

ECOLOGICAL, MORPHOLOGICAL AND GEOGRAPHIC PREDICTORS OF EXTINCTION RISK IN BATS

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**ECOLOGICAL, MORPHOLOGICAL AND GEOGRAPHIC PREDICTORS OF
EXTINCTION RISK IN BATS**

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ABSTRACT

Bats comprise a diverse and speciose order (Chiroptera) with over 1,400 species inhabiting every continent on earth except Antarctica. Globally, bat species are experiencing unprecedented declines due to factors such as habitat loss and degradation, climate change, direct persecution, and disease. Unfortunately, many bat species are found in parts of the world that are difficult to access (e.g., Africa, Amazonia), roost deep in caves or hollow trees, and are most commonly active at night, all of which pose challenges to data collection. As a result, little data on the population abundance of many species of bats is available. It is thereby difficult to assess the conservation risk of data deficient bat species, as conservation status is based largely upon changes in population abundance. In this project, we conducted a phylogenetically controlled analysis to examine 835 species of bats with an International Union for the Conservation of Nature (IUCN) listing status with respect to 20 morphological (e.g., body size and forearm length), ecological (e.g., mean annual temperature and precipitation of the species' range), and geographic (e.g., range size, latitude) variables. Our analysis suggests that species with primary diets of nectar/pollen, those that inhabit islands, and those with large forearms and hindfeet are at a higher risk of extinction.

Thesis Supervisor: Professor Matthew Reudink

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This research took place on the traditional lands of the Tk'emlúps te Secwépemc within Secwépemc'ulucw, the traditional and unceded territory of the Secwépemc.

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INTRODUCTION

Understanding extinction risk and the traits that predispose organisms to population decline is paramount for enacting effective conservation measures. Predicting vulnerability to extinction is especially important for species that are rare on the landscape or challenging to survey, as data on population abundance may be sparse or unavailable (Welch & Beaulieu 2018). The order Chiroptera, which encompasses all bat species, is particularly limited in data concerning population trends for many species. This lack of information is largely due to many species of bats being nocturnal and/or living in regions that are sparsely populated and difficult to survey (e.g., the Amazon basin and central Africa). Additionally, members of order Chiroptera often roost in locations like caves and hollow trees that are difficult to access and survey, creating additional challenges for data collection.

Approximately 200 of the over 1400 bat species recognized by the International Union for the Conservation of Nature (IUCN) are designated as vulnerable, endangered, or critically endangered (IUCN 2022). Bat species worldwide have been experiencing population declines due to stressors such as habitat loss and fragmentation, the destruction of roosts and hibernacula, disease, and hunting (Tuttle 2013). Deforestation is particularly problematic as species richness and abundance in bats is positively related to forest cover (García-Morales et al. 2016). In addition, climate change is negatively impacting population abundance of bat species via its effect on their access to food, rate and duration of energy use, reproduction, hibernation, and developmental timing (Sherwin et al. 2012).

In addition to habitat loss and climate change, the recent emergence and rapid spread of White Nose Syndrome has been having devastating effects on bat populations, particularly in North America where infected populations have decreased by 60-98% (Peuchmaille et al. 2011).

White Nose Syndrome, a fungal disease that affects hibernating bats with an observed mortality rate of 90-100% has killed millions of individuals (Hoyt et al. 2021).

Chiroptera is the 2nd largest order within the Class Mammalia; it includes over 1400 species that are widely dispersed globally (Arnaout et al.2022). Bat species are incredibly diverse in their behavior and ecology. However, it remains unclear whether bats exhibiting a particular behavior (e.g., foraging behavior), or ecology (e.g., diet, habitat), are more susceptible to population declines and at a higher risk of extinction than others. This information is particularly important as it can provide guidance for focussing conservation efforts on species that have not been assessed by the IUCN due to a lack of data on population abundance and trends. Jones et al. (2003) examined the traits associated with extinction risk of over 300 bat species and found smaller wing aspect ratios as well as smaller geographic ranges to be associated with a higher risk of extinction. They also noted that extinction risk is not distributed randomly throughout the Order Chiroptera; closely related species have a similar risk of extinction, and, at a broader taxonomic level, extinction risk differs between the suborders Megachiroptera and Microchiroptera. More members of Megachiroptera face a high risk of extinction than members of Microchiroptera.

In a recent study, Welch & Beaulieu (2018) examined predictors of extinction risk in bats and found that island endemism and small geographic ranges were associated with a higher risk of extinction. Using this information, the authors constructed a model to assess predicted extinction risk in comparison to the IUCN (International Union for Conservation of Nature) listed conservation category. This model was shown to be effective in predicting the risk of extinction with over 90% of bat species having the same threat level as the IUCN listed status. Like Jones et al. (2003), Welch & Beaulieu (2018) found that extinction risk is non-randomly distributed through the order, with closely related species sharing similar extinction risk, and suggested that

the degree of relatedness to other species may be a useful tool in inferring extinction risk for data deficient species.

Previous work on predicting extinction risk in bats has faced two major limitations. Neither the Jones et al. (2003) and Welch & Beaulieu (2018) analyses incorporated behavioural and ecological factors that may play an important role in influencing susceptibility to extinction; these include variables such as diet, habitat type, and climatic variables (e.g., annual precipitation, mean temperature of range annually, isothermality, etc.) associated with where the species is found. The lack of habitat information is particularly problematic as species richness and abundance in bat species decline in response to habitat loss (Muylaert et al. 2016). Furthermore, forests are being lost disproportionately in comparison to other habitats due to deforestation (Frick et al. 2019), which may put forest-dwelling bats at higher risk. Incorporating factors such as habitat, diet, and climate may be key in constructing models that effectively predict extinction risk in data deficient bat species.

To assess the influence of biological, behavioural, and ecological factors on extinction risk in bats, we compiled data with over 20 morphological, ecological, and geographic variables for 835 bat species that have been assessed by the IUCN. We then constructed a series of phylogenetically controlled models to assess the combination of factors that best predict the current IUCN threat category for data-rich species. Using this model, future work will then be able to extrapolate these findings to data-deficient species to generate a predicted extinction risk classification.

METHODS

Study Species

Order Chiroptera, which makes up 20% of all mammals consists of over 1400 species of bats that are widely distributed globally (Arnaout et al. 2022). This study concentrated on 835 species for which IUCN listing status, as well as information on morphology, behaviour, and ecology was available (IUCN 2022).

Data collection

To examine the possible relationship between various geographic, ecological, and morphological traits (Table 1) and extinction risk in bat species, data on over 1200 of the 1400 species of bats were obtained from the International Union for Conservation of Nature (IUCN 2022).

Table 1. All Variables used for analysis in this study listed with a brief description. All data was sourced from the International Union for Conservation of Nature (IUCN).

Variable:	Description:
Average Weight (g)	The average weight of an individual, measured in grams
Hindfoot (mm)	Length of hindfoot measured in millimetres
Altitudinal range lower (m)	Lowest point of altitudinal range measured in metres
Altitudinal range upper (m)	Highest point of altitudinal range measured in metres
Primary diet	The food source (insects, nectar/pollen, fruit, other) most frequently consumed by individuals.
Area (km)	The range size of the species, measured in kilometers
Area (m)	The range size of the species, measured in meters
Island/mainland classification	Classification if a species is either endemic to an island or is found on mainland environments.
Conservation category	Conservation category is listed from 1-5 and is characterized based upon the IUCN criteria.
Habitats	The most frequent habitat type for a species (Artificial/Terrestrial, Forest, Caves, Open, Savana, Aquatic)
Temp seasonality (C°)	The standard deviation in temperature annually multiplied by 100. Described in degrees Celsius.
Isothermality (C°)	A quantification for the oscillation in temperatures from day to night relative to the annual oscillation of summer and winter
Maximum temperature of warmest month (C°)	The maximum temperature of the coldest month in a species range, measured in degrees Celsius.
Minimum temperature of coldest month (C°)	The minimum temperature of the coldest month in a species range, measured in degrees Celsius.
Temperature of annual range (C°)	The annual temperature range of a species range, measured in degrees Celsius.
Annual precipitation (mm)	The precipitation that accumulates annually in a species range, measured in mm.
Forearm average (mm)	The average length of the forearm measured in millimetres
Head body average (mm)	The average length of the bat species measured nose to base of tail, in millimetres
X centroid (absolute value)	The x centroid of the species range, as an absolute value.
Y centroid (absolute value)	The y centroid of the species range, as an absolute value.

Conservation Risk

Conservation risk as assessed by the IUCN classifies species into categories that are rank on scale of 1-5: 1 (least concern), 2 (near threatened), 3 (vulnerable), 4 (endangered) and 5 (critically endangered). Conservation risk is determined by the IUCN based on characteristics concerning population size, species geographic range size, and extinction probability analysis (IUCN 2022). Numerical thresholds associated with these characteristics result in the designation of each species into one of the above categories of extinction risk (1-5) (IUCN 2022).

Phylogenetic Methods

To control for, and examine the influence of, phylogenetic effects on predicting extinction risk, we obtained a full mammalian phylogeny from Upham et al. (2019). Using this phylogeny, we pruned our phylogenetic tree to construct a phylogeny for the 835 bat species for which we had sufficient data for analysis. This phylogeny was paired with characteristics available from the IUCN to examine the predictors of extinction risk while controlling for non-independence across species due to common ancestry.

Statistical Analysis

All statistical analyses were conducted in R 3.5.3 (R Core Team 2017) and all figures were created using the *ggplot* package (Wickham 2016). To examine the factors predicting extinction risk in bats, we constructed a series of phylogenetic generalized least squares (PGLS) models using the *nlme* package (Pinheiro et al. 2018) to control for the effects of common ancestry (Symonds & Blomberg 2014). We constructed a series of full models to examine the effects of morphological, behavioural, and ecological variables, while not allowing highly correlated ($r > 0.7$) variables to

remain in the same model (e.g., temperature seasonality, minimum temperature of range, and Y centroid of range). Next, we used the stepAIC function in the *mass* package (Venables & Ripley 2002), to evaluate model fit for all potential combinations of predictor variables (Burnham and Anderson 2003). The model with the lowest AIC value was then selected as the top model. This was repeated for each correlated variable which produced 6 separate models and using the ANOVA function, we examined the significance of each predictor variable in the top models.

RESULTS

Because several morphological and climatic variables were highly correlated, we ran a total of six full models. Each model included a different variable from the correlated group, followed by a stepwise model reduction procedure to identify a best fit model. Regardless of the full starting model, each reduced top model included significant effects of habitat, diet, island/mainland classification, and range size (area in km). Bat species inhabiting caves, islands, and those with small ranges and a primary diet of nectar/pollen were more likely to have a higher IUCN listing status (Tables 2, Figures 1-6.). Bat species that primarily consume pollen/nectar appear to be at the highest conservation risk in contrast with other diets such as insects (Table 2, Figure 4). Of the body size metrics we examined, weight was not an important predictor of conservation status; however, hindfoot length (mm) and, to a lesser extent, forearm length (mm), were found to increase with conservation category. Of the climatic variables, only temperature of the coldest month was a significant predictor of conservation status (Table 2). Ranges with higher minimum temperatures were associated with greater conservation category.

Table 2. Top AIC models demonstrating the effect of different Climatic and Morphological variables on conservation risk category. Significant results ($P < 0.05$) are bolded.

Model/Correlate Group	Variable	Beta Coefficient	Std. Error	T-Value	P-Value
Model 1 - Using variables Average Weight for the morphological variable and Minimum Temperature of the coldest month as the climatic variable (AIC = 2993.03)	Habitats Artificial/Terrestrial	0.1140	0.3757	0.30	0.76
	Habitats Caves	0.9526	0.3827	2.49	0.013
	Habitats Forest	0.3242	0.3725	0.87	0.38
	Habitats Open	0.4029	0.3850	1.05	0.30
	Habitats Savana	0.4791	0.3957	1.21	0.23
	Primary Diet Insects	-0.4368	0.5740	-0.76	0.45
	Primary Diet Nectar/Pollen	-1.0058	0.3131	-3.21	0.0014
	Primary Diet Other	-0.0153	0.4375	-0.04	0.97
	Island/Mainland Classification	-0.3789	0.1073	-3.53	0.0004
	Minimum Temp. of Coldest Month	0.0012	0.0006	2.18	0.03
	Annual Precipitation	-0.0001	0.0000	-1.69	0.09
	Area (km)	<-0.000001	<0.0001	-7.20	<0.0001
Model 2 - Using variables Average Weight for the morphological variable and Temperature Seasonality as the climatic variable (AIC = 2994.36)	Habitats Artificial/Terrestrial	0.1170	0.3759	0.31	0.76
	Habitats Caves	0.9421	0.3828	2.46	0.014
	Habitats Forest	0.3325	0.3727	0.89	0.37
	Habitats Open	0.4043	0.3843	1.05	0.29
	Habitats Savana	0.4823	0.3958	1.22	0.22
	Island/Mainland Classification	-0.3638	0.1019	-3.57	0.0004
	Primary Diet Insects	-0.6421	0.5714	-1.12	0.26
	Primary Diet Nectar/Pollen	-0.9842	0.3133	-3.14	0.0017
	Primary Diet Other	-0.2006	0.4323	-0.46	0.64
	Average Weight	-0.0005	0.0003	-1.45	0.15
	Area (km)	<-0.000001	<0.0001	-7.17	<0.0001
Model 3 - Using variables Average Weight for the morphological variable and Y centroid as the climatic variable (AIC = 2994.36)	Habitats Artificial/Terrestrial	0.1170	0.3759	0.31	0.76
	Habitats Caves	0.9421	0.3828	2.46	0.014
	Habitats Forest	0.3326	0.3727	0.89	0.37
	Habitats Open	0.4042	0.3843	1.05	0.29
	Habitats Savana	0.4823	0.3958	1.22	0.22
	Primary Diet Insects	-0.6421	0.5714	-1.12	0.26
	Primary Diet Nectar/Pollen	-0.9841	0.3133	-3.14	0.0017
	Primary Diet Other	-0.2006	0.4323	-0.46	0.64
	Average Weight	-0.0005	0.0003	-1.45	0.15
	Island/Mainland Classification	-3.9340	0.1019	-3.57	0.0004
	Area (km)	<-0.000001	<0.0001	17.17	<0.0001
Model 4 - Using variables Forearm Length for the morphological variable and Temperature Seasonality as the climatic variable (AIC = 2992.21)	Habitats Artificial/Terrestrial	0.1241184	0.3811	0.20	0.84
	Habitats Caves	0.9529	0.3877	2.36	0.019
	Habitats Forest	0.3317	0.3776	0.75	0.45
	Habitats Open	0.4145	0.3887	0.96	0.34
	Habitats Savana	0.4721	0.4004	1.07	0.29
	Primary Diet Insects	-0.3811438	2.3868	-0.21	0.83
	Primary Diet Nectar/Pollen	-0.8619	2.4566	-0.28	0.78
	Primary Diet Other	-0.0145	2.4625	0.11	0.91
	Forearm Avg (mm)	0.0052	0.0026	2.03	0.043
	Island/Mainland Classification	-0.3893	0.1022	-3.78	0.0002
	Area (km)	<-0.000001	<0.0001	-7.20	<0.0001

Model 5 - Using variables Head/Body Size Average for the morphological variable and Temperature Seasonality as the climatic variable (AIC = 2994.49)	Habitats Artificial/Terrestrial	0.1214	0.3761	0.32	0.75
	Habitats Caves	0.9433	0.3830	2.46	0.014
	Habitats Forest	0.3329	0.3729	0.89	0.37
	Habitats Open	0.4129	0.3845	1.07	0.28
	Habitats Savana	0.4856	0.3961	1.23	0.22
	Primary Diet Insects	-0.5671	0.5694	-1.00	0.32
	Primary Diet Nectar/Pollen	-0.9602	0.3130	-3.07	0.002
	Primary Diet Other	-0.1300	0.4298	-0.30	0.76
	Island/Mainland Classification	-0.3720	0.1018	-3.65	0.0003
Model 6 - Using variables Hindfoot Size Average for the morphological variable and Temperature Seasonality as the climatic variable (AIC = 2983.2)	Area (km)	<-0.000001	<0.	-7.18	<0.0001
	Primary Diet Insects	-0.2192	0.5733	-0.38	0.70
	Primary Diet Nectar/Pollen	-0.9446	0.3108	-3.04	0.002
	Primary Diet Other	0.0833	0.4307	0.19	0.85
	Habitats Artificial/Terrestrial	0.1679	0.3736	0.45	0.65
	Habitats Caves	0.9813	0.3804	2.58	0.01
	Habitats Forest	0.3684	0.3703	0.99	0.32
	Habitats Open	0.4611	0.3820	1.21	0.23
	Habitats Savana	0.5121	0.3932	1.30	0.19
	Island/Mainland Classification	-0.3653	0.1011	-3.61	0.0003
	Hindfoot (mm)	0.0258	0.0071	3.63	0.0003
	Area (km)	<-0.000001	<0.0001	-7.18	<0.0001

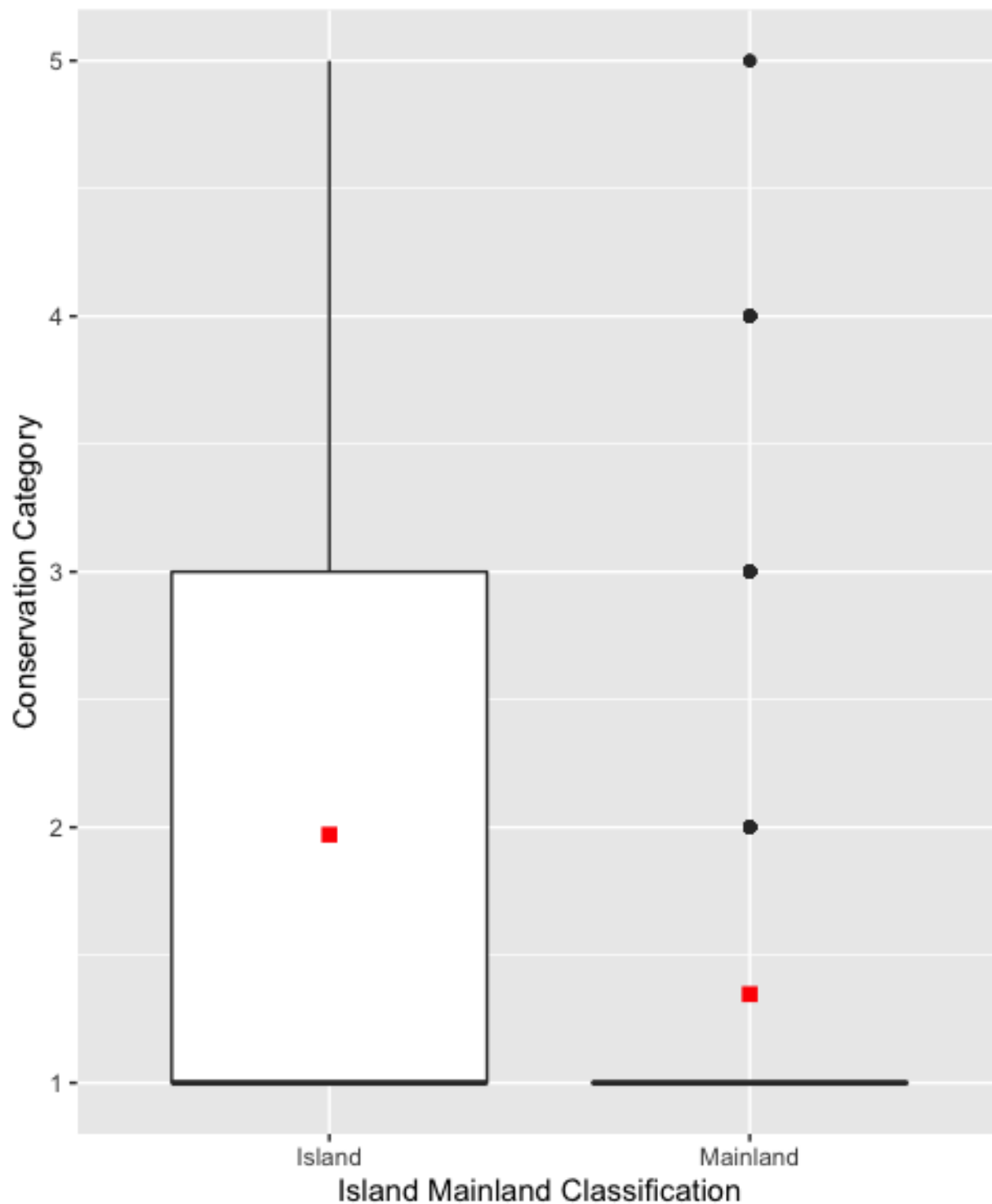


Figure 1. – Box plot showing the mean (small red box), IQR (box), 1.5x IQR (whiskers), and outliers (points outside of the 1.5x IQR) of the conservation category, based for island/mainland classification (N= 835). The IUCN conservation category is higher for species endemic to island habitats.

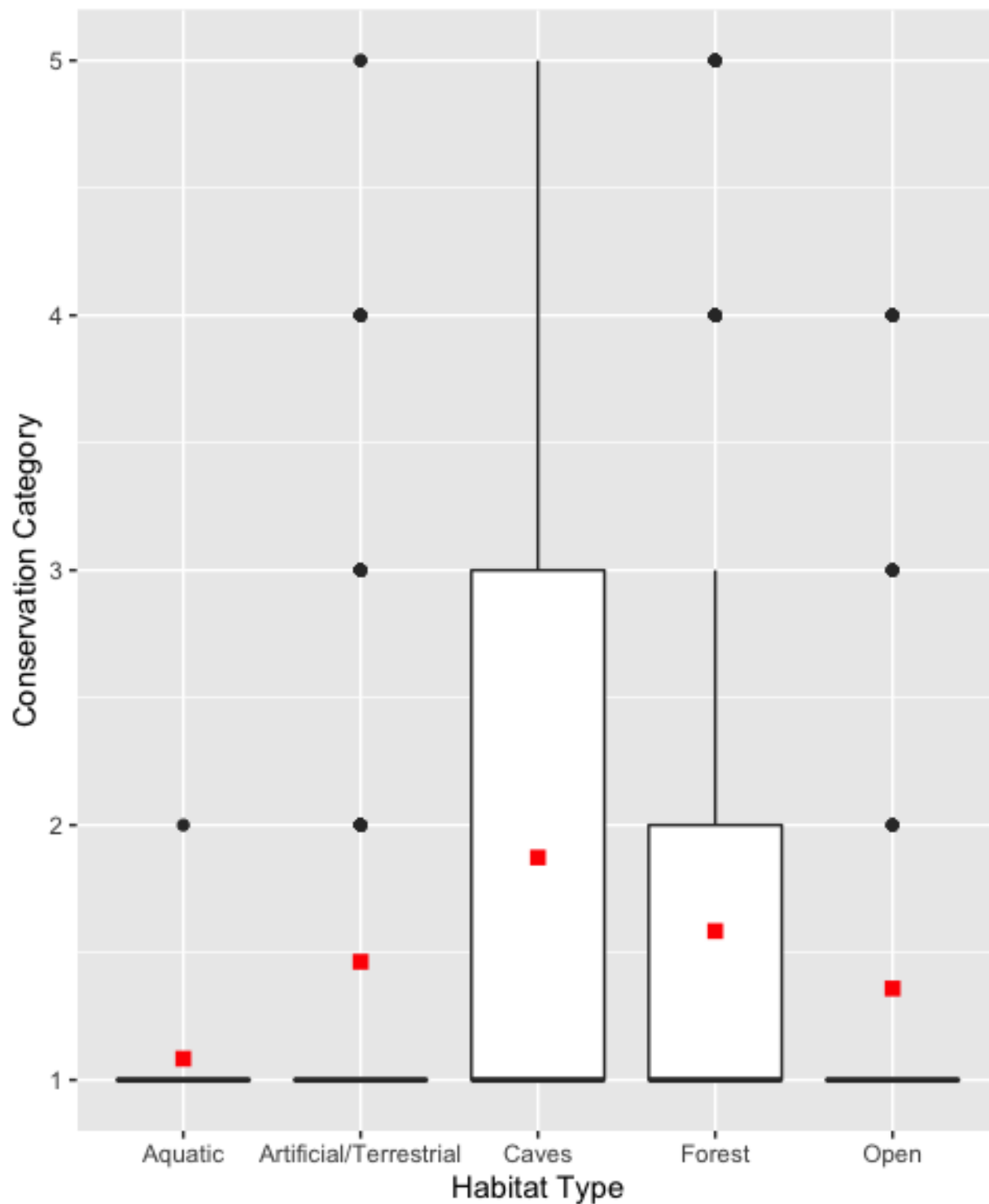


Figure 2. – Box plot showing the mean (small red box), IQR (box), 1.5x IQR (whiskers), and outliers (points outside of the 1.5x IQR) of the conservation category, based for habitat type (N= 835). Bat species which primarily inhabit caves have the highest conservation status.

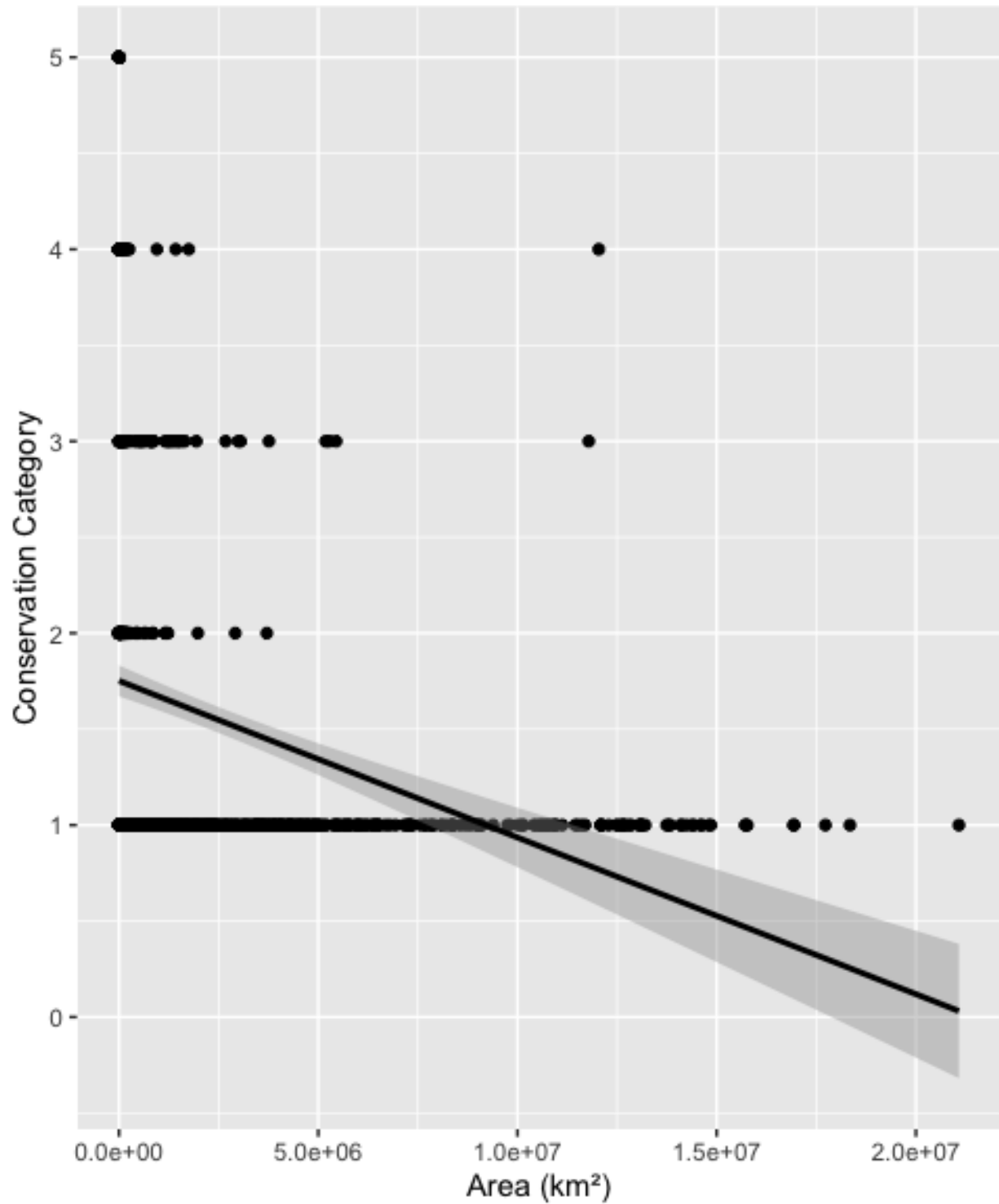


Figure 3. – Correlation between conservation category and area size (range in km) of N=835 bat species range. As a bat species range size decreases, it appears conservation category increases significantly.

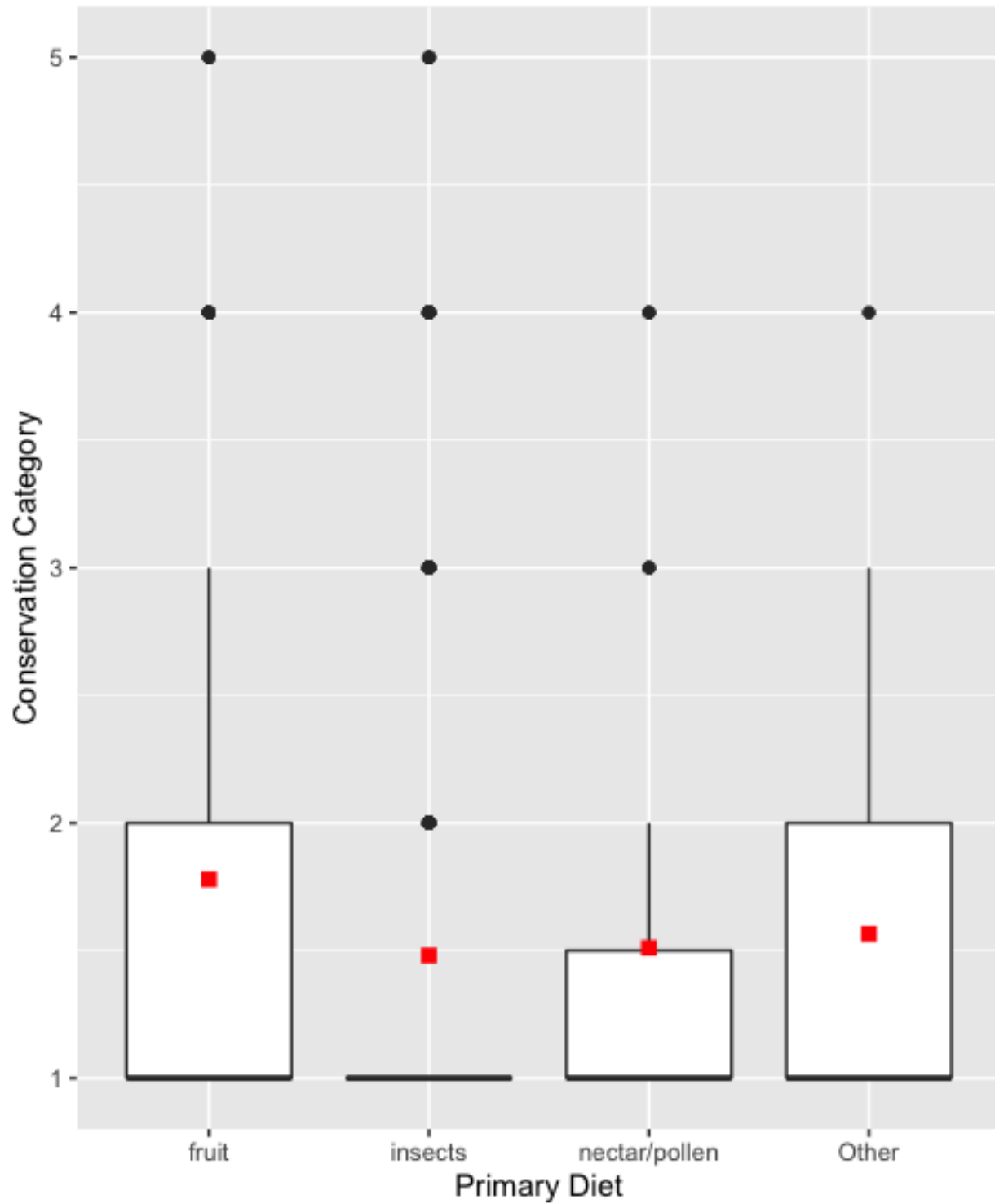


Figure 4. – Box plot showing the mean (small red box), IQR (box), 1.5x IQR (whiskers), and outliers (points outside of the 1.5x IQR) of the conservation category, concerning primary diet of a bat species (N= 835).

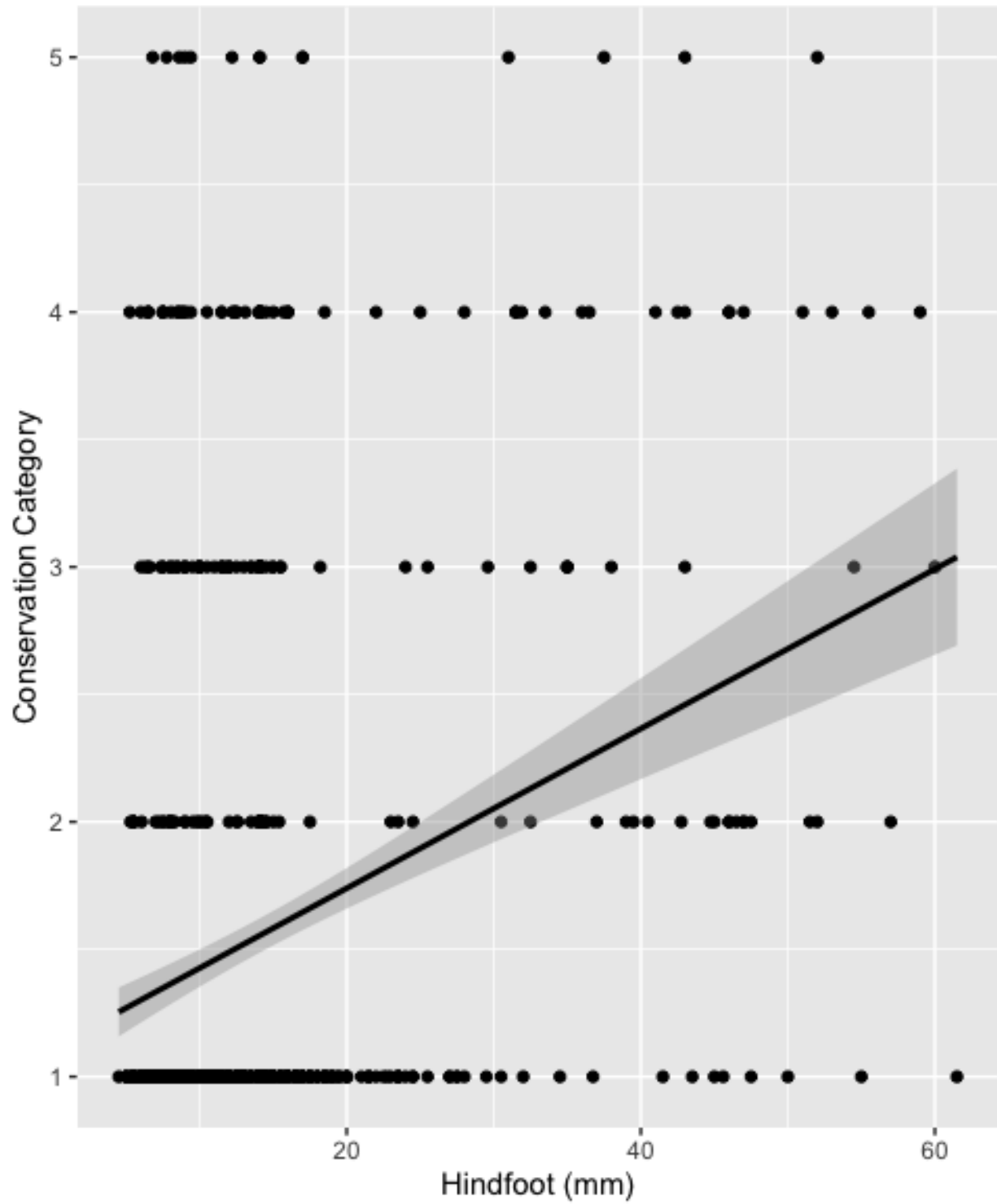


Figure 5. – Correlation between conservation category and hindfoot size (mm) of N=835 bat species. As hindfoot size increases, conservation category generally increases.

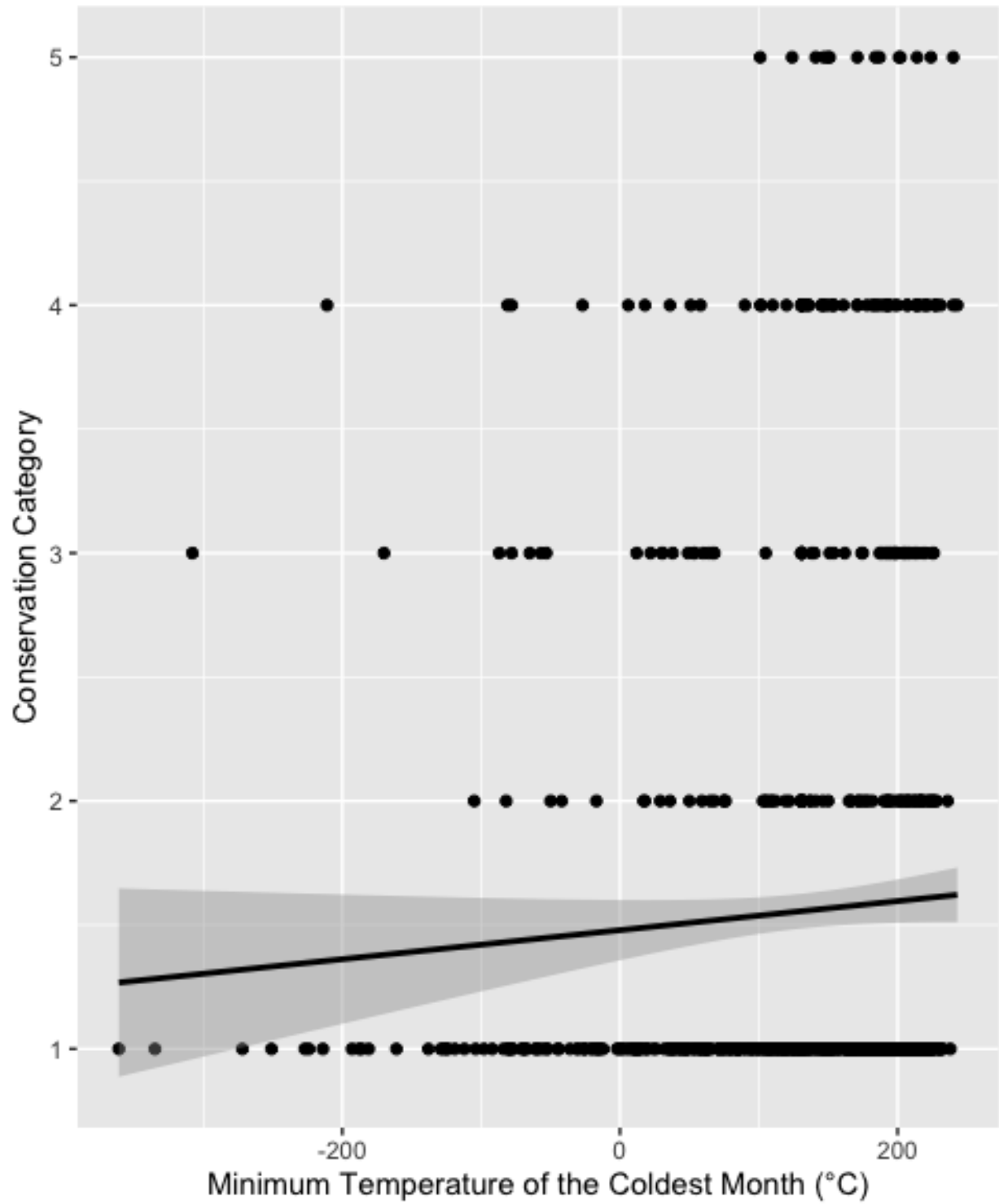


Figure 6. – Correlation plot between conservation category and minimum temperature of the coldest month (°C) of N=835 bat species.

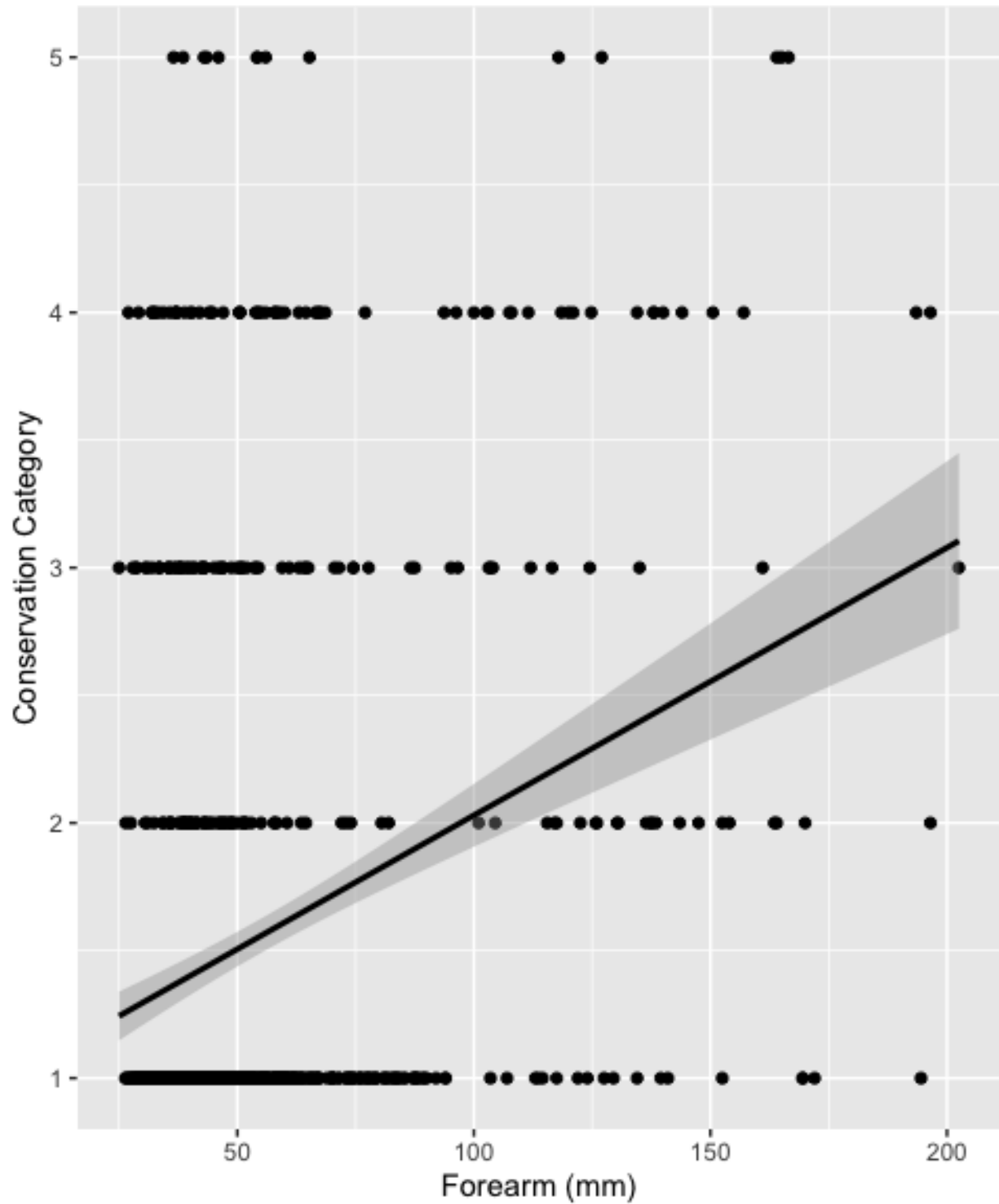


Figure 7. – Correlation plot between conservation category and forearm length (mm) of N=835 bat species. Conservation category appears to increase with forearm length.

DISCUSSION

Worldwide, bats are critical to ecosystem function through their role in myriad of ecological interactions, from pollination and seed dispersal to controlling insect populations. Unfortunately, many bat species are currently in decline, with 15% of the assessed bat species listed as threatened, endangered, or critically endangered, though 18% of bat species remain data deficient on the IUCN red list (IUCN 2022). With limited data on population abundance for many bat species and so many species remaining data deficient, it is difficult to establish protections and enact effective management for many potentially at-risk species. In this study, we conducted the largest and most comprehensive analysis to date on the predictors of extinction risk in bats, examining 835 bat species assessed by IUCN with the largest suite of biological, ecological, and geographic predictors yet tested. Our findings suggest that important predictors of extinction risk in 835 species of bats are range size (area in km), island endemism, habitat type, primary diet, body size (hindfoot length, forearm length), and minimum temperature of the coldest month. The strongest predictor in our study was range size and followed by island endemism. This finding is consistent with previous findings by Welch & Beaulieu (2018) as well as Jones et al. (2003), who found that both range size and island endemism were the strongest predictors of extinction risk in bats.

Small geographical range size is a key driver of population declines not only in bats, but thousands of other species, including those among plants (Staude et al. 2019), insects (Rocha-Ortega et al. 2020), birds (Harris & Pimm 2007) and other types of mammals (Collen et al. 2011, Staude et al. 2019). Species with smaller ranges are at a higher risk of extinction as the threats causing population decline, such as disease, natural disasters, lack of resources, etc., is more likely to affect the entire range of the species (Collen et al. 2016). Furthermore, island endemism is closely linked to range size, as species that are endemic to islands tend to have small range sizes (Jones et al. 2003). Threatened species that are endemic to islands also have lower genetic diversity

than related, nonthreatened, mainland species (Jamieson 2007). Therefore, genetic factors may be playing a role in the extinction risk of island species through processes such as inbreeding depression. Regardless of the mechanisms driving population declines in island endemics, our results reinforce the importance of continued efforts to protect these species.

Our results suggest that conservation measures should be enacted to protect cave habitats for bat species, as cave-dwelling species have more species at risk than any other habitat type. Cave-dwelling being of disproportionately high conservation concern may be a result of the impacts of White Nose Syndrome, as this disease disproportionately affects bats roosting in caves. For species that currently lack an IUCN listing status due to insufficient population abundance data, our results suggest that cave-dwelling species should be prioritized for population surveys and assessment.

Globally, pollinating species of both birds and mammals have been in decline (Regan et al. 2015). These declines are caused primarily by extensive habitat loss in recent years (Regan et al. 2015). Many other drivers of pollinator decline are currently recognized by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). These threats include pests and pathogens, ineffective management of pollinating species, pesticide use, land management, invasive species, GMOs, and climate change (Dicks et al 2021). Moreover, pollinating mammal species are more strongly affected by hunting than pollinating bird species (Ripple et al. 2016). These drivers of pollinator declines may provide insight into to why pollinating bat species appear to be at a high risk of extinction.

Larger bat species are commonly harvested for bushmeat in many parts of the world, including Southeast Asia, Africa, and South America (Ripple et al. 2016). Persecution of larger bat species may explain why bat species with larger hindfeet and forearms appear to be at a higher risk of extinction, as they are disproportionately affected by hunting. Moreover, larger species

typically occur in lower population densities, a factor related to elevated extinction risk (Cardillo et al. 2005).

Finally, we found species living in habitats with higher minimum temperatures during the coldest month of the year were at a greater risk of extinction. As the impacts of deforestation are most significant in the tropics, where temperatures are high year-round, the effects of deforestation, habitat loss, and reduced resource availability may be disproportionately high in these areas (Wang 2013). This, in turn, may be putting species inhabiting warmer climates at a higher risk of extinction. However, this may be related to deforestation and habitat loss as deforestation has been shown to result in increased temperatures of local climates (Prevedello et al. 2019).

Though our research highlights the importance of understanding the drivers behind population declines, the next step will be to construct a predictive model based on these findings to assign data deficient bat species to a putative conservation category. By doing so, we will be able to identify bat species in most urgent need of population assessment. By identifying these potentially at-risk species, we may be able to avoid extinctions and mitigate threats by producing effective conservation measures before it's too late.

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