Resource use by two morphologically similar insectivorous bats (*Nycteris thebaica* and *Hipposideros caffer*)

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Studies of morphologically dissimilar insectivorous bats have lead to the conclusion that morphology is the prime correlate of habitat use, and consequently of diet. This has lead to the prediction that morphologically similar bats should have similar diets. We examined the diet and morphology of two morphologically similar species, the slit-faced bat, *Nycteris thebaica*, and Sundevall's leaf-nosed bat, *Hipposideros caffer*, in the context of this prediction. Although both species foraged in the same habitat, they had distinctly different diets. The diet of *N. thebaica* consisted mainly of non-volant prey, primarily orthopterans and arachnids, and the diet of *H. caffer*, mainly of moths. Differences in wing design between the two taxa were small. The only significant difference was in aspect ratio. There were no differences in wing loading and wingtip shape ratio between the two species. The flying abilities reported for these two species are very similar, suggesting that these small differences in wing design do not translate into differences in flying ability, and cannot explain the dietary differences between these two species. On the other hand, there are marked differences in their prey detection systems which correspond to differences in their diets. *H. caffer* uses echolocation to detect the flapping wings of insect prey, whereas *N. thebaica* depends on prey-generated sounds (fluttering or scuffling) to locate its targets.

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Traditionally, studies of resource utilization by insectivorous bat communities have used wing morphology and/or echolocation call characteristics to predict differences in habitat use and, as a consequence, differences in foraging strategies and diets of insectivorous bats (McKenzie & Rolfe 1986; Aldridge & Rautenbach 1987; Norberg & Rayner 1987; Crome & Richards 1988; Fenton 1990). The theoretical basis of these predictions stems from studies of species with large differences in wing morphology and echolocation call design. For example, Aldridge & Rautenbach (1987) studied 26 sympatric insectivorous bat species and found that there was a significant correlation between wing morphology, echolocation call design, and foraging habitat, resulting in dietary differences. They concluded that insectivorous species with similar morphology would forage in similar habitats and therefore have similar diets.

However, ecological differences have been reported between species that are similar in morphology, echolocation call design, and habitat use (Saunders & Barclay 1992; Arlettaz & Perrin 1995; Hickey, Acharya & Pennington 1996; Arlettaz, Ruedi, Ibanez, Palmeirim & Hausser 1997). Saunders & Barclay (1992) suggested that morphology may influence the ecology of insectivorous bats at several levels. At one level, large morphological differences may influence foraging habitat by restricting some species to certain habitats, resulting in dietary differences. At another level, small morphological differences between species may influence the ability of the bat to exploit available prey within similar habitats, leading to dietary differences (Saunders & Barclay 1992). However, dietary differences might be caused by differences in the prey detection systems of morphologically similar species. Differences in such systems might make certain insect prey available to one species but not to another, even though they are morphologically similar and forage in the same habitat at the same time.

In this study we examined the diets of two morphologically similar insectivorous bat species (Aldridge & Rautenbach 1987, Group 2) that use very different prey detection systems. The slit-faced bat, *Nycteris thebaica* (E. Geoffroy 1813), and Sundevall's leaf-nosed bat, *Hipposideros caffer* (Sundevall 1846), co-exist in similar habitats over much of their range (Whitaker & Black 1976; LaVal & LaVal 1980; O'Shea & Vaughan 1980; Fenton 1985; Aldridge & Rautenbach 1987; Findley 1993) and have been observed sharing the same night roosts and foraging sites (LaVal & LaVal 1980; D.S. Jacobs pers. obs.). However, there are marked differences in their prey detection systems. *H. caffer* has a high duty cycle echolocation call and uses Doppler shifted echoes to detect the flapping wings of insect prey. *N. thebaica*, on the other hand, appears to depend upon prey-generated sounds, such as fluttering and scuffling, to detect insect prey (Fenton, Gaudet & Leonard 1983; Obrist, Fenton, Eger & Schlegel 1993). These differences in their prey detection systems might explain the differences in their patterns of habitat use. *H. caffer* usually uses continuous flight to capture airborne prey but will occasionally take prey from surfaces (Bell & Fenton 1984). *N. thebaica*, on the other hand, alternates between continuous flight and short flight from perches, and typically takes prey from surfaces (Aldridge, Obrist, Merriam & Fenton 1990).

If Aldridge & Rautenbach's (1987) conclusion is correct, then, given their similar morphology, these two species should have similar diets. Alternatively, the marked differences in the way they detect insect prey might result in their having very different diets. We specifically addressed two

questions. (1) Do *N. thebaica* and *H. caffer* use the same kind of insect prey? (2) Do differences that might exist in the diet of *N. thebaica* and *H. caffer* correspond to differences in their morphology, or to differences in their prey detection systems?

Methods

Study site

Field work was conducted in August 1995, at Mkuzi Game Reserve (32°E, 28°S) in the far north-eastern corner of the KwaZulu-Natal province of South Africa. Eleven specimens of *H. caffer* and nine of *N. thebaica* were captured using a hand-net. The two species were captured from two night roosts (Bube and Masinga Hides) which they shared. The hides were located approximately 500 m apart within a sand forest thicket. Sand forest is characterised by *Acacia, Albizia* and *Dichrostachys* trees, which seldom grow taller than 5 m and are often interspersed with grass. Bats were kept in cloth bags for approximately 1 h for the collection of faeces. Culled parts from insect prey were collected from the floor of the night roosts and used as part of a reference collection with which to compare insect fragments from bat faeces.

Morphology

The mass (to the nearest 0.5 g) and forearm length (FA, to the nearest 0.1 mm) were recorded for each bat. Bats were kept for at least 1 h after capture before being weighed, to ensure that their alimentary tracts were empty. The extended right wing of each bat was traced so that length measurements (see below) and wing area (including body area without the head, and the area of the uropatagium (after Saunders & Barclay 1992) could be measured using a Jandel digitizer with SigmaScan software (version 3.10). Wing measurements were repeated three times and the average used in statistical analyses.

Wing design was evaluated using wing span (B), wing area (S), wing loading ($WL = Mg/S$, where M is total body mass, g is acceleration due to gravity and S is wing area), and aspect ratio ($AR = B^2/S$; Norberg 1981). Wingtip shape ratio ($I = T_S/T_L - T_S$) was used to reflect flight manoeuvrability directly associated with the shape of the wingtip; rounded wingtips suggest greater manoeuvrability (Norberg & Rayner 1987). T_S is tip area ratio and T_L is the tip length ratio. $T_S = S_{hw}/S_{aw}$, where S_{hw} is handwing area, and S_{aw} is armwing area. $T_L = L_{hw}/L_{aw}$, where L_{hw} is handwing length, and L_{aw} is armwing length. Rounded or nearly square wingtips have high I values while pointed wingtips have low I values (Norberg & Rayner 1987).

Diet

Bat faecal pellets were teased apart under 70% ethanol and the arthropod exoskeleton fragments identified to order by comparing them to fragments obtained by crushing reference arthropod specimens (collected using a mercury vapour light trap) and culled parts of insects collected from the floor of the hides. A total of 185 and 413 faecal pellets were analysed for *N. thebaica* and *H. caffer*, respectively. The number of pellets varied considerably between individual bats (*N. thebaica*: 4–33 pellets, mean ± SD = 20.6 ± 10.8 and *H. caffer*: 6–70 pellets, mean ± SD = 37.5 ± 20.7). Prey items were classified as belonging to one of seven categories: Arachnida, Coleoptera, Blattodea, Orthoptera, Trichoptera, Lepidoptera, and all others. The last category consisted of unidentified insects as well as insects of other orders present in trace amounts. The percentage frequency of occurrence of each class of prey item in all faecal pellets collected for each bat, and the per cent volume that each category of prey item comprised of the total dietary volume for each bat, were calculated as described by Whitaker (1988). Only analyses performed on the per cent volume data are reported here because the per cent frequency data yielded essentially the same dietary patterns.

The food-niche breadth (FNB; Hickey *et al.* 1996) also called Simpsons's diversity index (Findley & Black 1983) for each species was calculated as:

$$FNB = 1/\sum_{i=1}^{n} P_i\, j^2$$

where P_i is the proportion of the i^{th} prey category of species j.

Two indices of niche overlap between N. thebaica and *H. caffer* were calculated: Schoener's (1970) niche overlap index;

$$overlap = 1 - (1/2)\left(\sum_{i=1}^{n} |P_i\, j - P_i k|\right)$$

where P_i is the proportion of the i^{th} prey category of species j and k, and Findley & Black's (1983), niche overlap index;

$$overlap = \sum_{i=1}^{n} P_{min}$$

where the lesser of the paired values for the proportional volume of each food category (P_{min}) is summed over all n food categories.

Statistical analysis

Morphology

Where the assumptions of normality and approximately equal variances held, t-tests were used to test differences in body mass, forearm length and wing design parameters. Where these assumptions did not hold, non-parametric Mann-Whitney tests were used (Zar 1996). The wing parameters of the two species were represented in aerodynamic space by plotting aspect ratio against wingloading, aspect ratio against the wingtip shape ratio, and wingtip length against wingtip area for all bats. To circumscribe each species' cluster of points, extreme points were connected by straight lines (after McKenzie & Rolfe 1986; Norberg & Rayner 1987; Crome & Richards 1988).

Diet

The percentage volume data obtained from faecal pellet analysis for both species was arcsine-transformed to correct for variance differences (Zar 1996), and was incorporated into a dietary data matrix. The dietary matrix consisted of the 20 individual bats (columns) and seven food categories (rows).

Cluster analysis was used to sort the bats into groups with similar diets. This was done as follows. The dietary matrix was converted to a triangular matrix of similarities between all possible pairs of bats by applying the Bray-Curtis measure

of similarity (Bray & Curtis 1957). The Bray-Curtis measure takes the form of:

$$\delta_{jk} = \sum|Y_{ij} - Y_{ik}| / \sum(Y_{ij} + Y_{ik})$$

where, Y_{ij} = the per cent volume for the i^{th} food category in the diet of the j^{th} bat; Y_{ik} = the per cent volume for the i^{th} food category in the diet of the k^{th} bat; δ_{jk} = dissimilarity between the diets of j^{th} and the k^{th} bats summed over all food categories. The Bray-Curtis measure is not affected by joint absences and was therefore deemed sufficiently robust for dietary analysis (Field, Clarke & Warwick 1982). The fact that this measure is unaffected by joint absences is important because of the large number of zeros usually present in a dietary data matrix. The inclusion of joint absences in the analysis has the effect of saying, for instance, that *N. thebaica* and *H. caffer* have similar diets because they both do not eat fruit.

The similarity matrix was subjected to a group-average sorting method which joins two groups of bats together at the average level of similarity between all members of one and all members of the other group. This results in a hierarchy of similarities which are displayed as a dendrogram in which the bats are clustered into distinct groups. The cut-off levels for each cluster are arbitrary and dependent on what is considered the most informative clustering pattern. For the purposes of this study, a level of 48% similarity was considered as the cut-off mark because it provided the most informative cluster pattern (Field *et al.* 1982).

The stability of the grouping in the dendrogram was checked by ordination because of the various disadvantages associated with dendrograms (Field *et al.* 1982). The preferred method of ordination is multi-dimensional scaling (MDS). Other ordination methods such as principal co-ordinate, reciprocal averaging, and correspondence analysis are not suitable because they are based on the eigenvalue method of principal component analysis, and are therefore relatively inflexible, particularly with regard to large numbers of zeros usually found in a dietary data matrix. MDS was used to obtain a simple ordination of the dietary data matrix in a specified number of dimensions. MDS represents the dissimilarity between each pair of bats as a distance in Euclidean space, and then seeks the best possible reconciliation of these inter-bat distances with the physical distances between these points on a two-dimensional representation of the ordination. A stress value is associated with MDS and can be thought of as the distortion involved in compressing the data into a smaller number of dimensions (Field *et al.* 1982). The result is a two-dimensional map of the relative positioning of the 20 individual bats based on the dissimilarity in their diets.

One-way analysis of similarities (ANOSIM) was performed on the groups identified by cluster analysis and MDS, to determine if significant differences in diet existed. Once data are represented as a dendrogram or ordination graph using cluster analysis or MDS the food category differences causing the patterns are lost (Field *et al.* 1982). This information was retrieved by performing similarity percentage analysis (*SIMPER*) on the untransformed dietary data matrix to assess which food categories were typical of the two groups, and which food categories were good discriminators between groups.

Cluster analysis, MDS, ANOSIM and SIMPER were performed with the aid of the PRIMER computer package (version 4.2; Plymouth Marine Laboratory 1994). General discussions of the above techniques can be found in Field *et al.* (1982), Clarke (1993), and Clarke & Warwick (1994).

Results

Interspecific differences in morphology

The plot of aspect ratio (*AR*) against wing loading (*WL*) and wingtip shape ratio (*I*) (Figure 1) indicates that *N. thebaica* and *H. caffer* were not separated by either *WL* or *I*. Some separation is apparent along the *AR* axis, with the *N. thebaica* individuals clustering at relatively low *AR* values (4.7–5.7) and all but one of the *H. caffer* individuals (C_{81}) clustering at relatively high *AR* values (5.7–6.6; Figure 1). The only significant difference between the two species was in aspect ratio (Table 1; Mann-Whitney, $U_{\alpha(2),9,11} = 94$, $p = 0.0007$). *Hipposideros caffer* had the larger aspect ratio. The heavier species, *N. thebaica*, has a slightly larger wingspan and wing area than *H. caffer* and, consequently, similar wing loading ($t = 0.9467$, $d.f. = 18$, $p = 0.37$). There was no significant difference in the

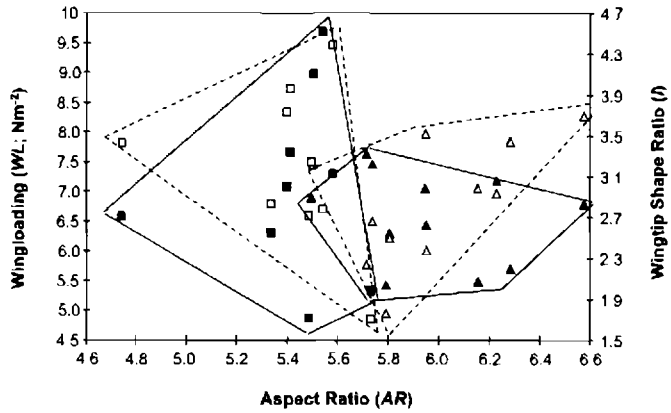

Figure 1 The distribution of *Nycteris thebaica* and *Hipposideros caffer* individuals in aerodynamic-space. Each polygon is the smallest that will encompass the range of *AR* × *WL* (solid lines) and *AR* × *I* (dotted lines) values for both species. The solid and open squares = *AR* × *WL* and *AR* × *I*, respectively for *N. thebaica*, and the solid and open triangles = *AR* × *WL* and *AR* × *I*, respectively for *H. caffer*.

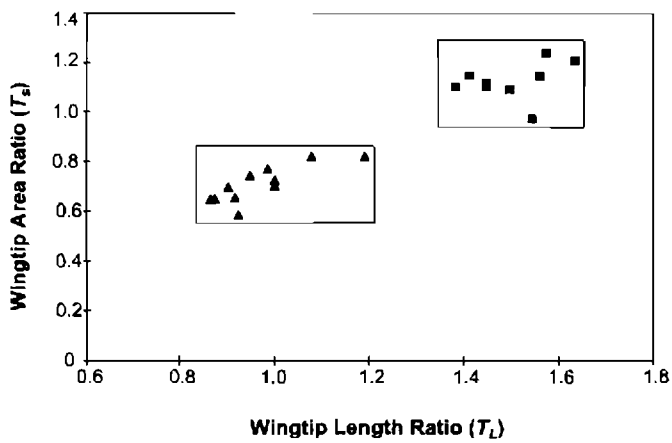

Figure 2 Representation in aerodynamic space of the component parts of the wingtip shape ratio (*I*) for *Nycteris thebaica* (solid squares) and *Hipposideros caffer* (solid triangles).

Table 1 Morphological characteristics (mean ± *SD*) of *Nycteris thebaica* and *Hipposideros caffer* captured at Mkuzi Game Reserve. a = *t*-test, b = Mann-Whitney test. NS = non-significant, 1 = $p < 0.05$, 2 = $p < 0.005$, 3 = $p < 0.001$, and 4 = $p < 0.0001$

Species	n	total[b3] mass, *M*/kg	forearm[b2] length *FA*/m	wing-[b1]span, *B*/m	wing[b3] area, *S*/m^2	aspect[b3] ratio, *A*	wing[aNS] loading, *Mg/S* Nm^{-2}	tip[b4] length ratio, l_L	tip[b4] area ratio, l_S	tip[aNS] shape ratio, *I*
N. thebaica	9	0.012 ± 0.0024	0.46 ± 0.012	0.30 ± 0.009	0.008 ± 0.0004	5.4 ± 0.3	7.1 ± 1.6	1.50 ± 0.084	1.13 ± 0.076	3.20 ± 0.80
H. caffer	11	0.009 ± 0.0007	0.48 ± 0.010	0.28 ± 0.013	0.007 ± 0.0004	6.0 ± 0.3	6.6 ± 0.8	0.972 ± 0.096	0.713 ± 0.075	2.85 ± 0.60

wingtip shape ratio between species ($t = 1.100$, $df. = 18$, $p = 0.29$). However, the plot of the two components of the wingtip shape ratio, wingtip length (T_l) and wingtip area (T_S), divided the two species into two distinct clusters, with *N. thebaica* having proportionately longer wingtips (Mann-Whitney, $U_{\alpha(2),9,11} = 99$, $p < 0.0001$), and wingtips of greater area (Mann-Whitney, $U_{\alpha(2),9,11} = 99$, $p < 0.0001$) than *H. caffer* (Figure 2).

Interspecific differences in diet

Composition, diversity, and niche overlap

The results of the faecal pellet analysis are summarised in Table 2. The only food category eaten in the same percentages by both species was Coleoptera. The diet of *N. thebaica* was dominated by Orthoptera (43.9%, mainly family Gryllidae) and Arachnida (35.9%), whereas that of *H. caffer* was dominated by Lepidoptera (79.5%). The food-niche breadth of *N. thebaica* was considerably wider than that of *H. caffer* (3.03 vs. 1.54; Table 2). The niche overlap between *N. thebaica* and *H. caffer* was 14.5% (Table 2).

Multivariate analysis of diet

At the 48% level of similarity, cluster analysis divided the 20 bats into two groups (Figure 3). The first group consisted of the 11 *H. caffer* individuals collected from both night roosts (Figure 3; roosts designated M = Masinga and B = Bube).

Table 2 Per cent composition by volume of diet for *Nycteris thebaica* and *Hipposideros caffer* at Mkuzi Game Reserve, South Africa

	H. caffer $n = 11^*$ (413)**	*N. thebaica* $n = 9^*$ (185)**
Coleoptera	7.9	8.0
Arachnida	0.7	35.9
Blattodea	0.4	5.7
Orthoptera	0.1	43.6
Trichoptera	1.0	1.3
Lepidoptera	79.5	2.7
All other	2.8	2.8
Food-niche breadth	1.54	3.03
Niche-overlap[1] (%)	14.5	
Niche overlap[2] (%)	14.5	

* number of bats sampled, ** number of faecal pellets analyzed. [1] Schoener (1970) niche overlap index; [2] Findley & Black (1983) dietary overlap index

The second group consisted of eight of the nine *N. thebaica* individuals collected from both night roosts. Bats from the different night roosts are randomly distributed in each of the two groups in Figure 3, indicating that there are no real differences in dietary composition for *H. caffer* or *N. thebaica* individuals collected from different night roosts. In subsequent analyses individuals from different night roosts were not considered separately.

The bat designated T_{B4} (Figure 3) could be considered a third group with a unique dietary composition, comprised of 17.5% Arachnida, 25% Lepidoptera, 32.5% Trichoptera and 25% of other insects. However, dietary composition for T_{B4} was based on the analysis of four faecal pellets, which was considerably less than the number of pellets analysed for the other *N. thebaica* individuals. In line with Whitaker (1988) we attributed the difference in the diet of T_{B4} to the small number of pellets analysed, and consequently considered T_{B4} to be an outlier of group 2 rather than a third group (Figure 3).

The associated stress level of the MDS ordination was very low (0.06) suggesting that the compression of the dietary matrix into 2-D space (Figure 4) accurately portrays the relationship between individual bats. As with cluster analysis, ordination divided the bats into two groups (Figure 4). However, one bat from each species (T_{B4} and C_{B2}) did not cluster

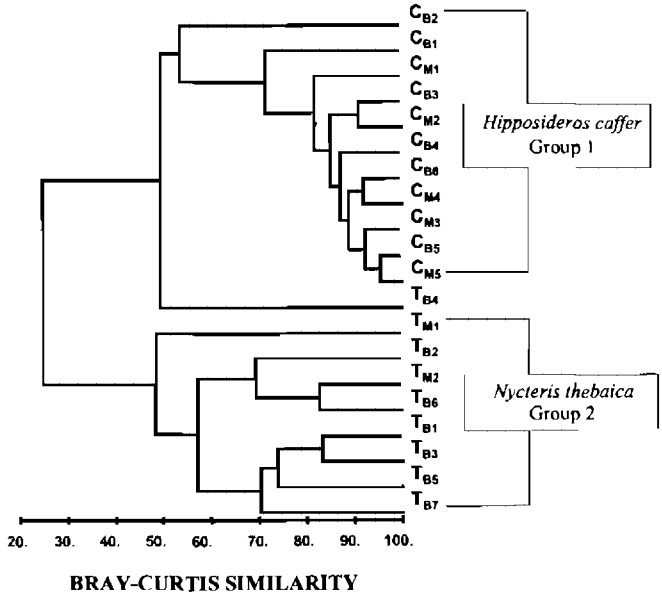

Figure 3 Dendrogram generated by cluster analysis of the percentage volume dietary data for *Nycteris thebaica* and *Hipposideros caffer* T = *N. thebaica*, C = *H. caffer*. B = Bube Hide, M = Masinga Hide. Numbers designate a specific bat.

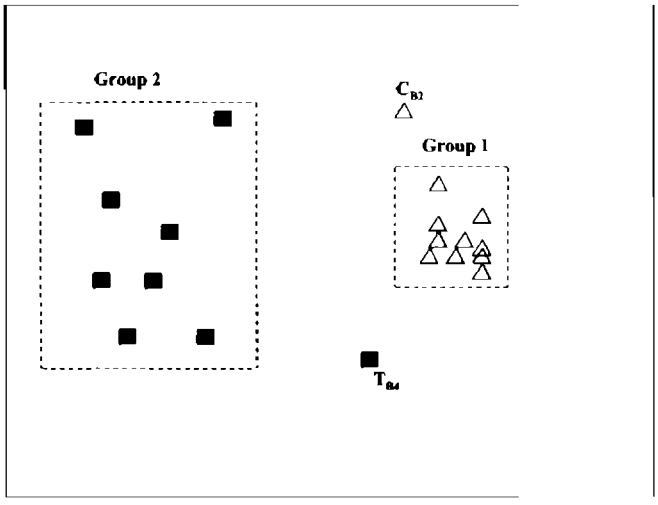

Figure 4 MDS ordination of the dietary data for *Nycteris thebaica* and *Hipposideros caffer*. Individual codes are as for Figure 3. Group 1 = *H. caffer* and Group 2 = *N. thebaica*.

with its respective species. As before, T_{B4} was classified as an outlier and not a separate group for the same reasons as outlined in the cluster analysis results. Coleoptera comprised 62.5% of the diet of C_{B2} and this is largely responsible for it not clustering with the other *H. caffer* individuals. Here too dietary analysis was based on a low number of faecal pellets (six) in comparison with other *H. caffer* individuals (11–70 pellets). We therefore considered C_{B2} to be an outlier of group 1 (*H. caffer*; Figure 4) rather than a separate group. Thus, with these exceptions, both cluster analysis and MDS separated the two species on the basis of diet. Furthermore, the diets of the two species were statistically different (ANOSIM: R-statistic = 0.891, $p < 0.001$).

Similarity percentage analysis (SIMPER) determined that *H. caffer* individuals were 77.93% similar in dietary composition, *N. thebaica* individuals were 54.04% similar in dietary composition, and the two species were 72.97% dissimilar in dietary composition (Table 3). Repeating the analysis without the outlier T_{B4} resulted in an increase in the within-group similarity for the *N. thebaica* individuals to 60.35%. The within-group similarity of the *H. caffer* individuals remained unchanged, but the dissimilarity in dietary composition between the two species increased slightly to 75.78%. The analysis was not repeated with the omission of C_{B2} as we deemed it to be uninformative because the two species ate similar quantities of Coleoptera (Table 2).

SIMPER analysis identified Lepidoptera (62.41%) and Trichoptera (16.52%) as the major categories defining the dietary niche of *H. caffer* (Table 3). The Arachnida (40.55%) and Orthoptera (39.4%) were identified as the most important food categories defining the niche exploited by *N. thebaica*. The relative percentage dissimilarity between species identified Lepidoptera (62.41%) as the most important food category separating the niche space occupied by each species, followed by Orthoptera (21.51%) and Arachnida (19.95%; Table 3). Repeating the analysis without the outlier T_{B4} yielded similar results to those presented in Table 3, with the exception that the Orthoptera now contributed a greater percentage (45.94%) to the dietary composition of *N. thebaica* than did the Arachnida (38.17%).

Table 3 Results of SIMPER analysis of the diets of *Nycteris thebaica* and *Hipposideros caffer*. Percentages in columns indicate the relative importance of the food categories contributing to either similarity within species or dissimilarity between species. Percentages in parentheses indicate either similarity within or between species

	Av. similarity within species groups		Av. dissimilarity between species groups
Food categories	*H. caffer* (77.93%) Per cent	*N. thebaica* (54.04%) Per cent	*H. caffer / N. thebaica* (72.97%) Per cent
Coleoptera	14.80	4.45	9.27
Arachnida	1.94	40.55	19.95
Blattodea	0.70	2.98	4.52
Orthoptera	—[a]	39.90	21.51
Trichoptera	16.52	—[a]	10.19
Lepidoptera	62.41	5.44	29.71
All other	3.24	6.02	4.85

[a] Present in only very small quantities

Discussion

Dietary differences

The substantial contribution of arachnids to the diet of *N. thebaica*, and the lack of Diptera in the diet of this bat is in marked contrast to the findings of other authors (Whitaker & Black 1976; LaVal & LaVal 1980; Fenton 1985). This suggests that *N. thebaica* may exhibit dietary plasticity depending on prey availability. Whitaker & Black (1976) found that insect larvae comprised 23.2% of the diet of *N. thebaica*. We found larvae present in only very small amounts and therefore included larvae in the 'all other' category. Our findings for *H. caffer* are in general agreement with those of other authors (Whitaker & Black 1976; Fenton 1985; Aldridge & Rautenbach 1987; Dunning & Krüger 1996), but differ from those of Aldridge & Rautenbach (1987) who found that Trichoptera comprised 50% of the diet of *H. caffer*, and Fenton (1985) who did not find any evidence of Trichoptera in the diet of *H. caffer*.

Our study highlights two of the potential drawbacks associated with faecal pellet analysis: (1) the bias that too small a sample of faecal pellets can cause, and (2) the under-representation of soft-bodied invertebrates in faeces. The individuals classified as outliers by cluster analysis and MDS (Figures 3 and 4), illustrate the bias associated with a too small faecal sample. This suggests that a minimum of 10 pellets per individual should be analysed to avoid such biases. The second difficulty is illustrated by the contrasting findings of our study and Whitaker & Black's (1976) study of the dietary composition of *N. thebaica*. Whitaker & Black's (1976) ana-lyses were based on stomach contents, and it is possible that because faeces are the end products of digestion, soft-bodied invertebrates were completely digested, and therefore under-represented in our study. Alternatively, the lack of larvae

could have occurred as a result of variation in seasonal abundance of larvae and would thus likely present a bias in the data, since sampling was only carried out during the month of August and not during the entire year. These caveats aside, the dietary differences between *N. thebaica* and *H. caffer* are large enough for us to draw conclusions about the ecological relationships between the two species that should not be invalidated by the potential increased importance of insect larvae in the diet of *N. thebaica*.

Our finding that *N. thebaica* has a greater food-niche breadth than *H. caffer* is supported by other studies (Whitaker & Black 1976; Fenton 1985), although actual values differed (*N. thebaica* FNB = 4.79, *H. caffer* FNB = 1.56, Whitaker & Black 1976; *N. thebaica* FNB = 2.0, *H. caffer* FNB = 1.94, Fenton 1985). The niche overlap reported by Whitaker & Black (1976) of 28% was slightly larger than our finding of 14.5%, while the niche overlap of 60% calculated from Fenton (1985) differed substantially from our findings. Both methods employed to calculate niche overlap agreed well when the dietary data were distributed amongst more than three food categories. At low numbers of food categories (i.e. low dietary diversity, e.g. Fenton 1985), Findley & Black's (1983) method resulted in a higher nich overlap value (80%) than that of Schoener (1970; 60%).

The dietary data demonstrate that these two species have very different diets (Tables 2 and 3, Figures 3 and 4) and consequently do not support Aldridge & Rautenbach's (1987) conclusion that bats foraging in similar habitats would have similar diets. The major difference between the diets of *N. thebaica* and *H. caffer* is that the former specialises on non-volant arthropods (orthopterians and arachnids) while the latter specialises in volant arthropods (moths).

Morphological similarity and foraging strategy

The major problem in having examined only two species is that it is difficult to determine how similar they are to each other, relative to other bat species. One way to do this is to compare them to a larger set of species by calculating relative distances in wing design parameters between species pairs. Aldridge & Rautenbach's (1987) study of 26 syntopic bat species, based on morphological and echolocation characteristics, clustered both *N. thebaica* and *H. caffer* into the same group, suggesting that, relative to other bat species, these two species are similar in wing design. Our results support this finding and show just how similar these two species are in terms of wing design. There was no significant difference in wingloading or wingtip shape, and although there was a significant difference in aspect ratio, the difference was small (*N. thebaica* $\bar{x} = 5.4$ $SD \pm 0.3$, *H. caffer* $\bar{x} = 6.0$ $SD \pm 0.3$).

This morphological similarity is reflected in the similar flight patterns reported for these two species. Both are capable of hovering (LaVal & LaVal 1980; Bell & Fenton 1984) and use a combination of aerial pursuit and gleaning to capture prey (LaVal & LaVal 1980; Fenton, Gaudet & Leonard 1983; Bell & Fenton 1984; Fenton 1985; 1986; Aldridge & Rautenbach 1987; Norberg & Rayner 1987). Furthermore, *H. caffer* is known to momentarily touch down on a surface with feet and wrists to capture prey (Bell & Fenton 1984). This suggests that *H. caffer* should also be able to exploit non-volant arthropods.

Thus, the interspecific differences in flight morphology (Table 1) between the two species do not translate into any known differences in flying ability. Furthermore, although both species display similar flying abilities, there are marked differences in their typical patterns of habitat use which cannot be adequately explained by the small differences in their aspect ratios. *H. caffer* usually uses continuous flight to capture airborne prey and will only occasionally take prey from surfaces (Bell & Fenton 1984). *N. thebaica*, on the other hand, alternates between continuous flight and short flight from perches, and typically takes prey from surfaces (Aldridge, Obrist, Merriam & Fenton 1990). Consequently, it seems unlikely that differences in flight morphology adequately explain differences in diet or differences in patterns of habitat use between the two species. An alternative explanation is interspecific differences in prey detection.

There are major differences in the prey detection systems of these two species. The echolocation calls of *H. caffer* are produced at high duty cycle, dominated by one narrow band frequency of short duration (7 ms; Fenton & Bell 1981; Fenton 1986; Aldridge & Rautenbach 1987). The generation of short calls that span an insect's wing beat cycle means that *H. caffer* receives a blend of weak and strong signals at different Doppler-shifts (Bell & Fenton 1984; Fenton 1985; 1990; Link, Marimuthu & Neuweiler. 1986), enabling accurate detection of a flying insect (or one that is stationary but flapping its wings). The dependence on wing flapping to detect insect prey (Bell & Fenton 1984) might explain why *H. caffer* typically uses continuous flight and only occasionally takes prey from surfaces.

N. thebaica, on the other hand, is known to use acoustic stimuli emanating from prey to detect targets (Fenton *et al.* 1983) and may not use its echolocation to detect, track or assess prey. Obrist *et al.* (1993) have shown that the pinnae of *H. caffer* are mechanically tuned to the frequencies dominating its echolocation calls, whereas the pinnae of *N. thebaica* are tuned to the lower frequency sounds (below those dominating its echolocation calls) associated with the scuffling and fluttering sounds of prey movement. This is supported by the large numbers of gryllid cercii in some of the *N. thebaica* faecal samples, suggesting that this species may be exploiting male cricket mating calls for target detection. The ability of *N. thebaica* to home in on prey-generated sounds would enable *N. thebaica* to feed on a greater variety of insect prey (including more non-volant prey) than would the Doppler-shift echolocation system of *H. caffer* which is specific for the detection of fluttering prey. This is reflected in *N. thebaica* having a greater food-niche breadth than that of *H. caffer* (Table 2).

Thus, it appears that differences in morphology are not the primary cause of the large dietary differences between *N. thebaica* and *H caffer*. The only difference in wing design between the two species is the lower aspect ratio of *N. thebaica*. This cannot explain the preponderance of non-volant prey in its diet and of volant prey in the diet of *H. caffer*. In contrast, there is a strong correspondence between the differences in the prey detection systems of the two species and differences in their diet. These two species therefore represent an exception to the rule (advanced by Aldridge & Rautenbach

1987) that morphologically similar bats should have similar diets.

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