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

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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.
5. 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.

Mots clés
chats *Felis catus*, chauves-souris Chiroptera, conservation de la biodiversité, espèces envahissantes, menace, perte de biodiversité, prédation

RESUMÉ EN FRANÇAIS

1. Les chats *Felis catus*, sous toutes leurs formes (domestiques, errants ou harets), ont été identifiés comme une menace mondiale majeure pour la biodiversité, en particulier pour les oiseaux et les petits mammifères. Cependant, l'ampleur de ce phénomène et l'impact de la prédation exercée sur les chauves-souris par les chats n'ont guère été pris en compte jusqu'à présent. En particulier la question de savoir si des caractéristiques spécifiques rendent certaines espèces de chauves-souris particulièrement vulnérables à la prédation par les chats reste en suspens.
2. Nous avons examiné l'impact des chats sur les chauves-souris, en croisant les informations issues de la littérature scientifique sur le sujet et celles disponibles dans la base de données de la liste rouge de l'Union Internationale pour la Conservation de la Nature (UICN). Notre objectif était de produire une synthèse mondiale visant à estimer dans quelle mesure les chats s'attaquent aux chauves-souris et constituent une menace. Nous avons également rassemblé les données disponibles sur le régime alimentaire des chats, qui fournissent des informations sur les taux de prédation des chauves-souris par les chats.
3. Peu d'études (n = 44) ont permis d'identifier des espèces de chauves-souris prédatées et/ou menacées par les chats, un nombre disproportionné d'entre elles concernent les écosystèmes insulaires. Ces études ont permis d'identifier 86 espèces de chauves-souris (environ 7 % des espèces mondiales) représentant des proies ou étant directement menacées par les chats ; environ un quart de ces espèces sont classées comme "quasi menacées" ou "menacées" (catégories de l'UICN : En danger critique d'extinction, En danger ou Vulnérable). Dans les évaluations de la Liste rouge de l'UICN, les chats sont plus fréquemment mentionnés comme une menace pour les espèces de chauves-souris menacées ou quasi menacées que pour les espèces non menacées (catégorie de l'UICN "Préoccupation mineure").
4. Dans les études analysant le régime alimentaire des chats (excréments, estomacs et tubes digestifs) la fréquence d'occurrence des chauves-souris dans les échantillons était en moyenne de 0.7 ± 2.1 % (moyenne ± écart-type ; n = 102). Dans de nombreux travaux, la taille des échantillons était trop petite pour permettre de détecter la prédation sur des chauves-souris.
5. Toutes les formes de chats s'attaquent aux chauves-souris, et cette prédation a été signalée dans tous les principaux habitats terrestres. En conclusion, la prédation des chauves-souris par les chats apparait être une menace sous-estimée au niveau mondial.

INTRODUCTION

With *ca.* 1400 known extant species, bats (Chiroptera) are the second-richest taxonomic order of mammals on Earth (Voigt & Kingston 2016, 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 importance: 1) the destruction and transformation of their natural habitats for agriculture, wood harvesting or residential and commercial development; 2) other forms of human intrusion and disturbance (including tourism); 3) mining and quarrying; 4) hunting for meat and traditional medicine; and 5) fires and severe weather events such as heat waves or tropical storms (O'Shea et al. 2016, Voigt & Kingston 2016, IUCN 2020). Further threats have been identified recently, such as emergent diseases (e.g. White Nose Syndrome), massive culling for crop protection, and human persecution in response to the risk of bat-borne diseases spreading to humans (Blehert et al. 2009, O'Shea et al. 2016, Aziz et al. 2017, Florens & Baider 2019, Zhao 2020). Several recent studies have also documented the direct or indirect impacts of invasive species on many bat species (Menchetti et al. 2014, Welch & Leppanen 2017, Hernández-Brito et al. 2018, Dorrestein et al. 2019). Among these more recently recognised threats, Welch and Leppanen (2017) highlighted an unexpected, understudied and probably underestimated threat to bats, namely the impact of invasive predators. Of all the invasive predators, the cat *Felis catus* is the species most frequently cited as potentially affecting bats (Welch & Leppanen 2017).

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

Bats typically have low reproductive rates, delayed maturity and long gestation periods, naturally 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 2016, 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 by cats (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). 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 individuals 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 in 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% 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

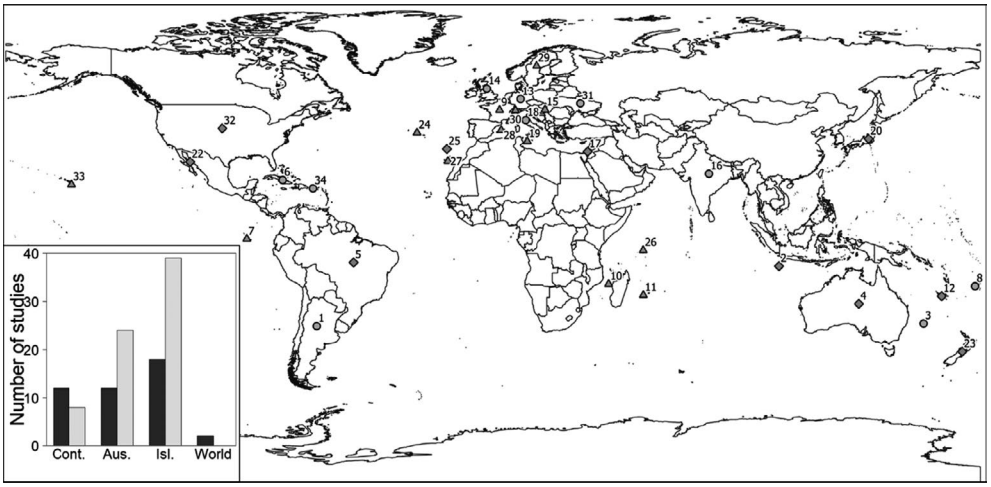

Fig. 1. Geographical distribution of studies where bat species were recorded as being preyed upon or threatened by cats (dot), found in cat diet studies (triangle) or both (diamond). Numbers next to dots refer to the site identification codes given in Appendix S2. Only one dot (and number) is shown per 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).

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

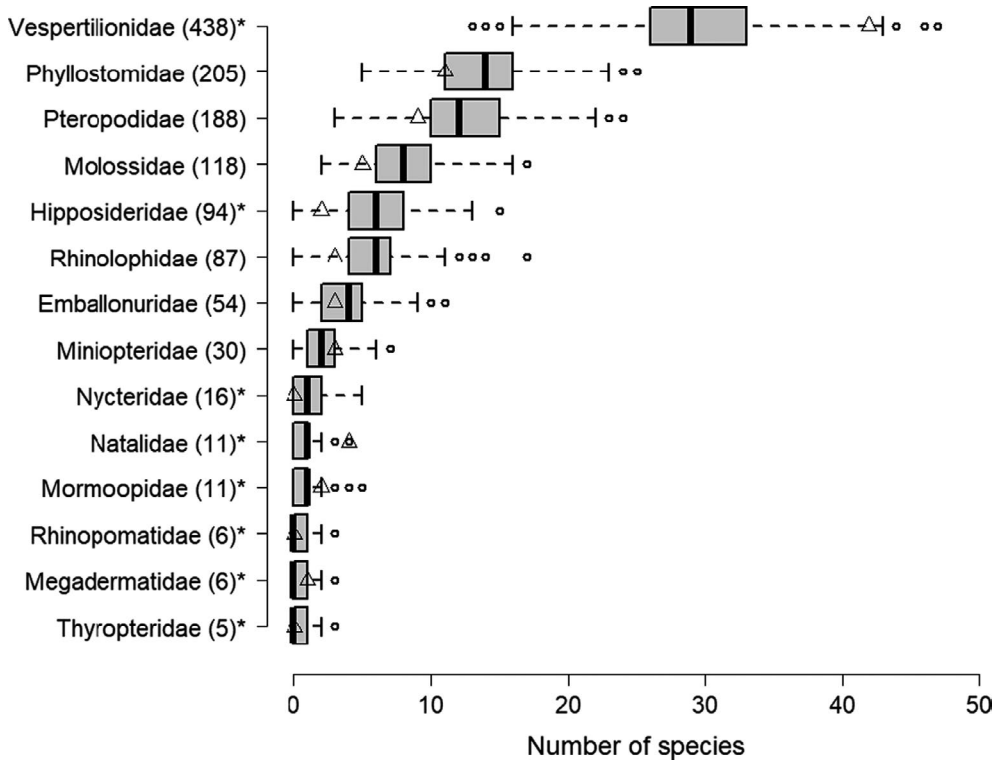

Fig. 2. Susceptibility of the different bat families to predation by cats (restricted to families with at least five species, species number in parentheses). The boxplots represent the distribution of the number of species expected to be preyed upon according to the overall percentage of cat prey species (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.

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

	Number of bat species		
IUCN categories	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%

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

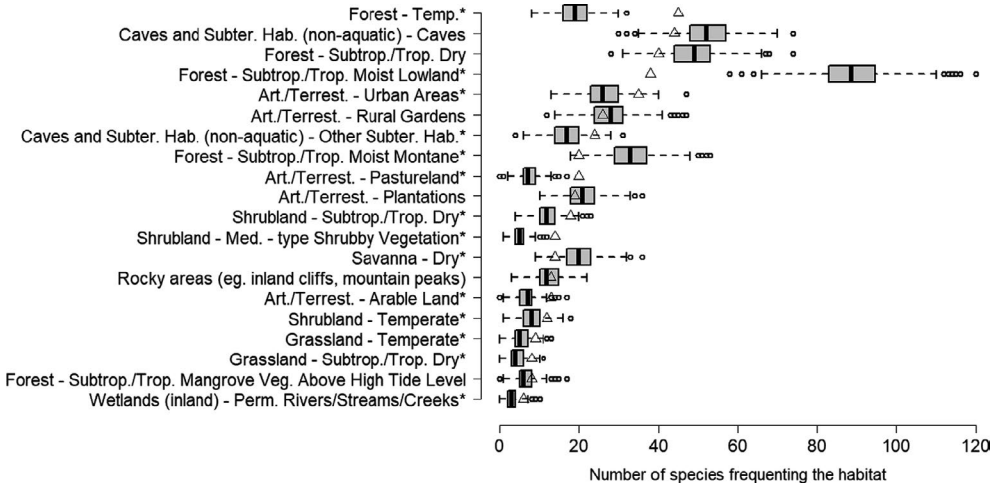

Fig. 3. Comparison of the distribution of bat species among the 20 habitat types recorded as mainly frequented by bats (International Union for Conservation of Nature database). The boxplots represent the distribution of the number of species frequenting the habitat expected according to the overall 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.

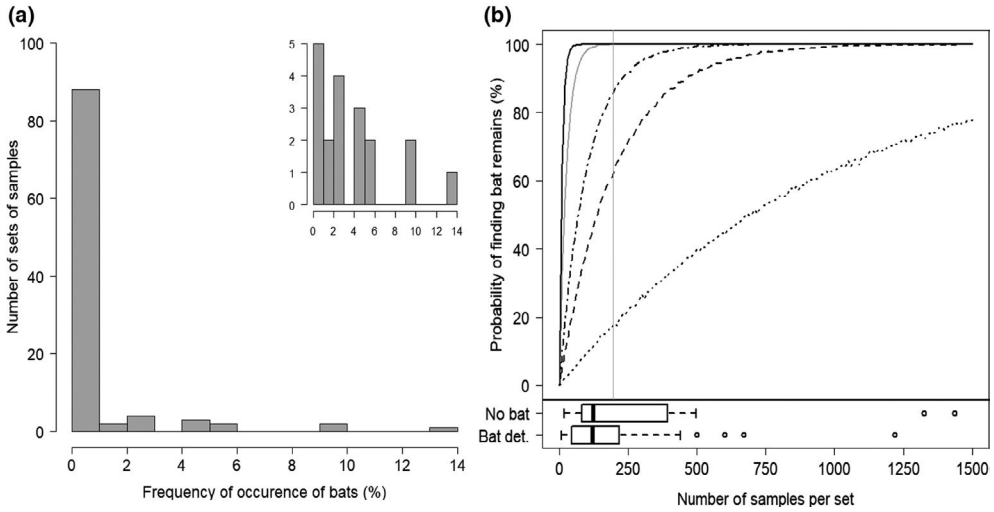

Fig. 4. (a) Distribution of the frequency of occurrence (FO%) of bats in the diet of cats, from the 76 cat diet studies in which bat FO% was calculated, representing 102 sets of samples. The main histogram represents the distribution of FO% for all sets of samples, while the inserted histogram represents the distribution of FO% for sets where bats were found (n = 19). (b) Estimation of the probability of finding bat remains in cat diet according to the number of samples per set, and the true FO% and comparison of the number of samples per set according to whether bats were detected. The solid line corresponds to a FO% of 10%, dot-dashed line to a FO% of 1%, short-dashed line to a FO% of 0.5%, dotted line to a FO% of 0.1% and the curved grey line to the average FO% of 3.9%. The vertical grey line represents the average number of samples per set. Boxplots represent the number of samples per set of diet studies where bats have been detected (Bat det.) or not (No bat).

detect bats (GLM, $\beta = 0.002 \pm 0.001$, $P = 0.052$; 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 underappreciated 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 underestimate 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.

Bat species preyed upon or threatened by cats

Predation of bats by cats appears to be a widespread phenomenon. Indeed, 86 bat species were identified as preyed upon or threatened by cats, and these species varied widely in terms of body mass, diet and preferred habitat. Our collation revealed that some of the world's largest bats (e.g. *Pteropus* species) are consumed by cats, consistent with records of predation by cats of mammals (in other taxonomic groups) that have a weight equal to or even greater than that of cats (maximum mass of mammalian prey, >5 kg *cf*. typical mass of cat, 3.3–4.2 kg; Kutt 2012, Fancourt 2015, Woinarski et al. 2019, Woolley et al. 2019). The bat species known to be preyed upon or threatened by cats belonged to 12 of the 20 bat families, but we found that they were better represented in certain families, notably in the most numerous bat family, Vespertilionidae: almost 10% of species in that family are preyed upon or threatened by cats (Fig. 2). Hence, it seems likely that some families are more susceptible to predation than others. As an example, Rodríguez-Durán et al. (2010) highlighted that, in a cave housing several species of bats, the relative proportion of bat species preyed upon by cats was not correlated with the abundance of each species. Welch and Leppanen (2017) suggested that, in this case, flight behaviour might influence susceptibility to predation by cats. There are also certain behaviours, particularly those relating to foraging, which could make certain species more susceptible to predation by cats, such as feeding on or near the ground; examples include *Pteropus melanotus natalis, Mystacina tuberculata*, *Antrozous pallidus* and Phyllostomidae (Ross 1961, Daniel 1979, Bonaccorso & Gush 1987, Tidemann 1987, Tidemann et al. 1994). A further possibility is that the unequal proportional representation of bat species preyed upon by cats across bat families may be a consequence of varying abundances of the bat species across families. For example, if Vespertilionidae are on average more abundant than bats in some other families, cats may be taking a higher proportion of Vespertilionidae simply because of a higher encounter rate.

About a quarter of the 86 bat species preyed upon or threatened by cats have threatened or Near Threatened conservation status (Red List categories: CR, EN, VU and NT; IUCN 2020) and so require special attention and a rapid assessment of the threat that cats can represent for them. One bat species known to be eaten by cats (*Pipistrellus murrayi*) became extinct in 2009; although predation by cats may have contributed, it was the cumulative impacts of habitat destruction and a range of invasive species which led this species to extinction (Tidemann et al. 1994, Woinarski 2018, IUCN 2020).

Bat predation by cats is poorly documented and remains largely neglected by conservationists interested in bats. For only 18 of the 86 species that we report as preyed or threatened by cats, the cat is listed as a threat in the IUCN Red List database. This may indicate that, for some bat species, predation by cats occurs but is rare or inconsequential with respect to their conservation status, or that there has been inadequate recognition to date of the threat posed by cats in these assessments.

We found more documents concerning predation of or threats to bats by domestic or free-roaming than feral cats; however, this result but may reflect some biases, for example bats taken by pet cats may be more readily identifiable than remains inside feral cat stomachs or scats. All types of cat, whether domestic, free-roaming or feral, appear to be potential predators of bats.

Our results suggest that bats occurring in some habitats, notably 'Forest – Temperate', 'Artificial/Terrestrial – Urban Areas' and 'Caves and Subterranean Habitats

(non-aquatic) – Other Subterranean Habitats', are more likely than others to be killed by cats. Cats may be more abundant in these habitats or may prefer to hunt there (Legge et al. 2020). Alternatively, these habitats may represent opportunities for regular encounters between cats and bats or for facilitated predation of bats by cats. How, when and where cats prey upon bats is still not well understood. The sparse information in the literature suggests that the predation of bats may occur in caves or buildings when they fall to the ground, from the air during emergence and return to roosts, or when bats feed near the ground (Tidemann 1987, Tidemann et al. 1994, Rodríguez-Durán et al. 2010, Ancillotto et al. 2013, Tuttle 2013).

Cat dietary studies and rates of predation of bats by cats

We found high variability in the FO% of bats in cat dietary studies. This variation may be due to the influence of site and habitat and potentially season, the abundance of bats in the areas studied, and the abundance of alternative prey. In New Caledonia (south-west Pacific), Palmas et al. (2017) reported FO% of bats in cat diet varying from 0 to 13%, depending on sampling site and habitat. These results are in accordance with the facts that the population-level impacts of predation can be variable (Welch & Leppanen 2017), and that bats are not usually the primary prey of invasive predators (Pitt & Witmer 2007).

The comparison of FO% of bats in cat diets showed no statistically significant difference between islands, mainland Australia and continents (no bats were reported in the 11 cat dietary studies conducted on continents). However, reports of bat predation by cats from continents do exist (unpublished data), and more work should be dedicated in this context to assess the level of impact. Additionally, most studies that identify bat species as being preyed upon or threatened by cats were from islands, and this was disproportionate to the small area of islands relative to continents. This may be due to: 1) the greater species richness of bats on islands, with more than half of bat species (60%) present on islands, and a quarter (25%) restricted to islands; 2) islands tending to have higher densities of cats than mainland areas (Jones et al. 2009, Conenna et al. 2017, Legge et al. 2017, Frick et al. 2019); and 3) a disproportionately large share of the world's threatened bat species occurring on islands, so that island bats may have been subject to a correspondingly disproportionate share of research, including on the factors that cause mortality.

There is only a relatively small number of cat dietary studies in which bats were reported as prey, and an even smaller number in which bat species were identified. The comparison of scat and stomach/gut samples suggests that there is a greater probability of detecting bat remains and identifying the species consumed when using stomach/gut samples than when examining scats, as previously reported by Murphy et al. (2019). We found that most cat dietary studies had insufficient sample sizes to detect bats reliably. The likelihood that sampling is inadequate to provide robust estimates of bat FO% in cat diet has probably caused some authors to exclude bats from reported items in their studies. Indeed, in our collation, most of the data on bat predation by cats were extracted from supplementary materials in studies, and bat predation was not mentioned in the main text. However, considering the density of cats and their ubiquity, and the local population sizes of some bats, even low FO%s can represent a considerable number of bats killed. We note that FO% of bats in cat dietary samples may under-estimate the incidence of cats killing bats, if cats kill bats but do not eat them. Conversely, predation rates may be over-estimated if cats are scavenging on bat carcasses, although consumption of carrion is relatively uncommon in cats (Woinarski et al. 2019).

The impact of predation by cats on bats

The genuine impact of predation by cats on bat populations remains to be assessed, but there are a number of reasons why we might expect predation by cats to have a significant impact on bats and to threaten their populations:

1. Bats have relatively few natural predators and show naïve behaviour towards some introduced predators (Durrell 1976, Tidemann 1987, Delpietro 1994, Baxter et al. 2006, Driessens & Siemers 2010, Lima & O'Keefe 2013).
2. Cats now occur across most of the Earth's surface, in all ecosystems frequented by bats (Global Invasive Species Database 2020, IUCN 2020). Cats are highly effective predators with strong abilities to jump and climb trees or walls, and can be arboreal predators (Case 2003, McComb et al. 2019). Furthermore, they exhibit some traits that make them well suited for efficiently hunting bats, such as the ability to hear high-frequency sounds (ultrasounds) and to see well at night (Heffner & Heffner 1985, Jones 1999, Jones & Holderied 2007); all bats are in the size range of prey taken by cats (Woinarski et al. 2019).
3. Bat populations are particularly sensitive to the loss of individuals because of their demographic attributes, such as relatively long lifespan and small litter size (McIlwee & Martin 2002, Kunz & Fenton 2005, Fleischer et al. 2017). In addition, there is evidence of predation by cats disproportionately affecting female bats, which could amplify demographic impacts (Ancillotto et al. 2013).

4. Quantitative studies of predation of bats by cats remain rare; however, the number of individual bats preyed upon by cats can be significant. For example, Woods et al. (2003) estimated that in five months, domestic cats in Great Britain killed at least 170000 bats (0.3% of an estimated 57 million mammalian prey). Scrimgeour et al. (2012) reported that an individual cat killed at least 102 bats in seven days. Murphy et al. (2019) developed estimates of the number of individuals in key mammal groups killed each year by feral cats in Australia. Although they did not estimate the numbers of bats killed, their dataset and methodology can be used to estimate that approximately 440000 bats are killed each year in Australia (0.7% of 459 million native mammalian prey; unpublished data).
5. The noise, odour and movement associated with bat roosts tend to attract cats. The presence of cats near a roost can severely affect a bat colony directly, through predation of individuals, notably young, which remain immobile for a long time, or indirectly, by influencing bat behaviour and possibly forcing bats to leave their roost (Kalcounis & Brigham 1994, Rydell et al. 1996, Lima & O'Keefe 2013, Welch & Leppanen 2017, Ancillotto et al. 2019). Roosts are a critical, and often limited, resource for bats, in which bats are regularly gathered and most vulnerable to predation (Tuttle & Stevenson 1982, Lewis 1995, Welch & Leppanen 2017).

CONCLUSION

Cats are now found almost throughout the world, in all ecosystems frequented by bats. They are able to prey upon bats of all sizes, from a range of bat families and in varied habitats. It is therefore likely that our review paints a fragmentary and only partial picture of the true impacts of cats on the world's bat species. The threat posed by cats to bats adds to the long list of threats already affecting this group of mammals, which fulfil key ecological functions in many ecosystems and provide essential ecosystem services, such as insect regulation, pollination and seed dispersal. This is particularly (but not exclusively) the case on islands, where bats are often the only native terrestrial mammals and therefore represent an irreplaceable biological group with many endemic species. The impact of cats on bats on continents may also be high, but it remains just as poorly understood as the impact on islands.

RECOMMENDATIONS

Our review indicates that predation by cats may be a more serious threat to the conservation of the world's bats than previously recognised. We found that many bat species have been reported as killed by cats, but predation by cats is recognised as a threat in IUCN conservation accounts for only a few of these species. We recommend that authors of those accounts give consideration to including predation by cats as a threat and enhanced management of cats as a priority conservation response. In some cases, uncertainty about the population-level impacts of predation by cats should be resolved through targeted quantitative studies of the extent and consequences of predation.

According to Williams et al. (2020), priority research must be aimed at assessing the extent of the threat and providing management solutions, not just situational awareness. Even before starting new research, conservation actions can be carried out to protect roosts. For example, bats in caves where cats are likely to attack can be protected by installing doors that prevent access to cats, but allow bats to enter safely (Tuttle 2013).

We propose four main lines of future research directions:

1. Finding and assessing conservation actions and tools to protect bats from predation by cats. A special effort should be made to raise awareness and educate people, notably pet owners, about the impact of cats on bats and other taxa, as this information is poorly known and sometimes denied, particularly in relation to domestic and stray cats (McDonald et al. 2015, McLeod et al. 2017, Loss et al. 2018, Linklater et al. 2019). In the particular case of domestic cat management, it has been shown that a collaborative approach to finding a compromise and a solution that takes into account the owners' opinions and practices is more productive than a confrontation between managers and owners (Crowley et al. 2020).
2. Identifying ecological and biological traits that may render particular bat species more susceptible to predation by cats than others.
3. Further assessing the extent of the threat posed by cats to bats by:
   a. Assessing the frequency and intensity of predation. This includes more studies of cat diet with sufficiently large numbers of samples analysed per season and per site. We recommend sets with at least 250 samples, in order to be able to find bats with a probability of 90% for a FO% of 1% and 70% for a FO% of 0.5% (Fig. 4b). Cat dietary studies based on the collection and analysis of scats are reliable and relatively low-cost methods of assessing the place of bats in the diet of cats, particularly feral cats, but may have lower likelihood of detecting bats than studies that sample cat stomachs.

b. Identifying bat species in cat dietary sampling where possible. This may be possible with fine-scale observation, but recent developments in molecular analysis of samples may help identify the species consumed. Furthermore, referencing and sharing observational data on predation of bats by cats and studies on capture even without consumption could be useful to identify the species of bat consumed and to understand the extent of this phenomenon more fully. The use of forensic DNA analysis techniques on injured or dead bats can complement observational data and provide additional information on the origin of injuries, to identify predation by cats (Khayat et al. 2020).
c. Identifying types of cat and estimating their density would be useful for estimating total numbers of bats preyed upon by cats. Such studies should also consider the extent to which consumption of bats by cats may be a result of predation, or may instead arise from scavenging by cats on already dead bats.
d. Identifying the extent to which predation on bats may be largely driven by individual cats that specialise on bats, the factors that influence such individual preferences, where such predation is focused (e.g. at bat roost sites), and how any such bat-specialist cats may best be controlled. Individual cats also differ in hunting behaviour and preference. Some individual cats may be responsible for very high rates of predation on particular species, including threatened mammals (Moseby et al. 2015), and including both common and threatened bat species (Scrimgeour et al. 2012, Khayat et al. 2020).
e. A better understanding of the population dynamics of various bat species is needed, in order to assess the consequences of cat-induced mortality on population viability.

4. Prioritise bat conservation by identifying and managing factors that magnify the impact of cats on bats, including consideration of:
   a. Where the bat species at greatest risk of extinction are found.
   b. Where cats occur in the highest densities.
   c. When bat FO% in cat diet is particularly high, and where other sources of prey for cats are less abundant.

In addition to these research suggestions, we recommend enhanced management of cats, in particular on islands, in areas important for threatened bat species, and at bat roost sites that may hold high proportions of the total population of some bat species. Such enhanced cat management may include curfews or containment of pet cats, intensive strategic trapping for unowned cats, prohibition of cat introductions to islands that do not currently have cats, and eradication of feral cats on islands with endemic bats.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. List of publications identifying bat species preyed upon or threatened by cats.
Appendix S2. Site identification codes related to the map of the geographical distribution of studies (Fig. 1).
Appendix S3. List of bat species with IUCN assessments in which cats are recorded as a threat (IUCN database downloaded in February 2020).
Appendix S4. List of the bat species preyed upon or threatened by cats.
Appendix S5. Distribution of species of bats preyed upon or threatened by cats and all bat species according to their taxonomic families (IUCN database downloaded in February 2020).
Appendix S6. List of published diet studies where bats are present in the sampling area.