Fig. 3. Bat species richness, showed as rarefaction curves. (*a*) The three main riverine (solid symbols) and woodland (open symbols) areas. Squares represent the Sabie sites, triangles the Letaba sites, and circles the Luvuvhu sites. (*b*) Data for combined woodland sites (×), riverine sites (+), and sites by area (symbols as in *a*). These curves are derived by predicting species-accumulation rates with increasing numbers of individuals as outlined in the text.

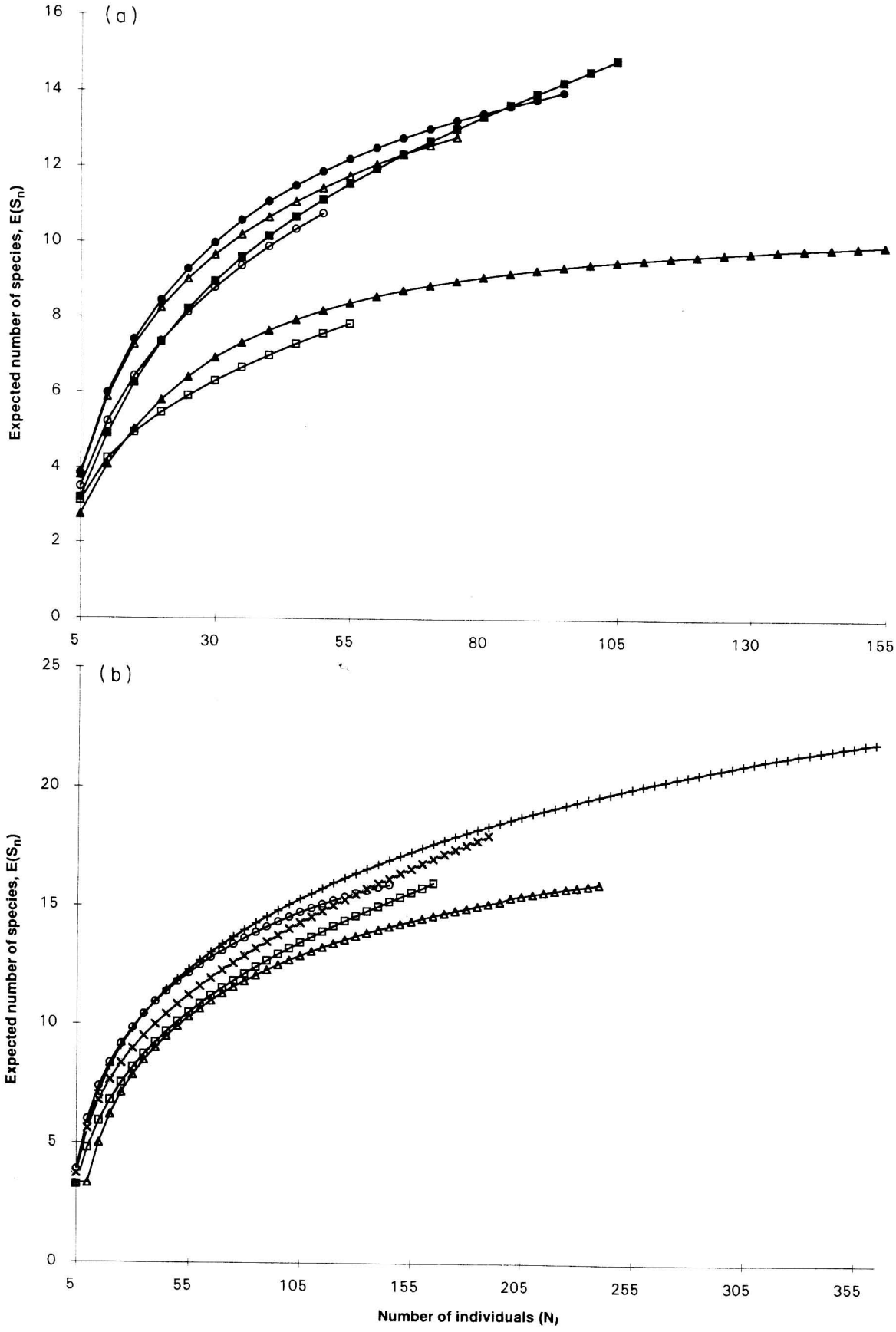


Fig. 4. Relative species-abundance curves for riparian sites (*a*), woodland sites (*b*), and combined riparian (+) and woodland (×) sites (*c*). Squares represent the Sabie sites, triangles the Letaba sites, and circles the Luvuvhu sites. Species ranks are shown, from most to least common, and the percentages of total individuals are depicted on a log scale.

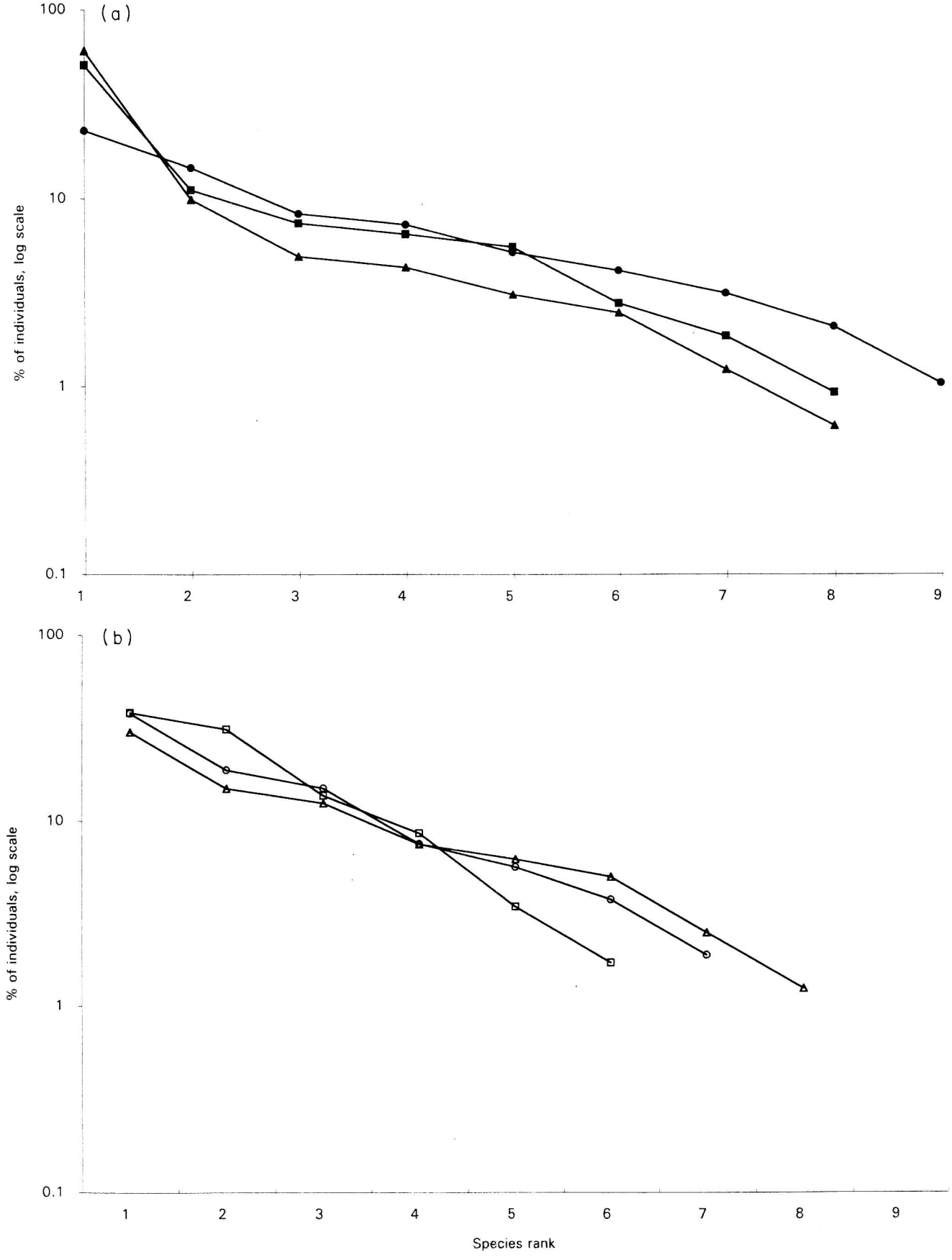
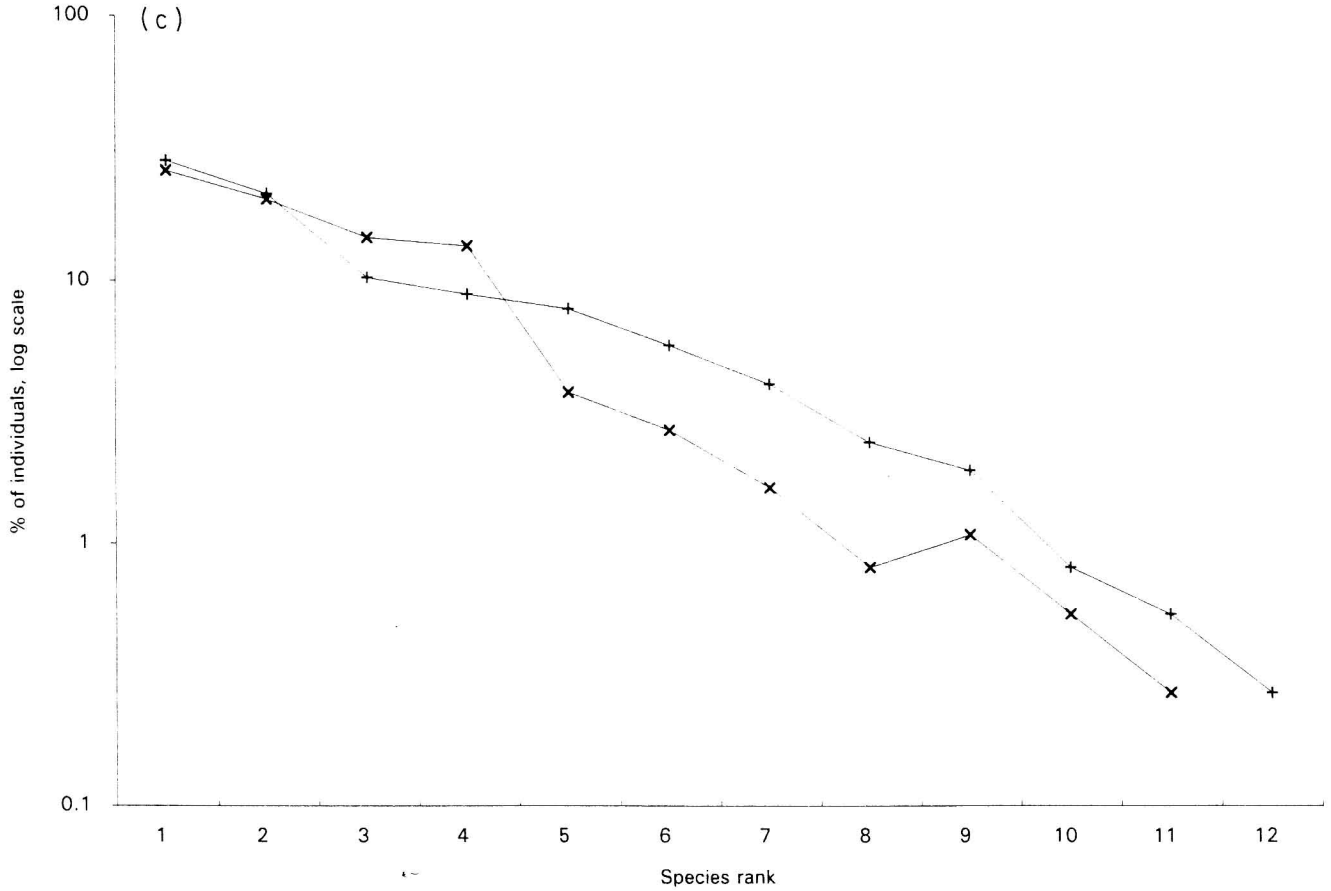


Fig. 4 *(concluded).*



National Park. Although the bat capture data showed higher numbers of bats in riverine than in dry woodland, the absence of rare or tropical species in the riverine catches suggests that river valleys do not provide special habitats for some species. Furthermore, the similarity in diversity and evenness between riparian and woodland sites does not indicate distinct bat communities in the river valleys. Some species of bats were almost ubiquitous (Table 1). Of the three areas, the Luvuvhu River appeared to have the most distinct community, with five species not found in other areas. These five, however, have been taken at more southerly locations in the park (Pienaar et al. 1987). The significant differences in bat captures between riverine and dry woodlands are not paralleled by differences with respect to insect abundance or bat activity as indicated by monitoring echolocation calls.

Our data provide no support for the proposal that increased habitat complexity has a significant effect on bat faunas. Furthermore, there was no evidence of a dramatic change in insect availability over the latitudinal distance we covered. The African situation may be strikingly different in areas where woodlands of any kind are restricted to river valleys. In these settings, habitat structural complexity will affect roosting opportunities (Humphrey 1975) and perhaps insect availability.

The statistically significant relationship between insectivorous bat activity and the numbers of insects attracted to black lights resembles the results of other studies. Rautenbach et al. (1988) showed a seasonal relationship between bat activity and insect availability along the Luvuvhu River. Many other studies have demonstrated that bats forage in artificial (e.g., at lights; Fenton and Morris 1976; Bell 1980; Rydell 1992) or natural (e.g., Gould 1978; Vaughan 1980; Ellis 1993) concentrations of insects. The echolocation calls of the bats often make these responses conspicuous (Rydell and Racey 1995). On 14 January, for example, between 22:00 and 23:15 in dry woodland at a site near the Sabie River, two small vespertilionids generated over 200 bat passes as they actively hunted for and attacked insects within 10 m of the mist nets. It was clear from the feeding buzzes (high pulse-repetition rates associated with attacks on airborne prey; Griffin et al. 1960) that the bats were foraging. Neither bat was caught in a mist net, because echolocating bats that are foraging are less often caught in mist nets than those flying to and from their roosts (e.g., Kunz and Kurta 1988). This illustrates the difficulty of associating bat activity with numbers of species or individuals.

Neither capture nor activity necessarily provides a complete picture of the bats in an area (e.g., Fenton et al. 1992), and neither is known to reflect population size in a predictable way (e.g., Kunz and Kurta 1988; Thomas and Laval 1988). Several factors affect captures of bats in mist nets. Some species are more adroit fliers than others (Aldridge and Rautenbach 1987), which may influence susceptibility to capture in mist nets. Our sample included relatively few rhinolophoids (Rhinolophidae, Nycteridae, and Hipposideridae), species often captured in the area when Tuttle traps

Fig. 5. Expected logarithmic series (Whittaker plots) of relative abundance. (*a*) All sites by habitat. Open symbols represent woodland and solid symbols riverine sites. Squares represent the Sabie sites, triangles the Letaba sites, and circles the Luvuvhu sites. (*b*) Data for combined riverine (+), woodland (×), and area sites (Sabie (squares), Letaba (triangles), Luvuvhu (circles)). Species ranks are shown, from most to least common, and the percentages of total individuals are depicted on a log scale.

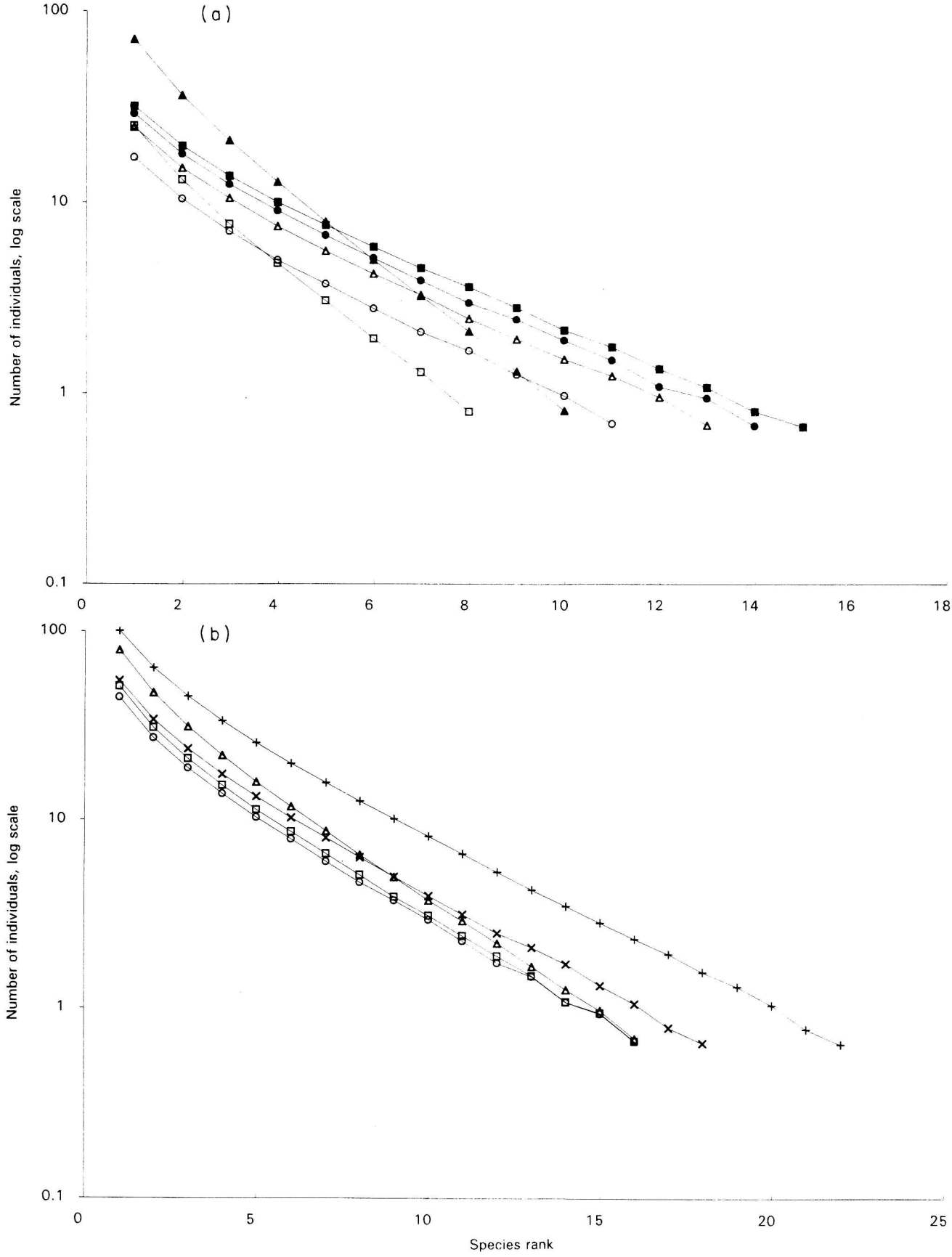


Table 2. Bat species diversity (α) and variance in riverine and dry woodlands along or near the Sabie, Letaba, and Luvuvhu rivers in the Kruger National Park (values are calculated from data in Table 1 using equations shown in the text).

	Diversity (α)	Variance	N_i	N_s
Sabie River				
Riverine	3.79	1.31	65	11
	4.88	2.38	33	10
	2.26	1.28	11	4
Woodland	1.97	0.77	23	5
	1.46	0.54	21	4
	3.98	2.64	14	6
Combined	4.48	1.23	167	16
CV	44.04			
Letaba River				
Riverine	3.51	1.23	57	10
	1.80	0.46	86	7
	3.49	1.52	31	8
Woodland	8.50	8.03	11	3
	3.68	1.36	52	10
	1.36	0.62	16	9
Combined	3.83	0.92	253	16
CV	81.46			
Luvuvhu River				
Riverine	3.14	1.41	25	6
	2.07	0.86	21	5
	5.07	2.14	49	12
Woodland	1.59	1.27	4	2
	2.34	0.91	28	6
	5.96	3.95	21	9
Combined	4.55	1.29	148	16
CV	33.04			
Riverine sites combined	5.09	1.18	378	22
Woodland sites combined	4.87	1.32	190	18

Note: CV is the coefficient of variation, N_i the number of individuals, and N_s the number of species.

(Tuttle 1974) are used instead of mist nets. Other bats, notably molossids, often forage above the canopy, so they are unlikely to be caught in mist nets set from the ground.

Other factors influence the picture of bat faunas provided by monitoring echolocation calls. Variation in the strengths of echolocation calls influences the detectability of bats by bat detectors (Ahlén 1981; Fenton and Bell 1981). Some species produce intense signals (e.g., many vespertilionids and molossids) and others much quieter ones (e.g., nycterids; Fenton and Bell 1981). At many of our sites, echolocation calls made it evident that molossids were abundant and active, yet these bats often formed a small portion of captured individuals (Table 1).

Roost availability affects bat distribution and diversity (Humphrey 1975). In some cases, such as at Letaba riverine sites, the captures of large numbers of *Tadarida* spp. probably reflected proximity to large colonies in bridges or buildings (Fenton et al. 1994). When foraging, larger species of *Tadarida*, (e.g., *T. midas*) may cover considerable distances ($\geq$20 km per night; Fenton and Rautenbach 1986), creating a roosting and foraging situation typical of refuging species (Hamilton and Watt 1970).

But roost availability does not necessarily explain the higher numbers of bats captured in riverine woodland. Along the Luvuvhu River, radio-tracking studies have shown that some bats which forage in riverine forest roost in dry woodland at least 5 km from the river (e.g., *Scotophilus borbonicus*), whereas others (e.g., *Rhinolophus hildebrandti*) do the opposite, albeit staying closer to the river (Fenton and Rautenbach 1986).

Bat-sampling programs should include captures and the monitoring of echolocation calls to obtain a more complete picture of the bat fauna and its patterns of habitat use (e.g., Fenton et al. 1992). In areas with fewer species, bat detectors can provide more detailed information about the specific identities of active bats there (e.g., Ahlén 1981; Fenton and Bell 1981) than would mist netting alone. In any case, the clear relationship between bat activity and insect availability illustrates the influence of prey on the activity patterns of insectivorous bats.

The availability of roosts and food limits the distribution and diversity of bats, which may also be affected by physiological constraints (Graham 1990). The abrupt latitudinal increase in the number of bat species as one moves south in North America reflects the bats' filling more trophic roles (Wilson 1974). Farther north in North America, bat diversity reflects habitat complexity, probably through roost availability (Humphrey 1975). Our data from Africa do not provide evidence of a similar clear impact of food or habitat complexity on bat diversity.

Acknowledgements

This study would not have been possible without the enthusiastic assistance of those participating in the Bat Conservation International Workshop: M. Ashby, G.S. Cumming, S. Ellis, J. Ferrigan, S. Gallo, M. Hovorka, C. Marks, G. Marks, A. Mercer, E. Muller, T. Murdoch, K. Saunders, M. Senkpiel, T. Tarlton, A. Tiessinga, L. Tomat, A. van Rychkenham, and G. Zippilli. We thank Dr. S.C.J. Joubert, Executive Director (Kruger National Park) and Dr. W.P.D. Gertenbach (General Manager, Nature Conservation) for permission to conduct this study, and Conservation Educationists I. Milne, M. Coetzee, K. van der Merwe, and B. Badenhorst for accompanying the group and sharing their extensive knowledge of the study areas. We also thank L. Acharya, J.L. Eger, and D.M. Syme, who read and commented on earlier drafts of the manuscript, which also benefitted from the attention of two anonymous reviewers.

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Appendix

The locations of the study sites were as follows: Sabie River riparian forests: 14 km east of Skukuza (24°57′S, 31° 41′E), 10 km west of Skukuza (24°58′S, 31°30′E), 5 km east of Skukuza (24°59′S, 31°38′E). Sabie dry woodland: 15 km northeast of Skukuza (24°52′S, 31°40′E), 17 km east-northeast of Skukuza (24°54′S, 31°41′E), 17 km southwest of Skukuza (25°03′S, 31°28′E). Letaba River riparian forests: 13 km north-northwest of Letaba (23°47′S, 31°33′E), 10 km north of Letaba (23°49′S, 31°35′E), 3 km east of Letaba (23°50′S, 31°37′E). Letaba dry woodland: 12 km northeast of Letaba (23°48′S, 31°37′E), 13 km west-northwest of Letaba (23°50′S, 31°26′E), 5 km south of Letaba (23°51′S, 31°34′E). Luvuvhu River riparian forest: 6 km west of Luvuvhu highwater bridge (22°26′S, 31°10′E), 6 km east of Luvuvhu highwater bridge (22°26′S, 31°17′E), 8 km east of Luvuvhu highwater bridge (22°26′S, 31°18′E). Luvuvhu dry woodland: 2 km south of the Luvuvhu highwater bridge (22°27′S, 31°13′E), 11 km west-southwest of Luvuvhu highwater bridge (22°31′S, 31°10′E), 5 km southeast of Punda Maria (22°44′S, 31°04′E).