
A Comparative Analysis of Specialization and Extinction Risk in Temperate-Zone Bats

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Abstract: *Identifying the factors that influence the extinction risk of animals is essential in conservation biology because they help identify endangered species and provide the basis for their preservation. We present a comparative study that uses data from the literature on the diet and morphological specialization of European and North American bat species to investigate the effect of specialization on extinction risk. We focused on bats because many species are endangered and their high ecological diversity makes them a good model system for our purpose. After correcting for phylogenetic inertia, we compared the influence of dietary niche breadth as a measure of food specialization and of wing morphology as a measure of foraging strategy, habitat adaptation, and migratory ability on the vulnerability of 35 insectivorous bat species. Our results do not support the hypothesis that a narrow dietary niche breadth is related to high extinction risk. Instead they suggest that habitat specialization, which is reflected in wing morphology, influences the extinction risk of bats. Our study shows that an initial risk assessment in temperate-zone bats could be based on data of wing morphology but not on dietary data obtained from fecal analyses.*

Key Words: Chiroptera, diet, fecal analysis, niche breadth, wing morphology

Un Análisis Comparativo de la Especialización y el Riesgo de Extinción en Murciélagos de Zonas Templadas

Resumen: *La identificación de factores que influyen en el riesgo de extinción de animales es esencial en biología de la conservación porque ayudan a identificar especies en peligro y proporcionan las bases para su preservación. Presentamos un estudio comparativo que utiliza datos de la literatura sobre la dieta y la especialización morfológica de especies europeas y norteamericanas de murciélagos para investigar el efecto de la especialización sobre el riesgo de extinción. Nos centramos en murciélagos porque muchas especies están en peligro y su alta diversidad ecológica los hace un buen modelo para nuestro propósito. Después de corregir la inercia filogenética, comparamos la influencia de la amplitud del nicho dietético como una medida de la especialización alimenticia y la morfología alar como una medida de estrategia de forrajeo, adaptación de hábitat y habilidad migratoria sobre la vulnerabilidad de 35 especies de murciélagos insectívoros. Nuestros resultados no sustentan a la hipótesis de que nichos dietéticos de amplitud estrecha están relacionados con alto riesgo de extinción. En cambio, sugieren que la especialización de hábitat, que se refleja en la morfología alar, influye en el riesgo de extinción de murciélagos. Nuestro estudio indica que una evaluación inicial de riesgo en murciélagos de zonas templadas podría basarse en datos de morfología alar, pero no en datos de la dieta obtenidos de análisis fecales.*

Palabras Clave: amplitud de nicho, análisis fecal, Chiroptera, dieta, morfología alar

Introduction

Identifying the traits that separate species with a high extinction risk from taxonomically related but not en-

dangered species is a key issue in conservation biology. Therefore, recent studies have made considerable efforts to identify the relevant factors leading to higher extinction risks (Laurance 1991; Landweber & Dobson 1999;

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Paper submitted April 4, 2003; revised manuscript accepted January 22, 2004.

Owens & Bennett 2000; Purvis et al. 2000; Cardillo & Bromham 2001; Jones et al. 2001; Crooks 2002; Dulvy & Reynolds 2002; Duncan et al. 2002; Harcourt et al. 2002).

The main factors that influence extinction risk are body size and degree of habitat and/or diet specialization (Owens & Bennett 2000; Purvis et al. 2000). Large body size generally results in a low reproduction rate and hence in a low ability to recover from population declines (Owens & Bennett 2000; Purvis et al. 2000). At the same time, large animals often have higher susceptibility to human persecution (Owens & Bennett 2000; Cardillo & Bromham 2001; Duncan et al. 2002). The second significant factor influencing extinction risk is niche differentiation. Through specialization on certain diets (i.e., niche breadth), foraging strategies, or habitat types, species avoid competition. But specialization also leads to an increment in the dependence on some specific resources (Begon et al. 1996). Hence, when relevant resources decline, specialists are likely to suffer more than generalists because generalists can switch to other available resources (Wilson et al. 1999; Harcourt et al. 2002; Hopkins et al. 2002).

A positive relationship between habitat specialization and extinction risk has been found in various taxa (e.g., insects: Hughes et al. 2000; reptiles: Foufopoulos & Ives 1999, birds: Owens & Bennett 2000; mammals: Harcourt et al. 2002). However, the relationship between dietary specialization and extinction risk is less clear. A few researchers have investigated the association between dietary specialization and conservation status but have provided contradictory results (Laurance 1991; Reed 1995; Wilson et al. 1999; Harcourt et al. 2002; Hopkins et al. 2002).

Their high ecological diversity makes bats (Microchiroptera) a good model for investigating the influence of foraging strategy and dietary specialization on extinction risk. Microchiroptera have a worldwide distribution, and the nearly 1000 species occupy a variety of ecological niches (Kunz & Pierson 1994; Hutson et al. 2001). Furthermore, bats are of high conservation interest because many species are endangered. Factors such as habitat destruction, pesticide use, and direct human persecution are thought to be the main causes for the observed population declines (Kunz & Racey 1998; Hutson et al. 2001). Some researchers have conducted comparative studies to investigate the factors influencing extinction risk in bats (Fenton 1997, 2003; Jones et al. 2003). To our knowledge, however, no publication has investigated quantitatively the relationship between dietary specialization and extinction risk in bats, although the necessary data are available for European and North American species.

The feeding behavior of bats is difficult to assess directly, owing to their nocturnal lifestyle. Instead, fecal analysis, as the standard noninvasive method, has been widely applied to gain information about the diet of bats (McAney et al. 1991). Furthermore, the foraging strategies

of bats are reflected by measurable characteristics of their wing morphology (Norberg & Rayner 1987). Among the comparatively well-studied insectivorous species living in Europe and North America, variation and pronounced differences in wing morphology exist. Species specializing in hunting flying insects in open space (aerial insectivores) usually fly fast and have relatively narrow and pointed wings. Hence, they have high wing loading values and aspect ratios but low wingtip areas and wingtip indices (Norberg 1986; Norberg 1987; Bininda-Emonds & Russell 1994; Norberg 1994). By contrast, bats that specialize in hunting insects close to the vegetation or the substrate (gleaners and water-surface foragers) usually fly slowly and have relatively broad wings (Baagøe 1987; Norberg & Rayner 1987; Fenton & Bogdanowicz 2002). Thus, compared with aerial insectivores, species foraging in cluttered space generally have low wing loading values and aspect ratios but high wingtip indices and wingtip areas.

Bats with broader wings have higher maneuverability but increased costs for commuting over long distances (Norberg & Rayner 1987; Neuweiler 1989; Norberg 1994). As a consequence, wing morphology may restrict bats to certain habitat types and possibly to certain prey taxa. Furthermore, wing morphology influences migratory behavior (Baagøe 1987; Norberg 1987; Fenton & Bogdanowicz 2002; Miller-Butterworth et al. 2003). For example, gleaners often hunt in forests and generally have low migration tendencies, whereas aerial insectivores cannot exploit flightless prey within vegetation and often migrate long distances.

Morphological and dietary specialization probably promoted the enormous adaptive radiation in bats (Neuweiler 1993; Arita & Fenton 1997; Miller-Butterworth et al. 2003). At present, however, specialization may be disadvantageous for the survival of bats in an environment affected by humans through fragmentation and rapid habitat alteration. Some previous work suggests that food specialization in bats (i.e., dietary niche breadth) may be correlated with the rarity of a species or its vulnerability to extinction (Sierro & Arlettaz 1997; Vaughan 1997). This idea assumes that specialized species can rarely switch prey types and that specialists, if the preferred prey becomes scarce, face an elevated extinction risk. Such a positive association between dietary specialization and rarity has been demonstrated for specialized phytophagous insects and highly monophagous mammals such as the Giant Panda (*Ailuropoda melanoleuca*: Carter et al. 1999; Hopkins et al. 2002) or the black-footed ferret (*Mustela nigripes*: Powell et al. 1985; Dobson & Lyles 2000).

Here, we present a comparative analysis of literature data on dietary specialization (niche breadth), wing morphology, and World Conservation Union (IUCN) conservation status (as a measure of extinction risk) of insectivorous temperate-zone bats. We restricted our analysis

to insectivorous bats living in Europe and North America because data on their morphology, diet, and extinction risk are better than those available for most tropical bat species. We obtained the relevant data for 35 bat species. We corrected for phylogeny, assessed the influence of dietary and morphological specialization on extinction risk, and tested whether species with specialized diets or wing morphology are threatened more often than generalists. Based on our results, we discuss which factors are likely determinants of extinction risk in temperate-zone microchiropterans and whether an initial risk assessment in bats could be based on wing morphology and/or diet. These two types of data are readily available from living animals and are, owing to the cryptic life of bats, more easily obtainable than detailed observations of habitat use.

Methods

Comparison of Different Fecal Analysis Methods

Using web-based search engines (Web of Science, Wildlife Worldwide, and Zoological Records) and references obtained directly from published studies, we searched for dietary analysis studies on European and North American insectivorous bats. We found 44 published fecal analysis studies of 35 bat species (for references, see Appendix 1). Because more fecal analysis data were available for European than for North American bats, the number of species in our data set is biased toward European bats (23 vs. 12 species). Some of the 44 studies contained only data from one study site in a specific year. Others contained data from several sites collected either in the same or in different years. To standardize studies, we defined a single "observation" for a given bat species to be the data collected from one particular site in 1 year. We obtained 125 observations for the 35 bat species. The number of observations per species ranged from 1 to 19; the average was 3.6 (sample sizes and diet volumes available from the authors upon request). The analyzed studies classified prey to the level of order in the case of adult insects and to the level of class for all the other prey types (e.g., juvenile stages).

In addition to their different methods of collecting samples, the 44 studies also differed in methods of analysis. Depending on the method applied, data were given as relative frequency of prey types (%*F*), frequency of occurrence of different prey types in bat droppings (%*O*), or volume percentage per prey type (%*V*). Percentage of occurrence (%*O*) is defined as the number of findings per prey type (N_i ; for $i = \text{category } 1 \text{ to } n$), divided by the number of analyzed droppings (D), multiplied by 100 (total $n > 100\%$) (McAney et al. 1991). Percentage frequency (%*F*) is defined as the number of findings of a particular prey type (N_i), divided by the total number of

occurrences of all prey types, multiplied by 100 (total $n = 100\%$) (McAney et al. 1991). Finally, percent volume (%*V*) is defined as the estimated volume per prey type in all analyzed fecal pellets (total $n = 100\%$) (Whitaker 1988).

To create a homogeneous data set, we converted %*O* values into %*F* values:

$$\%O_i = \frac{N_i}{D} \quad (1)$$

and

$$\%F_i = \frac{N_i}{\sum_{i=1}^n N_i} \quad (2)$$

From Eqs. 1 and 2 the result becomes

$$\%F_i = \frac{\%O_i \cdot D}{\sum_{i=1}^n (\%O_i \cdot D)} \quad (3)$$

For a given number of analyzed droppings (D) %*F* can be calculated as follows:

$$\%F_i = \frac{\%O_i}{\sum_{i=1}^n (\%O_i)} \quad (4)$$

Converting %*F* to %*V* values is not easy because the way the two values are inferred from fecal samples differs fundamentally. Ten of the 44 publications presented their results (which included 17 prey taxa) both as %*F* and %*V* for a given bat species (Kunz & Whitaker 1983; Bauerova & Ruprecht 1989; Whitaker & Clem 1992; Whitaker & Lawhead 1992; Sample & Whitmore 1993; Kunz et al. 1995; Lacki et al. 1995; Whitaker et al. 1996; Whitaker et al. 1997; Rydell & Petersons 1998). This allowed us to estimate the relationship between %*V* and %*F* values. The different ways of inferring %*F* and %*V* incur the possibility of method-specific biases (Robinson & Stebbings 1993) that are connected to the fact that different taxa have different detectability in feces and differ markedly in size (e.g., larger prey could occupy more space than smaller insects). To evaluate whether method-specific biases exist in our data set, we tested whether prey taxon and/or publication influenced the estimated values of %*V*. First, we searched for the curve estimation with the best fit by choosing, among all significant curve-estimation models, the one with the highest R^2 . Subsequently, in a mixed model we tested the effects taxon and publication on the model as random variables. The parameter estimations and mixed-model variance analyses were performed with generalized linear models (GLM), which then were used to convert all data into one cross-comparable form (%*V*).

Classification of Species-Specific Dietary Niche Breadth and Wing Morphology

We estimated dietary niche breadth from the data with Levin's index (Krebs 1998):

$$B = \frac{1}{\sum_{i=1}^n (\%V_i^2)}, \quad (5)$$

where B is Levin's measure of niche breadth and $\%V_i$ is the volumetric proportion of prey items of a category i from $i = 1$ to n categories. Dietary niche breadth was calculated with the average of all "observations" of a specific species. For simplicity, we used $\%O$, $\%F$, and $\%V$ values between 0 and 1 instead of percentage values. The relative proportion of prey categories ($\%V$) was log-transformed (Aitchinson 1982) prior to further analysis, except for the calculation of Levin's index.

Morphological Data

For the analysis of wing morphology, we used data from the most comprehensible and complete study available, the standard publication by Norberg and Rayner (1987). We used this data set exclusively because the authors present already standardized values of wingspan, wingtip length, and wingtip area. Furthermore they introduce the wingtip index, which describes the shape of the wings. Applying a single data set avoids biases, which can be caused by comparing several studies that use different measurement methods. However, by restricting our analysis to the data set of Norberg and Rayner (1987), we missed, completely or partly, morphological data for 6 of our 35 study species (*Eptesicus nilssonii*, *Hypsugo savii*, *Pipistrellus kublii*, *Rhinolophus blasii*, *Rhinolophus mehelyi*, and *Tadarida teniotis*).

Comparison of Dietary Niche Breadth, Wing Morphology, and Conservation Status

The assessment of extinction risk was taken from the 2001 IUCN Red Data Book for microchiropteran bats. This standard publication categorizes species either as lower risk-least concern (LRlc), lower risk-near threatened (LRnt), vulnerable (VU), or endangered (EN) (Hutson et al. 2001). To ensure that inclusion in risk categories reflects real endangerment and not limited knowledge, we excluded species listed by the IUCN as data-deficient (DD). Of the 35 European and North American bat species analyzed in our study, 22 were categorized by the IUCN as LRlc, 5 as LRnt, 6 as VU, and 2 as EN. The eight species categorized by the IUCN as threatened (EN and VU) were all assigned to their respective category because of population declines in the past or predicted for the future (Hutson et al. 2001). We treated the above levels as continuous characters, varying from 0 to 3. This assumes a continuous spectrum of extinction risk

underlying the IUCN categories, which represent discrete approximations (for a similar approach, see Purvis et al. 2000).

To account for the limited number of species, we first conducted a factor analysis on the morphology data to reduce the number of variables. All following statistical tests were performed on phylogenetic independent contrasts (Felsenstein 1985; Pagel 1999), generated with the CAIC software (Purvis & Rambaut 1995) and on data not corrected for phylogeny (treating the species as independent). We used the phylogeny provided by Jones et al. (2002) to infer the taxonomic relationship between the species used in this analysis. Branches were set to equal length (Garland et al. 1992). We used multiple regression together with model simplification to find the minimum adequate model (MAM) forcing the regression through the origin for the phylogenetic contrasts (Purvis & Rambaut 1995). Therefore, all variables were initially introduced as predictors. The predictor with the lowest reduction in variance was dropped at each step until all remaining predictors were significant. This way, we determined whether wing morphology, body size, and diet were correlated with conservation status. The statistical analyses were programmed on SAS-lab statistical package version 6.12 for Mac-OS (SAS Institute 1993).

Results

Fecal Analysis Methods and Dietary Niche Breadth

Comparing $\%F$ to $\%V$ values revealed that a cubic relationship yielded the best fit (Fig. 1). In a mixed model, we tested for the influence of the random effects of prey taxa and publication on the estimation curve (Table 1) and used the model to produce corrected estimates of the predictor variables of $\%F$ (Fig. 1). The mixed model showed that neither prey taxa nor publication had a significant influence on the model (Table 1).

We used another mixed model to test whether bat species had specific niche breadths, irrespective of the publication from which the data were taken (fixed effect, species: $F_{33,48} = 4.75$, $p = 0.0001$; random effect: publication estimate \pm SE = 0.09 ± 0.17 , $Z = 0.51$, $p = 0.61$). This shows that publication had no significant effect on niche breadth. Besides publication, sample size (sampling effort) theoretically could bias the dietary niche breadth of a species. For example, niche breadth might increase with increasing sample size. However, a generalized linear model (GLM) revealed that, in our data set, sample size had no significant effect on dietary niche breadth ($n = 35$, $F_{1,1.07} = 0.48$, $p = 0.5$). This suggests that, compared with the effect of species, sampling effort is negligible in our data set.

In two mixed models we tested the effect of dietary niche breadth on extinction risk, once weighting the

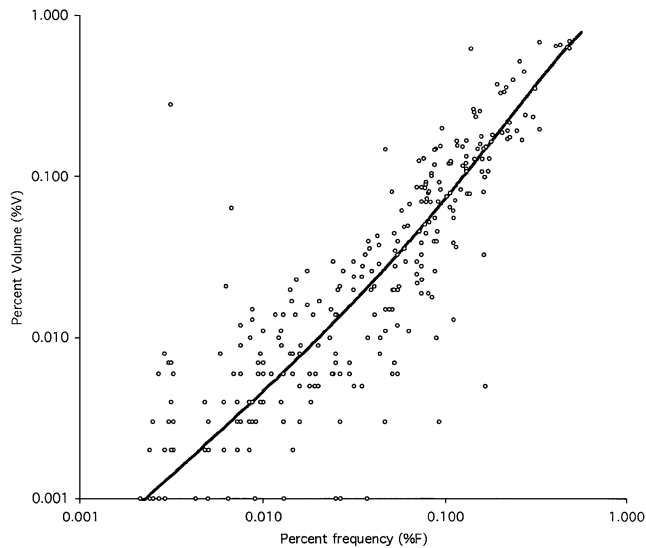


Figure 1. Curve estimation ($y = -2.59x^3 + 3.20x^2 + 0.43x$) of bat prey type inferred from fecal-analysis studies with results as percentage of frequency of prey types (%F) and percentage of volume per prey type (%V).

model with numbers of observations per species and once without. As suggested by the lack of a correlation between sampling effort and niche breadth, weighting for sample size per species had no significant effect ($N_{\text{species}} = 35$, weighted: niche \pm SE = 0.03 ± 0.11 , $T = 0.3$, $p = 0.76$; unweighted: niche \pm SE = 0.004 ± 0.10 , $T = 0.04$, $p = 0.96$)

Morphology and Correlates of Extinction Risk

Our cluster analysis of the morphological variables separated these into two distinct clusters. The first cluster contained size-dependent variables and the second cluster size-independent measures (Table 2).

In the multiple-regression analysis we included the two obtained clusters of morphology data and Levin's index of dietary niche breadth. Only the cluster containing the

Table 1. Mixed-model analysis of the data on bat fecal analysis^a to infer the best-fit curve estimation.^b

Effects ^c	Estimate \pm SE	p
Fixed effects		
%F	0.43 ± 0.12	0.0005
%F ²	3.20 ± 0.51	0.0001
%F ³	-2.59 ± 0.41	0.0001
Random effects		
prey taxon	0.001 ± 0.001	0.54
publication	0.001 ± 0.001	0.08

^a $N_{\text{samples}} = 290$, including 17 bat taxa in 10 publications.

^bSignificance level of coefficients and estimate of the slopes.

^cFrequency of prey types, %F.

Table 2. Cluster analysis^a separating bat morphological variables in to two clusters.^b

Cluster	Members	Scoring	% of total variance
1	mass	0.27	55
	wingloading	0.32	
	aspect ratio	0.31	
	wingtip length	0.27	
2	wingtip area	0.6	71
	wingtip index	0.6	

^a $N_{\text{samples}} = 29$; max Eigenvalue = 1; intercluster correlation = -0.27 .

^bScoring of variables and cumulative proportion of original variance explained by clusters.

size-independent morphological variables correlated significantly with the IUCN category. This cluster contained the variables wingtip index and wingtip area. The cluster increased significantly with higher extinction risk of a species, which means that species with a high wingtip index (i.e., rounded wings) and large wingtip areas (i.e., broad wings) tended to be higher in conservation status. This pattern was consistent, irrespective of whether the data were contrasted phylogenetically or whether species were treated as independent (Table 3). Dietary niche breadth remained nonsignificant. Thus, the only significant predictor of extinction risk was the cluster of size-independent wing measures (Table 3).

To check whether consumption of particular prey taxa correlated with IUCN status, we examined the significance of the log-converted prey-consumption data. In an exploratory procedure, we tested each prey taxon as a separate predictor. This was done with phylogenetic contrasts and treating species as independent variables. Our analysis resulted in nonsignificant correlations for all prey taxa (data not shown), which is in accordance with a lack of correlation between dietary specialization and IUCN status.

Table 3. Multiple-regression model testing the effect^a of cluster 1,^b cluster 2,^c and Levin's index of niche breadth on extinction risk in bats.

	Without phylogenetic correction ^d			With phylogenetic correction ^e		
	r	T	p	r	T	p
Cluster 1	-0.02	-0.16	0.88	-0.21	-0.64	0.53
Cluster 2	1.05	3.45	0.002	1.6	4.42	0.0008
Niche breadth	-0.1	-0.6	0.56	0.02	0.16	0.87

^aRegression coefficient (r), test statistics (T), and significance level of coefficients.

^bIncludes the size-dependent morphological variables of mass, wingload, aspect ratio, and wingtip length.

^cIncludes the size-independent morphological variables of wingtip area and wingtip index.

^d $N_{\text{samples}} = 29$.

^e $N_{\text{contrasts}} = 15$.

Discussion

Food Specialization and Extinction Risk

Our curve estimation revealed that it is possible to convert percent volume (%V) and percent frequency (%F) values into each other. Common prey categories that had high %F values also had large volumes (%V), irrespective of their taxonomy. Thus, expressing dietary data in percent volume (%V) apparently does not produce inherent biases (e.g., by different detectability of prey taxa in feces), as stated by Robinson and Stebbings (1993) in their criticism of the method. Furthermore, our results show that fecal analysis studies are likely to produce consistent data for a given species.

Although the analyzed bat species had species-specific dietary niche breadths, bats with higher extinction risk (according to their IUCN status) did not have narrower dietary niches than less threatened species. The observed lack of association between dietary specialization and extinction risk could be caused by two factors. First, fecal analysis—the current standard method of analyzing diet in bats—may not be precise enough to reflect the real dietary specialization of bat species. Alternatively, diet per se does not affect the vulnerability of bat species.

If bats specialize on certain prey species, rather than on a prey order as a whole, fecal analyses would not be fine-scaled enough to accurately describe the dietary niche of bat species. In this case, fecal studies are likely to underestimate niche breadth. With growing accuracy in the determination of dietary composition, niche breadth can only increase. Thus, fecal analyses provide a conservative estimation of a species' dietary niche breadth. Among the eight species with the highest conservation status (vulnerable & endangered), we found pronounced differences in dietary niche breadth. *Barbastella barbastellus*, *Corynorhinus townsendii*, *Myotis emarginatus*, and *Rhinolophus mehelyi* have relatively narrow dietary niches, whereas *Rhinolophus hipposideros*, *Myotis grisescens*, *Myotis sodalis*, and *Myotis bechsteinii* have intermediate to very wide dietary niche breadths (Appendix 1). This suggests that, unlike previously suspected by Vaughan (1997), bat species that are food specialists are not generally more vulnerable than species consuming a wide range of prey taxa.

Extinction risk in bats may not be influenced by dietary specialization because, in addition to food, bats depend on a variety of other resources within their habitat. Such resources are suitable day roosts for breeding, undisturbed hibernacula, and accessible mating sites (Altringham 1996). Thus, variables other than diet are likely determinants of extinction risk in temperate-zone bats. In some other animals, diet plays a key role in vulnerability and abundance—in phytophagous insects, for example, among which species are often highly specialized on a few or even one specific host plant (Hopkins et al. 2002).

For vertebrates, however, existing studies do not allow a general conclusion to be drawn about the relationship between dietary specialization and rarity or extinction risk (Blackburn et al. 1993; Owens & Bennett 2000; Cardillo & Bromham 2001; Dulvy & Reynolds 2002; Duncan et al. 2002; Johnson 2002).

Wing Morphology and Extinction Risk

In contrast to dietary niche breadth, characteristics of the wing morphology that are independent of body size were significantly correlated with the IUCN conservation status of the respective species. Bats with broader wings, as indicated by their increasing wingtip areas and wingtip indices, were more often in the categories of higher extinction risk than species with narrow or intermediate wing morphology (see also Jones et al. 2003). Thus, our data suggest that bats specialized on foraging close to or within vegetation on average face higher extinction risk than aerial insectivores or species with comparatively flexible foraging strategies. The fact that the eight most threatened species all forage in forests or at riparian vegetation (Barbour & Davis 1969; LaVal et al. 1977; Schober & Grimmberger 1998) is in line with this hypothesis. Loss of forest is believed to be an important reason for the decline of bats (Hutson et al. 2001); thus, species foraging in closed vegetation should be the first to suffer. This assumption is supported by habitat surveys, which suggest that human impact on woodlands affects bat abundance and diversity (Stebbins 1995; Walsh & Harris 1996; Kunz & Racey 1998; Russ & Montgomery 2002).

In addition to their effect on foraging strategy, wings that are broad, short, and rounded impose high costs on commuting flights. Thus, species with such wing morphology often have restricted migratory and dispersal abilities (Baagøe 1987; Norberg & Rayner 1987; Altringham 1996). This could limit their ability to recolonize areas where populations have gone extinct but that have become suitable again (Miller-Butterworth et al. 2003). In Europe the total area of woodlands has increased over the past 50 years. But such secondary forests may have lower quality and accessibility for bats than natural forests (Mayle 1990; Stebbings 1995). Whether habitat suitability or accessibility is more important in determining the current vulnerability of bat species cannot be answered with this study. To investigate this, we suggest further analyses that include variables such as echolocation characteristics, which allow a better separation between adaptation to cluttered habitat and dispersal ability (Neuweiler 1984, 1990).

Although body size is identified as a key factor influencing the extinction risk of animals, we found no evidence that this is the case in bats (see also Jones et al. 2003). Generally, body size is related to longevity and long reproductive cycles (i.e., slow life history) and hence low population density (Blackburn et al. 1993; Purvis et al. 2000).

In temperate-zone bats, body mass varies only between 5 and 40 g, and most species are monoparous and long-lived (Barbour & Davis 1969; Schober & Grimmberger 1998). Therefore, temperate-zone bats are exceptions to the rule of size-dependent generation time and can generally be regarded as species with slow life histories (Neuweiler 1993; Schober & Grimmberger 1998; Jones & MacLarnon 2001). The lack of a relationship between size and life history could explain why variables dependent on body size did not correlate with extinction risk in our study, which is in line with findings in Neotropical bats (Arita 1993).

Our results, in concordance with a recent study by Jones et al. (2003), suggest that bat species adapted to highly cluttered habitats face a higher extinction risk than average. However, exceptions exist on the level of single species. For example, bat species hunting over water (trawlers and water-surface foragers) have wing morphology similar to that of species hunting close to or within dense vegetation. Whereas the latter are often considered highly endangered, some species foraging over water are very common and may profit from anthropogenic factors that lead to an increase of eutrophic water bodies harboring large masses of insects (Hutson et al. 2001). This example makes it clear that wing morphology data alone cannot fully distinguish among different foraging strategies and habitat adaptations (cf. Saunders & Barclay 1992; Fenton & Bogdanowicz 2002). The second reason some species do not fit in the overall pattern is that they face specific threats. The Mexican free-tailed bat (*Tadarida brasiliensis*) is an aerial insectivore that forms huge aggregations of up to 20 million individuals, which makes the species potentially highly susceptible to human persecution and disturbance; it thus is considered by the IUCN as "lower risk-near threatened" (Hutson et al. 2001).

Conclusions

We sought to determine whether specialization influences extinction risk in temperate-zone bat species. Our data do not support the hypothesis that narrow dietary niche breadth is related to high extinction risk. Instead they suggest that habitat specialization, which is reflected in wing morphology, influences the extinction risk of temperate-zone bats. The underlying causes of the observed correlation between wing morphology and extinction risk are likely to depend on habitat availability and/or habitat accessibility. Our results show that an initial risk assessment in bats could be based on wing morphology data, but not on dietary data obtained from fecal analyses. Basing risk assessment on wing morphology has the great advantage that the relevant data can be obtained very easily. We did not intend to explain specific factors influencing the local situation of particular populations or species. Furthermore, we are aware of the fact that the

IUCN risk assessment—it although reflects the best of our knowledge and is widely used for action plans—may not be the ultimate statement about a species' real extinction risk (Hutson et al. 2001). Thus, besides global approaches as adopted in this study, detailed observations of habitat use and population dynamics remain a necessity, both for risk assessment of specific species or local populations and for designing robust conservation plans.

Acknowledgments

We thank F. Bontadina, D. Dechmann, M. B. Fenton, B. König, S. Krackow, A. McElligott, R. Medellín, J. Ortega, P. Pearman, and one anonymous referee for helpful comments and discussions on the manuscript. We are grateful to D. Hosken and S. Krackow for advice on the statistical analyses. K.S. is supported by Graduierten Kollegium: Wissensgesellschaft und Geschlechterbeziehung, Universität Zürich.

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Appendix 1. Percent volume (%V)^a of prey taxa in the diet of 35 bat species.^b

Species	N	Arachnida	Blattaria	Cblopoda	Coleoptera	Dermoptera	Diptera	Ephemeroptera	Hemiptera	Hymenoptera	Isoptera	Larvae	Lepidoptera	Neuroptera	Orboptera	Odonata	Plecoptera
		±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD	±SD
<i>Antrozous pallidus</i>	4	11	7.1	0	0	3.6	5.6	35.5	20.5	0	0	0	0.2	0.1	0	0	2.2
<i>Barbastellus barbastella</i>	4	0.8	1.5	0	0	0	0	0	0	0	0	0	9.1	6.3	0	0	0
<i>Corynorhinus townsendii</i>	3	0	0	0	0	0	0	1.8	1.2	0	0	0	1.8	1.8	0	0	0
<i>Eptesicus fuscus</i>	6	0	0	0	0	0	0	68.3	9.2	0	0	0	4	2.2	0	0	10.6
<i>Eptesicus nilssonii</i>	6	0	0	0	0	0	0	9.2	8.2	0.2	0.4	50.4	6.2	6.2	1.5	2	2.9
<i>Eptesicus serotinus</i>	3	0	0	0	0	0	0	69.8	31.1	0	0	13.4	7.7	0.4	0.2	0	4.3
<i>Hypsugo savii</i>	1	0	ND	0	ND	0	ND	0.9	ND	0	0	28.5	ND	ND	0	ND	7.6
<i>Lastarius borealis</i>	2	0.3	0.4	0	0	0	0	14.1	14.8	0	0	16.1	0	2.2	0	0	3
<i>Lastarius cinereus</i>	3	0	0	0	0	0	0	24	25.9	0	0	1.7	2.9	0	0	0	0.7
<i>Myotis bechsteinii</i>	2	3	4.3	1.3	1.9	2	2.8	6.5	0.9	5.2	3.1	20.3	2	0	0	0	2
<i>Myotis blythii</i>	2	0.6	0.7	0	0	0	0	13.6	7.3	2.8	3.9	1.6	0.1	0	0	0	0
<i>Myotis daubentonii</i>	9	2.9	2.1	0	0	0	0	3.6	2.2	0.8	0.7	74.1	12.3	0.5	0.4	2.4	3.6
<i>Myotis emarginatus</i>	1	39.5	ND	0	ND	0	ND	4.5	ND	0	0	74.3	ND	0	ND	0.3	ND
<i>Myotis grisescens</i>	2	0.2	0.3	0	0	0	0	35.7	35.5	0	1.3	11.5	0.8	1.1	1.4	0.6	0.6
<i>Myotis lucifugus</i>	3	5.6	9.7	0	0	0	0	7.3	4.9	0	0	28	26.6	3.1	2.4	3.1	3.2
<i>Myotis myotis</i>	5	10	11.8	0	0	0.5	1.1	68.4	18.7	1.8	3.3	2.7	4.4	0	0.1	0.1	0.1
<i>Myotis mystacinus</i>	2	17.7	0.8	0	0	0.2	0.3	7.4	7.8	0.3	0.3	56.5	4.6	0.6	5	4.1	4.1
<i>Myotis nattereri</i>	3	0	0	0	0	0	0	33.9	12.7	0	0	6.8	6	0.5	0.5	0.5	0.8
<i>Myotis septentrionalis</i>	1	0	ND	0	ND	0	ND	0	ND	0	0	25.5	ND	0	0.3	ND	ND
<i>Myotis sodalis</i>	1	0.1	ND	0	ND	0	ND	59.9	ND	0	0	5.5	ND	0	ND	5.7	ND
<i>Nycticeius humeralis</i>	19	2.9	3.1	0	0	0	0	10	10.1	0	0	72.8	22.3	0	0.1	0.1	0.1
<i>Nyctalus noctula</i>	6	0.3	0.4	0	0	0	0	23.8	24.7	0	0	20.8	14.7	5	6.9	8.1	8.1
<i>Pipistrellus kuhlii</i>	2	0	0	0	0	0	0	8.6	12.2	0	0	43.7	18.1	1.2	6.8	0.3	0.3
<i>Pipistrellus nathusii</i>	1	0	ND	0	ND	0	ND	0	ND	0	0	97.8	ND	0	ND	2.8	ND
<i>Pipistrellus subflavus</i>	1	0	ND	0	ND	0	ND	2.4	ND	0	0	31.1	ND	0	ND	3.5	ND
<i>Plecotus auritus</i>	3	9.7	8.4	0	0	1.2	1.9	4.4	3.1	5.7	3.5	36.2	6.3	0	0	0.7	1
<i>Plecotus austriacus</i>	3	0	0	0	0	0	0	8.8	6.5	0.1	0.1	15.6	12.7	0	0	0.1	0.1
<i>Rhinolophus blasii</i>	1	0	ND	0	ND	0	ND	0.1	ND	0	0	0.7	ND	0	ND	0	ND
<i>Rhinolophus ferrumequinum</i>	7	0.6	1	0	0	0	0	36.2	20.8	0	0	18.4	6.4	0	0	0.1	0.2
<i>Rhinolophus hipposideros</i>	4	0.4	0.9	0	0	0	0	1.6	0.9	0	0	42.8	10.4	0	0	0.8	0.8
<i>Rhinolophus mehelyi</i>	1	0	ND	0	ND	0	ND	0	ND	0	0	0	ND	0	ND	0	ND
<i>Tadarida brasiliensis</i>	2	0	0	0	0	0	0	36.3	14.1	0	0	7.6	9.8	0	0	6.9	8.2
<i>Tadarida teniotis</i>	2	0.3	0.4	0	0	0	0	0.5	0.7	0	0	0.5	0.7	0	0	6	8.5
<i>Vesperugo murinus</i>	7	0.1	0.4	0	0	0	0	3.9	3.7	0	0	60	24.8	0.7	1.5	0.3	2.4

continued

Appendix 1. (continued)

Species	Homoptera	Hymenoptera	Isoptera	Larvae	Niche	Lepidoptera	Neuroptera	Odonata	Orthoptera	Plecoptera	±SD
<i>Myotis nattereri</i>	0	3.4	3.2	0	0.3	8.1	6.9	0.6	0	0	0
<i>Myotis septentrionalis</i>	1.4	2.5	2.6	0	0	40.6	10.4	0.2	0	0	0
<i>Myotis sodalis</i>	0.2	ND	ND	0	ND	14.3	ND	ND	0	ND	0
<i>Nycticeius humeralis</i>	7	ND	ND	0	ND	19.7	ND	ND	0	ND	0
<i>Nyctalus leisleri</i>	0.6	1.4	2.7	0	0.2	11.7	17.1	6.4	0	0	0
<i>Nyctalus noctula</i>	0	1.1	1.8	0	0	15.2	10.8	4.1	0	0	0
<i>Pipistrellus kuhlii</i>	3.6	5	9.9	0	0	23.1	0.6	0.6	0	0	0
<i>Pipistrellus naubusii</i>	0	ND	ND	0	ND	0.5	ND	ND	0	ND	0
<i>Pipistrellus subflavus</i>	11.7	ND	ND	0	ND	14.1	ND	ND	0	ND	0
<i>Plecotus auritus</i>	0	0.8	0.7	0	0	38.6	10	0.8	0	0.1	0.2
<i>Plecotus austriacus</i>	0	0.5	0.9	0	0	75.9	2.7	0.9	0	0	0
<i>Rhinolophus blasii</i>	0	ND	ND	2.5	ND	96.5	ND	ND	0	ND	0
<i>Rhinolophus ferrumequinum</i>	0	0	6.1	5.2	0	38.8	13.7	1.2	0	0	0
<i>Rhinolophus hipposideros</i>	0	0.1	3.7	4.6	0	38.1	15.7	8.1	0	0	0
<i>Rhinolophus mehelyi</i>	0	ND	ND	0	ND	100	ND	ND	0	ND	0
<i>Tadarida brasiliensis</i>	4	0.4	10.3	14.4	0	34.5	1.5	0.2	0.1	0	0
<i>Tadarida teniotis</i>	0	0	0.5	0.7	0	77.6	13.1	17	0	0	0
<i>Vespertilio murinus</i>	2.4	4.4	0.6	0	0	11.8	13.9	4.1	0	0	0
Psocoptera											
<i>Antrozous pallidus</i>	0	0	0	0	2.70	0.58					
<i>Barbastella barbastella</i>	0.1	0.2	0	0	1.29	0.34					
<i>Corynorhinus townsendii</i>	0	0	0	0	1.10	0.10					
<i>Eptesicus fuscus</i>	0	0	1.1	1.4	2.07	0.43					
<i>Eptesicus nilssonii</i>	0	0	10	8.7	2.85	0.29					
<i>Eptesicus serotinus</i>	0	0	4.1	7	2.50	2.15					
<i>Hypsignathus</i>	0	ND	0.6	ND	4.19	ND					
<i>Lasturus borealis</i>	0	0	5.1	7.1	2.64	0.93					
<i>Lasturus cinereus</i>	0	2.3	0	0	2.31	1.17					
<i>Myotis bechsteinii</i>	0	0	0.2	0.3	9.31	0.19					
<i>Myotis blythii</i>	0	0	0	0	2.05	0.24					
<i>Myotis daubentonii</i>	0	0.1	30.2	19.6	1.47	0.23					
<i>Myotis emarginatus</i>	0	ND	0	ND	1.41	ND					
<i>Myotis grisescens</i>	0	0	11.7	8.6	3.67	1.78					
<i>Myotis lucifugus</i>	0	0	6.2	8.5	3.61	2.27					
<i>Myotis myotis</i>	0	0	0	0	1.98	0.62					
<i>Myotis mystacinus</i>	0.6	0.8	5.8	8.3	4.45	4.25					
<i>Myotis sodalis</i>	0	0	4.6	7.8	2.66	0.49					
<i>Myotis nattereri</i>	0	0	9.4	6.8	3.13	0.24					
<i>Myotis septentrionalis</i>	0	ND	55.1	ND	2.57	ND					
<i>Nycticeius humeralis</i>	0	ND	0.2	ND	2.45	ND					
<i>Nyctalus leisleri</i>	0	0	7	6.3	1.78	0.96					
<i>Nyctalus noctula</i>	0	0	17.6	15.1	4.35	1.84					
<i>Pipistrellus kuhlii</i>	0.5	0.7	8.2	11.6	3.59	1.56					
<i>Pipistrellus subflavus</i>	0	ND	2.8	ND	1.16	ND					
<i>Plecotus auritus</i>	0	ND	0	ND	6.11	ND					
<i>Plecotus austriacus</i>	0.6	1	4.2	4.3	3.42	1.20					
<i>Rhinolophus blasii</i>	0	0	1.5	2.6	1.62	0.16					
<i>Rhinolophus ferrumequinum</i>	0	ND	0	ND	1.07	ND					
<i>Rhinolophus hipposideros</i>	0	0	3.9	4.2	2.84	0.83					
<i>Rhinolophus mehelyi</i>	0.2	0.5	7	7.4	2.74	0.70					
<i>Rhinolophus brasiliensis</i>	0	ND	0	ND	1.00	ND					
<i>Tadarida teniotis</i>	0	0	0	0	3.43	0.90					
<i>Vespertilio murinus</i>	0	0	0.5	0.7	1.60	0.42					
	0	0	16.5	14.1	2.17	0.59					

^a Percent volume (%V) = volumetric proportion for each prey taxon found in all analyzed feces.

^b ND = no data available (sample size = 1).