Contributed Papers

Effects of roost specialization on extinction risk in bats

Maria Sagot† * and Gloriana Chaverri‡ *

†Department of Biological Sciences, State University of New York at Oswego, Oswego, NY 13126, U.S.A.,
email maria.sagot@oswego.edu
‡Universidad de Costa Rica, Golfito 60701, Costa Rica

Abstract: *Understanding causes and consequences of ecological specialization is of major concern in conservation. Specialist species are particularly vulnerable to human activities. If their food or habitats are depleted or lost, they may not be able to exploit alternative resources, and population losses may result. We examined International Union for Conservation of Nature (IUCN) Red List bat data and the number of roosts used per species (accounting for phylogenetic independence) to determine whether roost specialization is correlated with extinction risk. We found a significant correlation between the IUCN Red List category and the number of roost types used. Species that use fewer roost types had a higher risk of extinction. We found that caves and similar structures were the most widely used roost types, particularly by species under some level of risk of extinction. Many critically endangered, endangered, or vulnerable species used natural roosts exclusively, whereas less threatened species used natural and human-made roosts. Our results suggest that roost loss, particularly in species that rely on a single roost type, may be linked to extinction risk. Our focus on a single life history trait prevented us from determining how important this variable is for extinction risk relative to other variables, but we have taken a first step toward prioritizing conservation actions. Our results also suggest that roost specialization may exacerbate population declines due to other risk factors, such as hunting pressure or habitat loss, and thus that management actions to preserve species under risk of extinction should prioritize protection of roosting sites.*

Keywords: Chiroptera, endangered species, red list

Los Efectos de la Especialización de Dormidero sobre el Riesgo de Extinción de Murciélagos

Resumen: *Entender las causas y consecuencias de la especialización ecológica es una de las mayores preocupaciones de la conservación. Las especies especialistas son particularmente vulnerables a las actividades humanas. Si su alimento o sus hábitats son disminuidos o se pierden, es probable que no puedan explotar recursos alternativos y esto resulte en pérdida de poblaciones. Examinamos datos sobre murciélagos de la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) y el número de dormideros utilizado por especie (considerando la independencia filogenética) para determinar si la especialización de dormidero está correlacionada con el riesgo de extinción. Encontramos una correlación significativa entre la categoría de acuerdo a la Lista Roja de la UICN y el número de tipos de dormidero utilizados. Las especies que utilizan menos tipos de dormideros tuvieron un riesgo de extinción mayor. Encontramos que las cuevas y estructuras similares fueron el tipo de dormidero utilizado más comúnmente, particularmente por especies bajo algún nivel de riesgo de extinción. Muchas especies en peligro crítico, en peligro o vulnerables utilizaron exclusivamente dormideros naturales, mientras que las especies menos amenazadas utilizaron dormideros naturales y aquellos hechos por humanos. Nuestros resultados sugieren que la pérdida de dormideros, particularmente en aquellas especies que dependen de un tipo único, puede estar relacionada con el riesgo de extinción. Nuestro enfoque en un carácter único de la historia de vida nos impidió determinar cuán importante es esta variable para el riesgo de extinción en relación a otras variables, pero hemos dado el primer paso hacia la priorización de las acciones de conservación. Nuestros resultados también sugieren que la especialización de dormidero puede empeorar la declinación poblacional debido a*

otros factores de riesgo, como la presión de caza o la pérdida de hábitat, y por esto las acciones de manejo
para preservar especies bajo riesgo de extinción deberían priorizar la protección de los dormideros.

Palabras Clave: Chiroptera, especies en peligro, lista roja

Introduction

Ecological specialization is defined as the use of a restricted range of resources (Devictor et al. 2010). Understanding specialization is necessary for conservation because specialist species are particularly vulnerable to human activities. If their resources are depleted or lost, specialists may be unable to exploit alternative food items or habitats and populations may be extirpated (e.g., Henle et al. 2004; Safi & Kerth 2004; Clavel et al. 2010). Specialists are essential components of communities, and their loss could alter ecosystem functioning substantially (Clavel et al. 2010). Therefore, establishing conservation priorities requires knowledge not only of population trends but also understanding levels of resource specialization and the status of critical resources. Urgent actions to preserve these resources may be needed to save specialists.

Bats are essential components of communities because they are effective long-distance seed dispersers and pollinators, and by consuming a large number of potentially destructive insect pests, bats provide important services to humans (Kunz et al. 2011). At least 24% of all known species of bats are under threat as a result of human activities, including introduction of non-native species, hunting, loss of foraging habitat, and loss of roosts (Jones et al. 2003; Racey & Entwistle 2003). Roosts are essential resources for bats because they spend at least half their time in these structures, and roosts serve as refuge from predators and inclement weather (Lausen & Barclay 2002; Ferrara & Leberg 2005). Roosts also provide an important, if not exclusive, venue for social interactions such as copulation, feeding, and grooming (Wilkinson 1986; Kerth et al. 2003; Chaverri & Kunz 2006). One of the most widely recognized functions of roosts is habitat for rearing young (Kunz & Lumsden 2003; Altringham 2011). Thus, roosts are critical for the reproduction and survival of individuals.

Bats use a diversity of structures for roosting, including caves, hollow trees, foliage, and excavated termite nests, among others (Altringham 2011). Some species use several roost types. For example, the evening bat (*Nycticeius humeralis*) uses caves, trees cavities, tree-bark cracks, foliage, leaf litter, and human-made structures (Watkins 1972; Menzel et al. 2001; Perry & Thill 2008). Other roost-specialists use only one type of structure. For example, Spix's disc-winged bat (*Thyroptera tricolor*) roosts only inside the developing furled leaves of plants such as heliconias (Wilson & Findley 1977; Chaverri & Kunz 2011),

and the Mexican funnel-eared bat (*Natalus stramineus*) roosts only in caves (Arita & Vargas 1995; Pedersen et al. 2007).

We tested the hypothesis that species that use fewer roost types are at greater risk of extinction, as defined by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2013). Although other studies show that food and habitat specialization are correlated with extinction risk in temperate bats (Safi & Kerth 2004; Boyles & Storm 2007), we examined the relationship between resource specialization and extinction risk in bats worldwide. Finding these correlative patterns, especially at large scales, is a vital first step in revealing the mechanisms that produce them. These large-scale patterns are also important in prioritizing habitats, regions, and species for conservation. Based on the number of citations, research of this nature (e.g., Owens & Bennett 2000; Harcourt et al. 2002; Safi & Kerth 2004) has influenced greatly understanding of the effects of specific species' traits in extinction risk under current and future environmental change. Although research on species extinction has benefited from considering evolutionary history (i.e., phylogenies [Purvis 2008]), this approach has not been explored extensively. Thus, we looked for a large-scale correlative pattern between extinction risk and roost specialization that could be used to further explore the mechanisms behind, as well as the relationship between, specialization and other important species traits in producing the observed pattern. We explored this correlation from a phylogenetic perspective by accounting for phylogenetic nonindependence as well as for some life history traits that show phylogenetic signal. We sought to provide additional evidence of the important role roosts play in the lives of bats and to show that loss of these resources could bring concomitant losses of bat populations and the critical ecosystems services they provide.

Methods

Red List and Literature Search

From the IUCN Red List of Threatened Species (IUCN 2013), we obtained the conservation status of 385 bat species in Fritz et al.'s (2009) super tree. We assigned numerical values to the categories: 3, critically endangered; 4, endangered; 5, vulnerable; 6, near threatened; and 7, least concern. We also conducted a Web of Knowledge literature search (in February 2012) for publications that

described the roost types used by each of the species that had information on their conservation status (i.e., status other than data deficient). Keywords in the search were the species name and *roosts*. A total of 532 peer-reviewed journal publications matched our criteria. Once we had the detailed list of roost types used by each of the species, we classified them (13 categories) based on the most common terms used in the literature: 1, caves, cliffs, and crevices (opening or fissure in a rock); 2, tree cavities; 3, banks and ledges; 4, tree bark; 5, human-made buildings and structures; 6, leaf litter; 7, tree boles; 8, bamboo culm; 9, modified leaves and stems; 10, foliage and plant structures; 11, termite nests; 12, bird nests; and 13, furled leaves. Furled and modified leaves and stems were considered a separate category because species using these structures present special morphological and behavioral adaptations necessary to use these roosts (Wilson & Findley 1977; Schliemann & Maas 1978; Kunz & Lumsden 2003). To test for interaction among red-list categories and species range sizes, we classified range sizes (5 categories): 1, 1–50,000 km^2; 2, 51,000–100,000 km^2; 3, 101,000–500,000 km^2; 4, 5,01,000–20,000,000 km^2; 5, 21,000,000–43,000,000 km^2.

Analytical Approach

We used the continuous module within BayesTraits (Pagel 1994) to test for a correlation between red-list category and the number of roosts used by each species of bat. Continuous is a phylogenetic general linear square method (GLS) that estimates the variance of evolutionary change (i.e., Brownian motion parameter [Pagel 1997, 1999]) and the covariance of changes between pairs of traits to test for correlation. To do this, the program runs 2 separate models, one in which correlation between traits is assumed (using the GLS approach) and one where the correlation is set to zero. For both models, we assumed a random walk. BayesTraits does not test hypotheses automatically; it uses Markov chain Monte Carlo methods to derive log likelihoods. Thus, as part of the results, continuous provides log likelihoods for the model of correlated evolution and for the model where the correlation was assumed to be zero. These 2 likelihoods were compared using a likelihood ratio test normally distributed as a χ^2 with 1 df to determine which model fits the data better.

Within the model, λ (lambda), κ (kappa), and δ (delta) transformations, which allow one to test tempo, mode, and phylogenetic associations of trait evolution, respectively, take a default value of 1.0. These constant values are based on the assumption that the phylogeny and its branch lengths have a constant variance. If trait evolution has not followed the topology or the branch lengths, these values will depart from 1.0. Thus, incorporating them into the analysis substantially improves the fit of the data to the model (Pagel 1997, 1999). Consequently, we calculated these parameters while testing

for correlated evolution of extinction risk and number of roosts used. Lambda transformation estimates whether the phylogeny correctly predicts the patterns of covariance among species on a given trait. A value of 1 corresponds with the original, untransformed branch lengths, whereas $\lambda = 0$ corresponds with complete absence of phylogenetic structure. Kappa is used to test for punctuational versus gradual mode of trait evolution in branches of different lengths. Kappa values >1 indicate that longer branches contribute more to trait evolution. When $\kappa = 0$, trait evolution is independent of the length of the branch. Delta detects whether the rate of trait evolution has accelerated or slowed over time as one moves from the root to the tips. Delta values <1 suggest that shorter paths contribute disproportionately to trait evolution, whereas values >1 indicate that longer paths contribute more to trait evolution.

Both the red-list category and roost variables were treated as dummy variables. Body size, brain size, and metabolic rate show phylogenetic signal in bats (Capellini et al. 2010; Rojas et al. 2013; Safi et al. 2013). Thus, when controlling for phylogeny, we not only controlled for phylogenetic independence but also, to some extent, for these life history traits. Because we focused on only one correlate of extinction risk, we could not quantify the importance of this variable relative to others in determining extinction risk or test for interactions between this variable and others.

Results

We found conservation status and roost type data for 385 bat species (18 families and 128 genera) distributed worldwide (except in polar regions and on isolated islands, particularly from Oceania). The body mass of the species ranged from 22 mm (*Craseonyteris thonglonyai*) to 289 mm (*Pteropus poliocephalus*), and species exhibited a diverse range of diets (carnivorous, piscivorous, sanguinivorous, nectarivorous, insectivorous, and frugivorous).

Kappa transformation did not depart from 1, suggesting that both traits evolved gradually across the phylogeny ($\kappa = 1.057$, $p > 0.05$). Lambda and δ departed from 0, suggesting that phylogenetic history had a minimal effect on trait evolution ($\lambda = 0.30$, $p < 0.05$; $\delta = 2.96$, $p < 0.001$). Maximum likelihood analysis indicated there was a significant correlation between the red-list category and the number of roost types used after controlling for phylogenetic independence. The correlated model fits the data better than the independent model (log likelihood –955.21 vs. –1005.72, $p < 0.05$), and red-list category was not associated with range size ($T_{390} = 1.847$, $p = 0.06$). Species that used fewer roost types had a higher risk of extinction. All three species considered critically endangered used a single roost type.

Table 1. Number of bat species and average number of roost type per species for each red-list category.

Category*	No. of species	No. roost types (range, median)
Critically endangered	3	1 (1)
Endangered	11	1.67 (1–4, 1)
Vulnerable	31	1.40 (1–4, 1)
Near threatened	33	2 (1–5, 2)
Least concern	303	2.31 (1–6, 3)

*International Union for Conservation of Nature categories (IUCN 2013).

Table 2. Number of species that roost exclusively in human-made structures, natural structures, or both. Status refers to range of concern status for species within that roost category.

Roost	No. of species	Conservation status[a]	Percent threatened[b]
Human made	2	LC	0
Natural	178	CR-LC	28
Both	205	EN-LC	14

[a] Range of conservation statuses for species within that roost category (CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern).
[b] Percentage of species within that roost category considered critically endangered, endangered, or vulnerable.

Endangered and vulnerable bats used 1.66 and 1.40 roost types, respectively, and a maximum of 4 (Table 1).

The average number of roost types used per species was 2.17 (SD 1.11, range 1–6). All bat species considered belonged to 1 of 5 conservation status categories (Table 1). Of the 178 species that used natural roosts exclusively, 20% were critically endangered, endangered, or vulnerable (Table 2). In contrast, the only 2 species that used human-made roosts exclusively were categorized as least concern. Moreover, of the 205 species that used both human-made and natural roosts, 5.3% were endangered or vulnerable (Table 2). We found that all critically endangered bat species lived on islands and thus had a small or very restricted range size (Table 3). Around 60% of species considered endangered and 50% of vulnerable species occurred only on islands. The major threats for the species with highest extinction risks (critically endangered, endangered, or vulnerable) were predominantly habitat degradation and roost loss (Table 3). Other important threats included hunting and introduction of novel predators.

Caves and similar structures such as cliffs and crevices were the most widely used roost types (Table 4) across all land regions (Table 5). Use of cave roosts was particularly common in species under some level of risk of extinction (vulnerable up to critically endangered) (Fig. 1). Banks, ledges, and foliage roosts were widely used by species considered endangered (critically or not) and vulnerable. Human-made structures were more commonly used by

species of least concern. Other roost types, such as leaf litter, tree boles, bamboo culm, termite nests, and furled leaves were exclusively used by species of least concern (Table 4). Species categorized as least concern used an average of 2.31 roosts and up to 6 different types. The number of roost types used was significantly different between concern categories ($F_{1,383} = 26.06$, $p < 0.001$).

Discussion

Our results suggest that roost specialization may be an important correlate of extinction risk in bats that may exacerbate the effect of other risk factors such as hunting pressure and habitat fragmentation and loss (O'Grady et al. 2004; Machado & Loyola 2013). Specialization increases dependence on specific resources (Begon et al. 1996). Thus, when relevant resources decrease, populations of specialists may decline because they cannot 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 a range of terrestrial and marine animals (e.g., insects, Hughes et al. 2000; reptiles, Foufopoulos & Ives 1999; birds, Owens & Bennett 2000; mammals, Harcourt et al. 2002). However, most of the studies on the extinction risk of specialized species have focused on broad resources, such as habitat use (e.g., Korkeamäki & Suhonen 2002; Bonin 2012; Suhonen et al. 2014). A few researchers have investigated the association between dietary specialization and conservation status, but their results were contradictory (e.g., Laurance 1991; Reed 1995; Harcourt et al. 2002; Safi & Kerth 2004; Boyles & Storm 2007). These mixed results may be related to the fact that in addition to food, animals depend on a variety of other resources within their habitat.

Roosts are extremely important to the fitness of bats and other animals because they provide protection from inclement weather and predators and a venue for social interactions (e.g., Kunz & Lumsden 2003; Kerth 2008; Pavey et al. 2014). Some species invest a substantial proportion of their time locating new roost sites and in the process may lose previous associates (Chaverri & Kunz 2011), with concomitant effects on group cohesion and performance (Mullen & Copper 1994). In addition, finding new roosts may be difficult or too costly for many species if these resources are rare (e.g., Li & Martin 1991; Beissinger 1996; Jones et al. 2003) or if the species has behavioral or morphological adaptations that restrict its use of roosts sites to a specific type (Chaverri & Kunz 2011). Thus, although roosts are an extremely important component of fitness and life history traits, ours is the first study to examine the association between extinction risk and specialization in roost use. Bats are ideal to test this relationship because roost specialization is likely to be related to extinction risk in bats (many species show

Table 3. Major threats (IUCN 2013) to bat species with highest extinction risk considered in our study.

Species	Red-list status	Island status[a]	Roost type[b]	roost loss or disturbance	habitat degradation or loss	hunting	introduced predators
Aproteles bulmerae	CR	Y	1	X		X	
Coleura seychellensis	CR	Y	1	X	X		X
Pteropus pselaphon	CR	Y	10	X	X		X
Acerodon jubatus	EN	Y	10	X	X	X	
Emballonura semicaudata	EN	Y	1, 3	X	X		
Myotis pruinosus	EN	Y	2		X		
Pipistrellus maderensis	EN	Y	1, 5	X	X		
Plecotus teneriffae	EN	Y	1, 5	X	X		
Pteropus livingstonii	EN	Y	10	X	X		
Pteropus mariannus	EN	Y	10			X	X
Acerodon leucotis	VU	Y	9			X	
Acerodon mackloti	VU	Y	10		X	X	
Chalinolobus tuberculatus	VU	Y	1, 2, 4, 5	X	X		X
Eidolon dupreanum	VU	Y	1, 10			X	
Macroderma gigas	VU	Y	1, 5	X	X		
Mystacina tuberculata	VU	Y	1, 2	X			X
Notopteris macdonaldi	VU	Y	1	X		X	
Pteropus melanotus	VU	Y	10		X	X	X
Pteropus ornatus	VU	Y	10			X	
Pteropus poliocephalus	VU	Y	10		X		
Pteropus pumilus	VU	Y	10		X	X	
Rhinolophus canuti	VU	Y	1	X	X		
Rousettus obliviosus	VU	Y	1	X			
Rousettus spinalatus	VU	Y	1	X	X		
Hipposideros halophyllus	EN	N	1	X	X	X	
Latidens salimalii	EN	N	1	X		X	
Leptonycteris nivalis	EN	N	1, 2, 5	X	X		
Myotis sodalis	EN	N	1, 2, 4, 5	X			
Rhinolophus maclaudi	EN	N	1		X	X	
Balantiopteryx io	VU	N	1	X	X		
Craseonycteris thonglongyai	VU	N	1	X			
Hipposideros marisae	VU	N	1, 3, 5	X	X		
Hipposideros ridleyi	VU	N	2, 5		X		
Leptonycteris curasoae	VU	N	1, 5	X	X		
Murina aenea	VU	N	10		X		
Musonycteris harrisoni	VU	N	1, 5		X		
Myotis capaccinii	VU	N	1, 5	X	X		
Myotis vivesi	VU	N	1		X		X
Rhinolophus guineensis	VU	N	1	X	X	X	
Rhinolophus mehelyi	VU	N	1	X	X		
Taphozous hildegardeae	VU	N	1	X	X		
Tomopeas ravus	VU	N	1	X			

[a] *Island status refers to whether species are endemic to islands: Y, yes; N, no.*
[b] *Key: 1, caves, cliffs and crevices; 2, tree cavities; 3, banks and ledges; 4, tree bark; 5, human-made buildings and structures; 6, leaf-litter; 7, tree boles; 8, bamboo culm; 9, modified leaves and stems; 10, foliage and plant structures; 11, termite nests; 12, bird nests; and 13, furled leaves.*

roost-specific adaptations and may not be able to adapt to new roost conditions [e.g., Wilson & Findley 1977; Schliemann & Maas 1978]) and because of the extreme dependence of bats on these resources (Lausen & Barclay 2002; Ferrara & Leberg 2005).

One of the most important correlates of extinction risk in mammals, and bats in particular, is a small geographic range size (Jones et al. 2003; Cardillo et al. 2006), which is not surprising (or informative) given that range size is a variable commonly used to determine IUCN Red List status, the dependent variable we used for extinction risk.

Our results showed that some of the most threatened bat species were restricted to islands. For example, the only 3 critically endangered species were *Coleura seychellensis, Aproteles bulmerae*, and *Pteropus pselaphon*, which are endemic to the Seychelles Islands, Papua New Guinea, and the Ogasawara Islands in Japan, respectively. Considering that dispersal restrictions force island populations to use only resources found in these relatively small territories and that roost choices are already limited for roost specialists, protecting essential roosting habitats should be a conservation priority on islands.

Table 4. Number of bat species and range of red-list categories (IUCN 2013) for the 13 different roost types considered.

Roost type	Species	Category*
Bamboo culm	8	LC
Banks, ledges	9	EN-LC
Bird nest	9	NT-LC
Caves, cliffs, and crevices	284	CR-LC
Tree cavities	144	EN-LC
Foliage and plant structures	95	CR-LC
Furled leaf	7	LC
Human structures	208	EN-LC
Leaf litter	6	LC
Modified leaves and stems	28	VU-LC
Termite nest	8	LC
Tree bark	27	EN-LC
Tree bole	6	LC

Abbreviations: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern.

Studies have provided strong evidence to suggest that forest loss is one of the main correlates of population decreases in bats, and we found that this is a major threat to most of the endangered bats we considered (Table 3). Yet, IUCN's assessment of major threats to endangered bats suggests that these species may be also particularly vulnerable to population decreases due to roost disturbance (Table 3). Most of the threats suggested for threatened cave-dwelling bats were related to human activities in these habitats, such as extraction of guano (McCracken 1989; IUCN 2013). Use of cave roosts is common in bat species that are under some level of risk of extinction (vulnerable up to critically endangered). Thus, to minimize or curtail the negative effects of human visitation on bat populations, particularly those that are most threatened, caves should be considered a conservation priority.

Another widely used roost type in our study was human-made structures. For some species, their few known roost sites were located in such places. Although these structures provide an alternate roosting habitat for species that have lost roost sites, reducing their risk of extinction, the use of human dwellings may exacerbate human–bat conflicts (Razafindrakoto et al. 2010; Altringham 2011). If these conflicts are to be reduced, natural roost sites used by bats that typically inhabit human dwellings need to be protected or alternatives, such as artificial bat boxes, need to be provided (Brittingham & Williams 2000). In addition, effective and humane ways of evicting unwanted bat colonies from human dwellings in countries or regions where such methods are unknown by the general public should be promoted.

One limitation of our study is that we focused on only one life history trait. Thus, we were unable to determine how important this variable is for extinction risk, relative to other variables. In addition, we were unable to determine if roost specialization interacts with other life history traits, threat factors, or demographic characteristics. A lack of detailed information on roosting ecology, especially from Asia and Oceania, is also a limitation. Although we have identified, for example, some of the roosting resources that are used by many species, detailed knowledge of other potential alternatives and how bats respond to loss of their main roosting habitats is still lacking. Murray et al. (2014) suggest better ways to asses species extinction risk, including intrinsic (life history and ecology) and extrinsic (environment and threats) factors in the evaluation. However, for multiple taxa, including bats, such analyses are difficult to perform because there is no detailed and accurate information on threats.

Table 5. Number of bat species* that use specific roost types in the 12 International Union for Conservation of Nature (IUCN) land regions.

IUCN region	Caves, cliffs, crevices	Tree cavities	Banks and ledges	Tree bark	Human-made, structures	Leaf litter	Tree boles	Bamboo culm	Modified leaves and stems	Foliage and plant structures	Termite nests	Bird nests	Furled leaves
Caribbean Islands	45	32	0	2	35	1	3	0	7	15	2	1	1
East Asia	2	2	0	0	2	0	0	0	0	4	0	0	0
Europe	61	31	0	5	50	1	0	2	4	10	0	2	1
Mesoamerica	76	55	0	11	72	2	4	0	12	16	4	1	1
North Africa	23	11	0	1	22	0	0	0	0	1	0	0	0
North America	34	23	0	12	34	3	1	0	0	7	0	1	0
North Asia	23	16	0	4	23	1	0	0	0	1	0	1	0
Oceania	39	19	3	2	26	1	1	3	1	25	1	5	0
South America	59	52	1	3	47	0	3	0	14	17	4	0	1
South and Southeast Asia	89	28	3	3	51	1	1	7	9	32	2	3	2
Sub-Saharan Africa	55	26	2	6	52	1	1	0	1	21	1	2	4
West and central Asia	40	22	0	3	40	0	0	0	2	7	0	1	1

Most species we considered occupy more than one land region; thus, total number of species does not equal the number of species in our study.
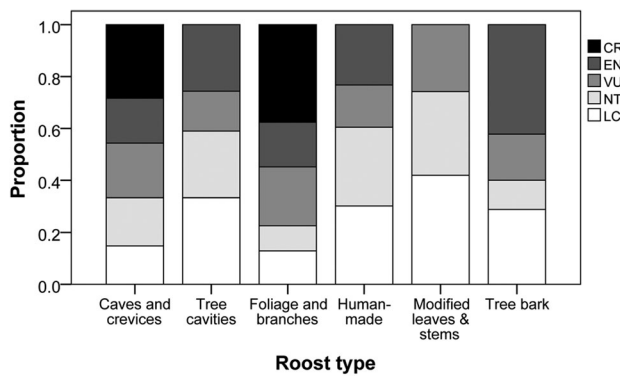
Figure 1. Proportion of roost types used by bats within each International Union for Conservation of Nature Red List category (IUCN 2013) (CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern). Bars show the relative importance of a particular roost type for bats within a given red-list category. For example, whereas 2 critically endangered and 224 least concern bats use caves and crevices, the bar for the former is larger because only 3 bats overall are considered critically endangered, whereas 304 are considered of least concern. Only the most commonly used roost types (i.e., those with the largest number of data points) are included.

Bats are important components of communities. They provide essential ecosystem services because they are efficient hunters of potentially damaging insect pests, are effective long-distance flower pollinators, disperse a large number of seeds from many important plant species, and provide valued products such as fertilizers (Kunz et al. 2011). Our results, and those of other studies (Jones et al. 2003; Safi & Kerth 2004; Boyles & Storm 2007), suggest that bats that specialize in the use of a narrow set of available resources have a higher risk of extinction than bats that do not specialize. To protect these essential resources would not only mean protecting the species that depend on them but also preserving the critical ecosystem services bats provide and preserving other organisms that use these resources.

Our results suggest that roost specialization in bats may be an important correlate of extinction risk. Although roosts have traditionally been considered important resources (e.g., Kunz & Lumsden 2003; Kerth 2008; Pavey et al. 2014), there is still scant information on whether and how animals cope with roost loss. Recent findings relative to bats suggest that loss of critical roosting resources may decrease colony size, social cohesion, and increase energetic expenditure and mortality (Borkin et al. 2011; Chaverri & Kunz 2011). Roost loss and disturbance of populations at roost sites are considered the most recurrent causes of population declines in most threatened bat species (IUCN 2013). Therefore, there is enough

evidence to assume that roost loss, particularly for species that rely on a single roost type, is an important cause of extinction risk. Notwithstanding the limitations of our study, it represents an important step toward introducing an additional factor that may influence extinction risk in bats.

Supporting Information

Raw data on roost type and IUCN status (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Altringham JD. 2011. Bats: from evolution to conservation. Oxford University Press, Oxford, United Kingdom.

Arita HT, Vargas JA. 1995. Natural history, interspecific association, and incidence of the cave bats of Yucatán, México. Southwestern Naturalist **40:**29–37.

Begon ME, Harper JL, Townsend CR. 1996. Ecology. 3rd edition. Blackwell Science, Oxford, United Kingdom.

Beissinger SR. 1996. On the limited breeding opportunities hypothesis for avian clutch size. The American Naturalist **147:**655–658.

Bonin M. 2012. Specializing on vulnerable habitat: *Acropora* selectivity among damselfish recruits and the risk of bleaching-induced habitat loss. Coral Reefs **31:**287–297.

Borkin KM, O'Donnell C, Parsons S. 2011. Bat colony size reduction coincides with clear-fell harvest operations and high rates of roost loss in plantation forest. Biodiversity and Conservation **20:**3537–3548.

Boyles JG, Storm JJ. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLOS ONE **2:**e672. DOI: 10.1371/journal.pone.0000672.

Brittingham MC, Williams LM. 2000. Bat boxes as alternative roosts for displaced bat maternity colonies. Wildlife Society Bulletin **28:**197–207.

Capellini I, Venditii C, Barton RA. 2010. Phylogeny and metabolic scaling in mammals. Ecology **91:**2783–2793.

Cardillo M, Mace GM, Gittleman JL, Purvis A. 2006. Latent risk and the future battlegrounds of mammal conservation. Proceedings of the National Academy of Sciences of the United States of America **103:**4157–4161.

Chaverri G, Kunz TH. 2006. Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). Journal of Zoology **270:**650–656.

Chaverri G, Kunz TH. 2011. Response of a specialist bat to the loss of a critical resource. PLOS ONE **6:**e28821.

Clavel J, Julliard R, Devictor V. 2010. Worldwide decline of specialist species: Toward a global functional homogenization? Frontiers in Ecology and the Environment **8:**222–228.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villeger S, Mouquet N. 2010. Defining and measuring ecological specialization. Journal of Applied Ecology **47:**15–25.

Ferrara FJ, Leberg PL. 2005. Characteristics of positions selected by day-roosting bats under bridges in Louisiana. Journal of Mammalogy **86:**729–735.

Foufopoulos J, Ives AR. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. The American Naturalist **153**:1–25.

Fritz SA, Bininda-Emonds ORP, Purvis A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecology Letters **12**:538–549.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization and extinction in primates. Journal of Biogeography **29**:445–456.

Henle K, Davies KF, Kleyer M, Margules C, Settele J. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation **13**:207–251.

Hopkins GW, Thacker JI, Dixon AFG, Waring P, Telfer MG. 2002. Identifying rarity in insects: the importance of host plant range. Biological Conservation **105**:293–307.

Hughes JB, Daily GC, Ehrlich PR. 2000. Conservation of insect diversity: a habitat approach. Conservation Biology **14**:1788–1797.

International Union for Conservation of Nature (IUCN). 2013. The IUCN red list of threatened species. Version 2013.2. IUCN, Gland, Switzerland.

Jones KE, Purvis A, Gittleman JL. 2003. Biological correlates of extinction risk in bats. The American Naturalist **161**:601–614.

Kerth G. 2008. Causes and consequences of sociality in bats. BioScience **58**:737–746.

Kerth G, Almasi B, Ribi N, Thiel D, Lüpold S. 2003. Social interactions among wild female Bechstein's bats (*Myotis bechsteinii*) living in a maternity colony. Acta Ethologica **5**:107–114.

Korkeamäki E, Suhonen J. 2002. Distribution and habitat specialization of species affect local extinction in dragonfly Odonata populations. Ecography **25**:459–465.

Kunz TH, Lumsden LF. 2003. Ecology of cavity and foliage roosting bats. Pages 3–87 in Kunz TH, Fenton, MB, editors. Bat ecology. The University of Chicago Press, Chicago.

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Science **1223**:1–38.

Laurance WF. 1991. Ecological correlates of extinction proneness in Australian tropical rain-forest mammals. Conservation Biology **5**:79–89.

Lausen CL, Barclay RMR. 2002. Roosting behaviour and roost selection of female big brown bats (*Eptesicus fuscus*) roosting in rock crevices in south-eastern Alberta. Canadian Journal of Zoology **80**:1069–1076.

Li P, Martin TE. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. AUK **108**:405–418.

Machado N, Loyola RD. 2013. A comprehensive quantitative assessment of bird extinction risk in Brazil. PLOS ONE **8**:e72283.

McCracken GF. 1989. Cave conservation: special problems of bats. Bulletin of the National Speleological Society **51**:49–51.

Menzel MA, Carter TC, Ford WM, Chapman BR. 2001. Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the Upper Coastal Plain of South Carolina. American Midland Naturalist **145**:112–119.

Mullen B, Copper C. 1994. The relation between group cohesiveness and performance: and integration. Psychological Bulletin **115**:210–227.

Murray KA, Verde Arregoitia LD, Davison A, Di Marco M, Di Fonzo MMI. 2014. Global Change Biology **20**:483–494.

O'Grady JJ, Burgman MA, Keith DA, Master LL, Andelman SJ, Brook BW, Hammerson GA, Regan T, Frankham R. 2004. What are the best correlates of predicted extinction risk? Conservation Biology **18**:1624-1635.

Owens IPF, Bennett PM. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97**:12144–12148.

Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London B Biological Sciences **255**:37–45.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. Zoologica Scripta **26**:331–348.

Pagel M. 1999. Inferring the historical patterns of the biological evolution. Nature **401**:877–884.

Pavey CR, Cole JR, McDonald PJ, Nano CEM. 2014. Population dynamics and spatial ecology of a declining desert rodent, *Pseudomys australis*: the importance of refuges for persistence. Journal of Mammalogy **95**:615–625.

Pedersen SC, Larsen PA, Genoways HH, Morton MN, Lindsay KC, Cindric J. 2007. Bats of Barbuda, northern Lesser Antilles. Special Publications, Museum of Texas Tech University **271**:1–19.

Perry RW, Thill RE. 2008. Diurnal roosts of male evening bats (*Nycticeius humeralis*) in diversely managed pine-hardwood forests. American Midland Naturalist **160**:374–385.

Purvis A. 2008. Phylogenetic approaches to the study of extinction. Annual Reviews in Ecology, Evolution and Systematics **39**:301–319.

Racey PA, Entwistle AC. 2003. Conservation ecology of bats. Pages 680–743 in Kunz TH, Fenton MB, editors. Bat ecology. The University of Chicago Press, Chicago.

Razafindrakoto N, Harwell A, Jenkins RKB. 2010. Bats roosting in public buildings: a preliminary assessment from Moramanga, eastern Madagascar. Madagascar Conservation and Development **5**:85–88.

Reed JM. 1995. Relative vulnerability extirpation of montane breeding birds in the Great-Basin. Great Basin Naturalist **55**:342–351.

Rojas D, Mancina CA, Flores-Martínez JJ, Navarro L. 2013. Phylogenetic signal, feeding behaviour and brain volume in Neotropical bats. Journal of Evolutionary Biology **26**:1925–1933.

Safi K, Kerth G. 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. Conservation Biology **18**:1293-1303.

Safi K, Meiri S, Jones KE. 2013. Evolution of body size in bats. Pages 95–115 in Smith FA, Lyons SK, editors. Animal body size: linking pattern and process across space, time, and taxonomic group. The University of Chicago Press, Chicago.

Schliemann H, Maas B. 1978. Myzopoda aurita. Mammalian Species **116**:1–2.

Suhonen J, Korkeamäki E, Salmela J, Kuitunen M. 2014. Risk of local extinction of Odonata freshwater habitat generalists and specialists. Conservation Biology **28**:783–789.

Watkins LC. 1972. Nycticeius humeralis. Mammalian Species **23**:1–4.

Wilkinson GS. 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. Animal Behaviour **34**:1880–1889.

Wilson DE, Findley JS. 1977. Thyroptera tricolor. Mammalian Species **71**:1–3.

Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agriculture Ecosystems and Environment **75**:13–30.