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Cats Felis catus as a threat to bats worldwide: a review of the evidence

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Abstract :

1. Cats Felis catus, in all their forms (domestic, free-roaming/stray and feral), have been identified as a major global threat to biodiversity, especially birds and small mammals. However, there has been little previous consideration of the extent and impact of predation of bats by cats, or of whether specific characteristics make certain species of bats particularly vulnerable to predation by cats.

2. We reviewed the impact of cats on bats, based on a collation of scientific literature and the International Union for Conservation of Nature (IUCN) Red List database. Our aim was to produce a synthesis of the extent to which cats prey upon and threaten bats. We also collated available data on cat diet, which provide information on predation rates of bats by cats.

3. Few studies (n = 44) have identified bat species preyed upon or threatened by cats, with a disproportionate number of studies from islands. In these studies, 86 bat species (about 7% of the global extant tally) are reported as preyed upon or threatened by cats, and about one quarter of these species are listed as Near Threatened or threatened (IUCN categories Critically Endangered, Endangered, or Vulnerable). In IUCN Red List assessments, cats are more frequently mentioned as a threat to threatened or Near Threatened bat species than to non-threatened species (IUCN category Least Concern).

4. In studies reporting on the incidence of bats in cat dietary samples (scats, stomachs and guts), the frequency of occurrence of bats in samples averaged 0.7 ± 2.1% (mean ± standard deviation; n = 102). Many studies had sample sizes that were too small to be likely to detect bats. All forms of cat are reported to kill bats, and such predation has been reported in all major terrestrial habitats. We conclude that predation by cats is an under-appreciated threat to the world's bat species.

Keywords : bats Chiroptera, biodiversity conservation, biodiversity loss, cats Felis catus, invasive species, predation, threat

INTRODUCTION

With *ca.* 1400 known extant species, bats (Chiroptera) are the second-richest taxonomic order of mammals on Earth (Voigt & Kingston 2015, Burgin et al. 2018). Among them, at least 1280 species have had their conservation status assessed by the International Union for Conservation of Nature (IUCN). Of these species, 21% are currently considered Near Threatened or threatened (Critically Endangered, Endangered, or Vulnerable) worldwide, and another 19% are Data Deficient (Frick et al. 2019, IUCN 2020). At least five bat species have also been driven to extinction since the year 1500 (Frick et al. 2019, IUCN 2020). The main threats facing bats are, in decreasing order of

121 importance: 1) the destruction and transformation of their natural habitats for agriculture, wood
122 harvesting or residential and commercial development; 2) other forms of human intrusion and
123 disturbance (including tourism); 3) mining and quarrying; 4) hunting for meat and traditional
124 medicine; and 5) fires and severe weather events such as heat waves or tropical storms (Voigt &
125 Kingston 2015, O'Shea et al. 2016, IUCN 2020). Further threats have been identified recently, such
126 as emergent diseases (e.g. White Nose Syndrome), massive culling for crop protection, and human
127 persecution in response to the risk of bat-borne diseases spreading to humans (Blehert et al. 2009,
128 O'Shea et al. 2016, Aziz et al. 2017, Florens & Baider 2019, Zhao 2020). Several recent studies
129 have also documented the direct or indirect impacts of invasive species on many bat species
130 (Menchetti et al. 2014, Welch & Leppanen 2017, Hernández-Brito et al. 2018, Dorrestein et al.
131 2019). Among these more recently recognised threats, Welch and Leppanen (2017) highlighted an
132 unexpected, understudied and probably underestimated threat to bats, namely the impact of invasive
133 predators. Of all the invasive predators, the cat *Felis catus* (Linnaeus, 1758) is the species most
134 frequently cited as potentially affecting bats (Welch & Leppanen 2017).

135 The cat is a medium-sized carnivore domesticated approximately 9500 years before present in
136 the Middle East, and derived from individuals of the African wild cat *Felis silvestris lybica* (Vigne
137 et al. 2004, Driscoll et al. 2007). It has been transported by humans to all permanently inhabited
138 continents and many islands throughout the world, wreaking havoc on native fauna in a variety of
139 environments, from urban to remote natural habitats (Turner & Bateson 2013). Cats can be
140 categorised into three different forms: 1) domestic, i.e. owned by people, with most or all of their
141 needs supplied by their owners; 2) free-roaming (or stray), i.e. unowned cats found in and around
142 cities, towns and rural properties and mainly fed by humans (voluntarily or not); and 3) feral, i.e.
143 unowned cats that live and reproduce in the wild, often remaining remote from humans (Loss et al.
144 2013, Department of the Environment Australia 2015). Feral cats are cats that are descended from
145 domestic cats but are no longer domestic: they returned to the wild state and typically feed on wild
146 prey without interaction with humans. The cat, in all its forms, is recognised as one of the most
147 damaging to biodiversity of all invasive or commensal species (e.g. Lowe et al. 2000, Loss et al.
148 2013, Doherty et al. 2016), especially on islands (Medina et al. 2011, Nogales et al. 2013, Doherty
149 et al. 2017, Woinarski et al. 2017, 2018, Murphy et al. 2019). As an example, the cat has
150 contributed to 26% of recent (since the year 1500) vertebrate extinctions, i.e. 63 species (40 birds,
151 21 mammals and two reptiles), mostly on islands. Another 430 vertebrate species are currently
152 considered as threatened by cats (Doherty et al. 2016).

153 Bats typically have low reproductive rates, delayed maturity and long gestation periods, naturally
154 compensated for by long lifespans (Racey & Entwistle 2000, Wilkinson & South 2002, Barclay &

Harder 2003). Slow life histories make them particularly vulnerable to additional sources of mortality, including anthropogenic threats (McIlwee & Martin 2002, Voigt & Kingston 2015, Fleischer et al. 2017). Moreover, the gregarious behaviour of many bat species at diurnal resting sites leads to large proportions of populations congregating in very small areas, making them particularly vulnerable to repeated predation events and rare disturbance events (Kunz & Fenton 2005, Welch & Leppanen 2017).

Several studies have shown at least occasionally high rates of predation by cats of bats, including threatened species; such predation could be a major threat. For example, Scrimgeour et al. (2012) reported that a single cat was responsible for killing >100 individuals of the Vulnerable New Zealand endemic short-tailed bat *Mystacina tuberculata* at a tree roost site over a seven-day period. From an analysis of nearly 100 cat dietary samples (scats and stomachs) on Christmas Island, Indian Ocean, Tidemann et al. (1994) reported that the endemic subspecies of the Vulnerable Blyth's flying-fox *Pteropus melanotus* was present in 10% of samples. In New Caledonia, Palmas et al. (2017) analysed 5356 cat scats from 14 sites and found that the three species of *Pteropus* occurring on the island (*Pteropus ornatus, Pteropus tonganus* and *Pteropus vetulus*) were present in nine sites and in up to 13% of cat scats at a humid forest site. These examples suggest that the cat may represent a major predator of a range of bat species.

We undertook a global review of the available evidence of the impact of cats on bats through collation of the scientific literature and from evidence in the IUCN Red List database (IUCN 2020). The aims of our paper are fivefold:

1. To provide a comprehensive synthesis of records of bats being preyed upon or threatened by cats. In such an assessment, we note that there may be records of cats preying upon bats, but such predation does not necessarily demonstrate a population-level impact. Conversely, some conservation assessments for individual bat species cite cats as a threat to bat populations, although there may be no published record of predation by cats.
2. To identify whether any family of bats suffers a higher (or lower) incidence of predation by cats than others.
3. To identify whether there is variation in the incidence of predation of bats by cats occurring in different habitats.
4. To evaluate the frequency of occurrence of bats in the diet of cats.

5. To identify knowledge gaps, and to recommend research and conservation priorities that could improve our understanding of, and help reduce, the impact of cats on bat populations.

METHODS

Bat species killed or threatened by cats

We searched publications that identified bat species that are: 1) preyed upon (i.e. for which there is direct evidence of predation); and/or 2) threatened by cats (including instances where cats are reported to be a threat without direct evidence of predation published). For that purpose, we searched the Google Scholar database (http://scholar.google.com) in February 2020. We identified additional papers in the references listed in selected publications. Review papers were also checked as they sometimes provided data in a more appropriate form than original studies. The literature search was based on all combinations of the following three categories of words (a + b + c) in English, French and Spanish: a) 'bat' or 'Chiroptera'; b) 'cat' or '*Felis catus*'; and c) 'predation' or 'threat' or 'diet'. For each species of bat identified, a complementary search was made by searching all combinations of the two categories of words (d + e): d) the species' scientific name 'Genus species'; and e) 'cat' or '*Felis catus*'. For each publication, we extracted the following information:

1. Whether the study was conducted in a continental, insular or mainland-Australian context. We treated the mainland of Australia as a distinct category because Australia is the smallest continent and largest island, and because numerous studies of cat diet have been conducted there (Woinarski et al. 2019). Classifying it as a continent or island would have tipped the balance of data towards one category or the other.
2. The type of cat considered in the study with four different categories: domestic or free-roaming (stray), feral, both and any or unknown when the source did not mention any specific type of cat.

We complemented this literature search with a search of the IUCN Red List database (updated in February 2020) to identify bat species for which cats are mentioned as a threat, by searching for 'cat' or '*Felis catus*' in the threats referenced for each bat species for which an IUCN assessment had been published (n = 1280).

Then, we gathered the following information for all bat species recorded in one of the above steps:

1. Family, IUCN category, habitat, roosting types (extracted from the IUCN Red List database).
2. Mean adult body mass (extracted from the literature by searching the combination of the scientific name of the species 'Genus species' and 'weight' in Google Scholar and Google Books, http://books.google.com). Most of the data on mean adult body mass of bats captured by cats were extracted from the electronic supplementary material of Moyers Arévalo et al. (2020; n = 63). For the remaining species (n = 23), when more than one reference was available for body mass, we calculated the mean of these values. The fact that the sample size was not systematically mentioned prevented us from calculating weighted means.
3. The type of corroborating evidence allowing us to identify the predation level of cats on the species, according to four categories: 'listed as a threat' for sources where the cat was mentioned as a threat but no documentation of predation was found; 'anecdotal predation', where we found only one record of predation; 'multiple predation', where we found at least two documented records of predation; and 'not available' where no information about the number of records of predation on the bat species was available (e.g. bat species occurring in the list of prey of cats with no available data on the number of individual consumed).
4. The type of reference found for each case, according to three categories: published papers only, the mention of cats as a threat in the IUCN assessment only, and the combination of the two previous categories.

Cat dietary studies and rates of predation of bats by cats

Independently of the previous literature search, we identified peer-reviewed papers by searching in Google Scholar for publications containing different combinations of three categories of words (e + f) in English, French and Spanish: e) 'cat', 'feral cat' or '*Felis catus*'; and f) 'diet'. The objective was to assess the capacity of bat detection in cat dietary studies and incidence of predation of bats by cats. The frequency of occurrence (FO%) is the percentage of individual diet samples (scats, stomachs or guts) that contain remains of a particular prey species (Bonnaud et al. 2007). In this part of our review, we only considered studies based on cat scats, stomachs or guts with macroscopic or microscopic sample analyses. We excluded studies based on prey remains (e.g. bats brought home by pet cats or non-ingested remains of bats killed by cats), as this approach suffers from study-specific biases precluding comparisons of FO% among cat dietary studies. Publications with several sets of samples pooled were broken down by sample type (scats or stomachs/guts) and/or study site and/or seasons when possible. For studies that did not report the FO% of bat remains in cat diet, we checked the presence of bat species in the area studied, in accordance with

the information available on IUCN databases and by searching on Google Scholar the combination of the name of the location with 'bat' or 'Chiroptera'.

Data analyses

We carried out permutation tests to assess whether there was variation, across families and IUCN categories, in the proportion of bat species known to be preyed on by cats. Considering the proportion of cat prey species among all bat species, random models were built for each family or IUCN category by sampling binomial distributions (1000 repetitions). We considered only families with at least five species (14 out of 20 families). The observed number of species reported as captured by cats in a given family or IUCN category was then compared to the random distribution to estimate whether cat prey species are over- or under-represented, at a probability of 0.05. We performed a similar procedure for the 20 types of habitat most frequently used by bats as assessed by the IUCN. We tested whether IUCN assessments differed in terms of the identification of cats as a threat, by comparing bat species in the IUCN categories Critically Endangered, Endangered, and Vulnerable (threatened) and Near Threatened with species in the category Least Concern (non-threatened). For diet studies, we assessed if the number of samples differed between cat dietary studies reporting or not reporting bats, with a binomial Generalised Linear Model. We performed a Kruskal-Wallis chi-squared test to compare bat FO%s between islands, mainland Australia and continents. Finally, we used simulations (10000 repetitions) to estimate the probability of finding bat remains in cat dietary studies according to the sample size analysed and for different frequencies of occurrence of bat remains. All statistical analyses, graphics and simulations were performed in R 3.6.0 (R Core Team 2019).

RESULTS

Bat species preyed upon or threatened by cats

We identified 44 scientific publications which reported at least one and up to 24 bat species being preyed upon or threatened by cats (see Appendix S1 for a complete list of references). Among these publications, only four (9%) were specifically dedicated to the study of predation of bats by cats. A total of 28 publications (64%) reported finding dead and/or injured bats (14), bat remains in scats, stomachs and/or guts of cats (13), or both (1). Ten publications (23%) reported opportunistic observations of predation of bats by cats, and six publications (14%) mentioned cats as a threat to bats without providing direct evidence of predation.

Among the 44 publications, 18 were from islands (41%), 12 from mainland Australia (27%), 12 from continents (27%) and two were worldwide studies (5%; Fig. 1; Appendix S2). Forty-one publications specified the type of cat involved in bat predation: 17 concerned domestic or free-roaming (stray) cats, 20 concerned feral cats and four concerned any/unknown cats.

Cats were recorded as a threat in IUCN Red List assessments for 18 bat species (n = 1280, 1.4%, Appendix S3). For eight of these 18 species, our literature search failed to identify published records of predation by cats.

We identified 86 species of bats as preyed upon or threatened by cats. This represents 6.1% of all known bat species, from 12 of the 20 bat families (Fig. 2, Appendices S4, S5) and includes bats with various feeding habits (nectarivorous, frugivorous and insectivorous). The average adult weight of bat species preyed upon or threatened by cats was 53.7 g ± 137.8 (mean ± standard deviation), ranging from some of the smallest known bats (2.8 g, *Chilonatalus micropus*) to some of the largest bats (716 g, *Pteropus poliocephalus*). Among the 14 bat families comprising at least five species, the proportional incidence of bat species taken by cats was significantly higher (permutation test, $P < 0.05$, Fig. 2, Appendix S5) for Vespertilionidae (number cat prey species/number of species in the family = 42/438 [9.6%]), Natalidae (4/11 [36%]),Mormoopidae (2/11 [18%]) and Megadermatidae (1/6 [16.7%]) and significantly lower for Hipposideridae (2/94 [2.1%]), Nycteridae (0/16 [0%]), Rhinopomatidae (0/6 [0%]) and Thyropteridae (0/5 [0%]).

Of the 86 species preyed upon or threatened by cats, the IUCN category of one species was Extinct (EX) (*Pipistrellus murrayi*) and 22 were threatened or Near Threatened (NT) (26%; four Critically Endangered [CE], four Endangered [EN], 12 Vulnerable [VU] and two NT). Sixty-three species were non-threatened (73%; 61 Least Concern [LC]), one Data Deficient (DD) and one Not Evaluated (NE; Table 1)). Without considering the three EX, DD and NE species, these percentages are similar to the conservation status frequency distribution for all bat species. Threatened or Near Threatened species (Critically Endangered, Endangered, Vulnerable, or Near Threatened) represent 27% of bat species preyed upon or threatened by cats, and 26% of bats overall (permutation test: P = 0.09). Non-threatened (Least Concern) bats represent 73% of bat species preyed upon or threatened by cats, and 74% of bats overall (permutation test: P = 0.29).

Of the 86 bat species recorded as being preyed upon or threatened by cats, 78 were identified through mentions in scientific publications. Among these, only ten species also have predation by cats mentioned as a threat according to the IUCN. For eight species, evidence of predation by cats came only from their IUCN assessments without any reference to primary evidence of predation by cats. Without considering the three EX, DD and NE species, threatened and Near Threatened (CR,

EN, VU and NT) species had a higher percentage (55%, $n = 22$) of species with cats mentioned as a threat by the IUCN than non-threatened species (LC; 8%, $n = 61$), a highly significant difference (binomial GLM, $\beta = 2.60 \pm 0.63$, $P < 0.001$).

For 40 of the 86 bat species identified as preyed upon or threatened by cats, the evidence came from multiple reports of predation ('multiple predation'), for ten species, predation was reported only once ('anecdotal predation'), and, for 12 species, cats were mentioned as a threat to the species in a published paper or in the IUCN Red List assessment but we were unable to find any primary evidence of predation in the published literature ('listed as a threat'). There was no quantitative information available in publications for another 24 bat species ('not available').

For the 86 bat species identified as preyed upon or threatened by cats, the type(s) of cat involved was reported for 60. Domestic or free-roaming (stray) cats were involved in most instances ($n = 34$ bat species), followed by feral cats ($n = 22$) and both types ($n = 4$).

The 20 habitat types most frequently used by the 86 bat species preyed upon or threatened by cats differed from the 20 habitats most frequently used by all bats (Fig. 3). Bat species recorded as preyed upon or threatened by cats were more likely than expected (permutation tests, $P < 0.05$) to occur in the following habitats, in decreasing order of importance: 'Forest – Temperate', 'Artificial/Terrestrial – Urban Areas', 'Caves and Subterranean Habitats (non-aquatic) – Other Subterranean Habitats', 'Artificial/Terrestrial – Pastureland', 'Shrubland – Subtropical/Tropical Dry', 'Shrubland – Mediterranean-type Shrubby Vegetation', 'Artificial/Terrestrial – Arable Land', 'Shrubland – Temperate', 'Grassland – Temperate' and 'Grassland – Subtropical/Tropical Dry'. By contrast, bats were less likely to be recorded as preyed upon or threatened by cats than expected (permutation tests, $P < 0.05$) if they used, in order of importance: 'Forest – Subtropical/Tropical Moist Lowland', 'Forest – Subtropical/Tropical Moist Montane' and 'Savanna – Dry'.

Cat dietary studies and rates of predation of bats by cats

We found 77 studies focusing on cat diet, providing 103 different sets of samples (studies broken down by sample type, site or season) in which bat species could have been detected (i.e. bats are present in the sampling area; Appendix S6). Bat remains were found in 20, including 19 where FO% information was available, of the 103 sets of samples (19%), across 10 studies. This included 17 sets of samples in which bats were identified to the genus or species level. Across studies, the FO% of bat remains in cat diet (scat or stomach/gut) averaged 0.7 % ± 2.1 (mean ± standard deviation), but was highly variable, ranging from 0 to 13% (Fig. 4A, $n = 102$). We found no statistically significant differences in average FO% of bats in cat diets between islands (mean ± standard deviation FO% 1.0% ± 2.7; $n = 55$), mainland Australia (mean ± standard deviation FO%

of 0.5% ± 1.3; n = 37) and continents (no bats found in any studies, n = 11; Kruskal-Wallis chi-squared = 1.03, df = 2, P = 0.60).

The number of cat dietary samples per set averaged 196 ± 246 (mean ± standard deviation; median = 124, n = 102). We found that the number of samples per set of cat diet studies that did not record bats as a dietary item was smaller than the sample size for studies that did detect bats (GLM, β = 0.002 ± 0.001, P = 0.052; Fig. 4B). Considering the average FO% for sets of samples where bat remains have been found of 3.9%, our simulation analysis revealed that 84% of sets had a sufficient number of samples to have 80% probability of detecting bat remains (Fig. 4B, n = 102). However, only 3% of the sets provided a number of samples sufficient to have 50% probability to detect the lowest non-zero FO% recorded of 0.1%, and the average number of samples per set of 196 ensures only an 18% detection probability of a true 0.1% FO% (Fig. 4B).

DISCUSSION

Published data relating to predation of bats by cats are scarce, with a disproportionate number of studies from islands. This limited information base is likely to give a very fragmentary view of the global impact of predation by cats on bat populations. Notwithstanding this, we were able to identify 86 bat species (about 7% of the global tally) that are preyed upon or threatened by cats, about one quarter of which are threatened with extinction. We also found that, in IUCN Red List assessments, cats were more frequently mentioned as threats for threatened or Near Threatened bat species than for non-threatened species. We conclude that predation by cats is an under-appreciated threat to the world's bat species.

Our research highlights a lack of dedicated studies on the impacts of predation of bats by cats. Information from such studies is needed to improve assessment and understanding of the magnitude of the threat that cats pose to the survival of some bat species. A constraint on our review was that many cat dietary studies did not identify bats preyed upon by cats to the species level, at least in part because the morphological features distinguishing bat species may no longer be apparent in fragments in cat stomachs or faeces. For example, Woolley et al. (2019) reported that 64% of Australian cat dietary studies that reported bats in cat samples did not identify the species of bat consumed. Hence, our results are likely to under-estimate the variety of bat species killed by cats substantially. Since cats generally prefer to catch and consume live prey rather than to eat carrion (Woinarski et al. 2019), we assume that most of the bats consumed by cats were killed by them.

Figures

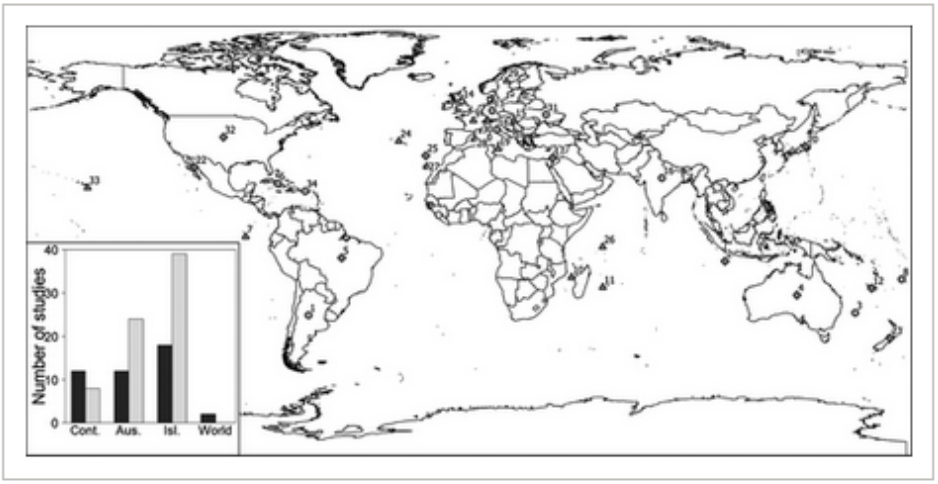

Fig. 1 Open in figure viewer | PowerPoint

Geographical distribution of studies where bat species were recorded as being preyed upon or threatened by cats (dot), found in cat diet studies (triangle) or both (diamond). Numbers next to dots refer to the site identification codes given in Appendix S2. Only one dot (and number) is shown per country or island. Inset: Comparison of the number of studies according to geographic setting and study type. The dark grey bars represent studies in which bat species were found to be preyed upon or threatened by cats; the light grey bars represent cat dietary studies (in which bat remains were, or were not found). Studies were grouped according to whether they came from continents (Cont.), the Australian mainland (Aus.), or islands (Isl.), or had a worldwide focus (World).

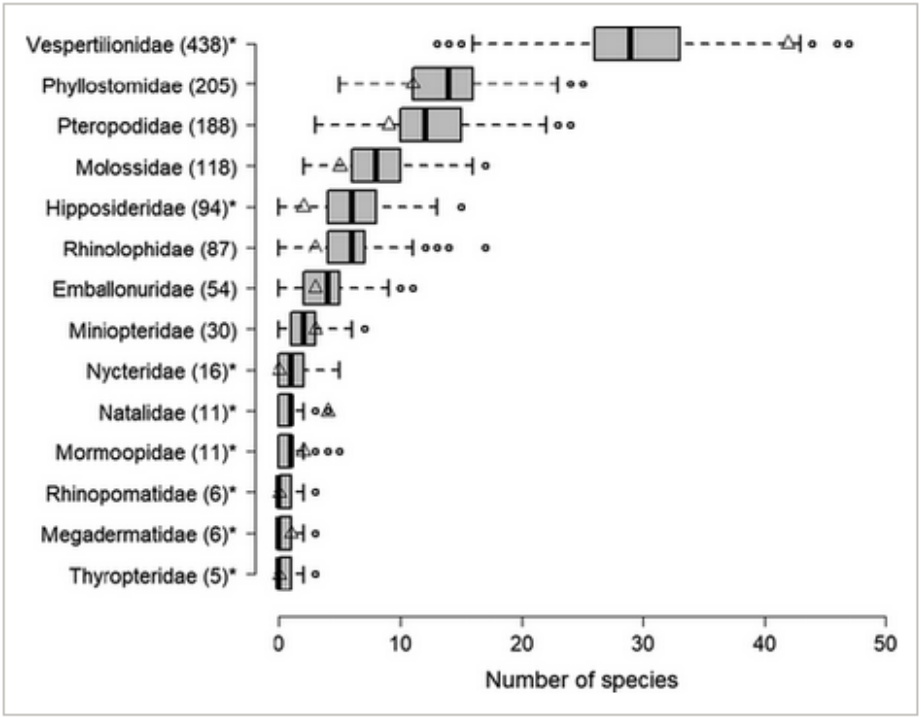

Fig. 2

Susceptibility of the different bat families to predation by cats (restricted to families with at least five species, species number in parentheses). The boxplots represent the distribution of the number of species expected to be preyed upon according to the overall percentage of cat prey species (6.7%; permutation test with 1000 repetitions). The triangles represent the actual number of species recorded as preyed upon or threatened by cats. The asterisks identify the families with a significant departure from random expectations (higher in Vespertilionidae, Natalidae, Mormoopidae and Megadermatidae; lower in Hipposideridae, Nycteridae, Rhinopomatidae and Thyropteridae). The boxes indicate the upper and lower quartiles, the whiskers indicate the ranges of the bottom 25% and top 25% of the data values and the unfilled circles indicate outliers.

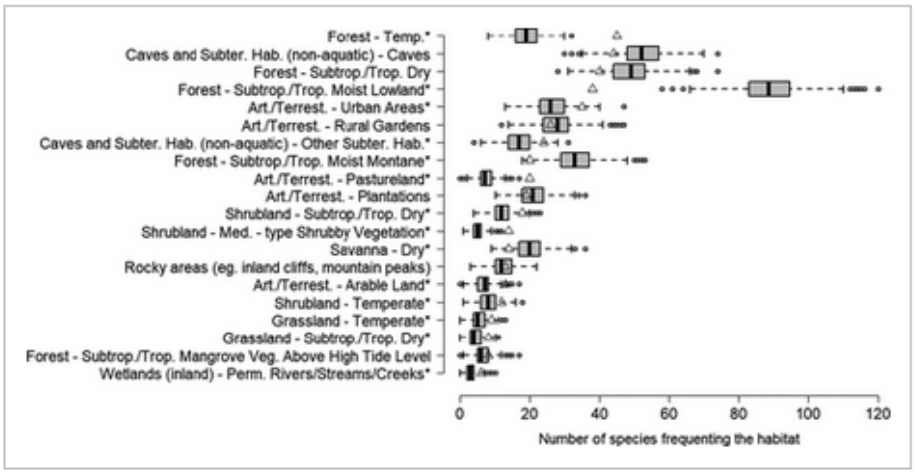

Fig. 3

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Comparison of the distribution of bat species among the 20 habitat types recorded as mainly frequented by bats (International Union for Conservation of Nature database). The boxplots represent the distribution of the number of species frequenting the habitat expected according to the overall proportion of predicted species (11%; permutation test with 1000 repetitions). The triangles represent the actual number of species frequenting the habitat recorded as preyed upon or threatened by cats. The asterisks identify the habitats with a significant departure from random expectations, either way. Note that the 20 habitat types mainly frequented by bats represent 87% of habitats for bat species preyed upon or threatened by cats and 85% for all bat species. The boxes indicate the upper and lower quartiles, the whiskers indicate the ranges of the bottom 25% and top 25% of the data values and the unfilled circles indicate outliers.

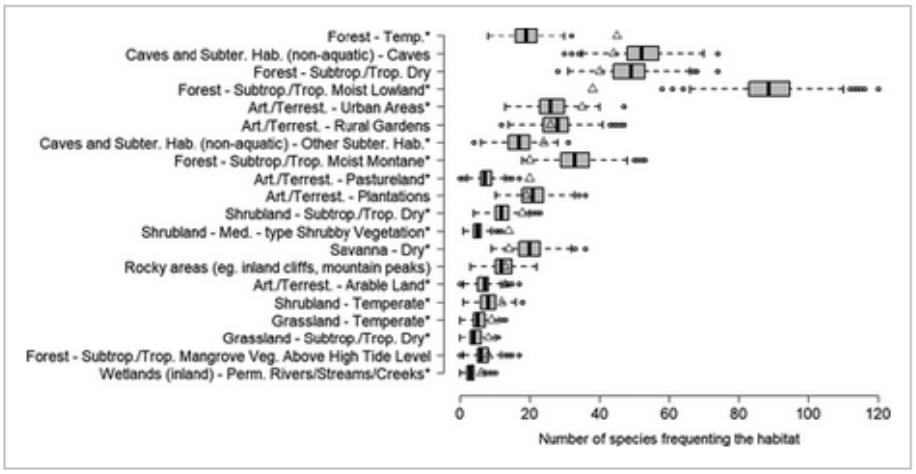

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Table 1. International Union for Conservation of Nature (IUCN) Red List conservation status of all 1281 bat species that have been placed in a category, and of the 86 species that are identified as being preyed upon or threatened by cats

IUCN categories	Number of bat species		
	All	Preyed upon or threatened by cats	Percentage of bat species preyed upon or threatened
Extinct (EX)	5	1	20%
Critically Endangered (CR)	23	4	17%
Endangered (EN)	60	4	6.7%
Vulnerable (VU)	109	12	11%
Near Threatened (NT)	80	2	2.5%
Least Concern (LC)	759	61	8.0%
Data Deficient (DD)	244	1	0.4%
Not Evaluated (NE)	1	1	100%
Total	1281	86	6.7%