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Biological and extrinsic correlates of extinction risk in Chinese lizards

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Abstract

China is a country with one of the most species-rich reptile faunas in the world. However, nearly a quarter of Chinese lizard species assessed by the China Biodiversity Red List are threatened. Nevertheless, to date, no study has explicitly examined the pattern and processes of extinction and threat in Chinese lizards. In this study, we conducted the first comparative phylogenetic analysis of extinction risk in Chinese lizards. We addressed the following 3 questions: (1) What is the pattern of extinction and threat in Chinese lizards? (2) Which species traits and extrinsic factors are related to their extinction risk? (3) How can we protect Chinese lizards based on our results? We collected data on 10 species traits (body size [BS], clutch size, geographic range size, activity time, reproductive mode, habitat specialization [HS], habitat use, leg development, maximum elevation, and elevation range) and 7 extrinsic factors (mean annual precipitation (MAP), mean annual temperature, mean annual solar insolation, normalized difference vegetation index (NDVI), human footprint, human population density, and human exploitation). After phylogenetic correction, these variables were used separately and in combination to assess their associations with extinction risk. We found that Chinese lizards with a small geographic range, large BS, high HS, and living in high MAP areas were vulnerable to extinction. Conservation priority should thus be given to species with the above extinction-prone traits so as to effectively protect Chinese lizards. Preventing future habitat destruction should also be a primary focus of management efforts because species with small range size and high HS are particularly vulnerable to habitat loss.

Key words: body size, extinction risk, habitat specialization, precipitation, range size, Red List

Global biodiversity is increasingly threatened and we are in the midst of the sixth mass extinction (Wake and Vredeburg 2008; Ceballos et al. 2015). The current species extinction rate is estimated 100–1,000 times higher than the pre-human background rate (Pimm et al. 2014). However, the extinction is taxonomically nonrandom and species with particular traits may be more prone to extinction (McKinney 1997; Purvis et al. 2000a, 2000b). Identifying species life-history and ecological traits that render species prone to extinction could help us predict their extinction risk and make species protection and conservation planning more efficient (Cardillo and Meijaard 2012; Chichorro et al. 2019). Therefore, the relationship

between species traits and extinction risk has been a study focus of conservation biologists and applied ecologists in the several past decades (McKinney 1997; Purvis et al. 2000b; Verde Arregoitia 2016; Chichorro et al. 2019).

Theoretical and empirical evidence suggest that species with particular traits are more prone to extinction than others (Verde Arregoitia 2016; Chichorro et al. 2019). For example, large body size (BS), small geographic range, high habitat specialization (HS), small clutch size, and restricted elevational range, are frequently associated with high extinction risk (Table 1; Henle et al. 2004; Siliceo and Díaz 2010; Tingley et al. 2013; Chen et al. 2019a).

Table 1. Species traits and extrinsic variables used to analyze the extinction risk in Chinese lizards

Predictor variables	Expected mechanisms	References
Intrinsic traits		
Geographic range size	Small-ranged species tend to have narrow niches and may be more easily affected by a single threat process across the entire range	Cooper et al. (2008); Böhm et al. (2016b)
Body size	Species with large BS often have low population density, large home range, slower life-history and are particularly prone to anthropogenic threats	Owens and Bennett (2000); Purvis et al. (2000b); Reed and Shine (2002)
Clutch size	Species with small clutch size are less able to compensate for increased mortality with increased fecundity	Purvis et al. (2000b)
Habitat specialization	Habitat specialists are less capable of dealing with novel environmental challenges and thus are at higher extinction risk	Murray et al. (2011); Böhm et al. (2016b)
Reproductive mode	Viviparous species tend to be larger than oviparous species and more likely to be hunted	Dunham et al. (1988); Böhm et al. (2016b)
Activity time	Diurnal species are vulnerable because they have a suite of extinction-prone traits, e.g., large BS, large home ranges, and being easier to be exploited	Purvis et al. (2000b); Chen et al. (2019b)
Habitat use	Species living in aquatic habitats are susceptible to predators and to regular or stochastic perturbations than species living in terrestrial habitats	Hero et al. (2005); Todd et al. (2017)
Leg development	Longer limbs increase the maximal sprint speed, which has a profound impact on the expression of many behaviors essential for survival, such as capturing prey and evading predators	Garland and Losos (1994); Husak et al. (2006); Foster et al. (2018)
Maximum elevation	Lizards are sensitive to elevation; high minimum elevation suggests smaller, more restricted range	Fischer and Lindenmayer (2005); Böhm et al. (2016b)
Elevational range	Species with restricted elevational ranges may have fewer refuges, less food resources, lower population size, and often fail to recolonize suitable habitats	White and Bennett (2015); Li and Pimm (2016); Chen et al. (2019a)
Extrinsic variables		
Mean annual precipitation	Areas with high levels of precipitation have higher productivity and potentially higher human disturbance	Tingley et al. (2013); Böhm et al. (2016b)
Mean annual temperature	Reptiles are solar ectotherms and have slower life histories and lower reproduction in lower temperature areas	Böhm et al. (2016b)
Normalized difference vegetation index (NDVI)	NDVI is a proxy for productive environmental energy; species that live in areas with lower NDVI have fewer food resources	Davies et al. (2006); Chen et al. (2019c)
Mean annual solar insolation	Lizards are solar ectotherms; low heat tolerances of lizards are associated with increased sensitivity to habitat modification	Nowakowski et al. (2018)
Human footprint	Higher levels of human footprint suggest higher cumulative human pressure on the environment, leading to increased extinction risk	Di Marco et al. (2018)
Human population density		Cardillo et al. (2008); Chen et al. (2019c)
Human exploitation	Species live in areas with higher human population density are exposed to higher human disturbance, resource use, and increased habitat damage	Ruland and Jeschke (2017); Chen et al. (2019b)
	Higher human exploitation indicates higher human disturbance and impacts, such as pet trade, medicine, research, and food purpose	

For each variable, the expected mechanism and references are listed. SUN, mean annual solar insolation.

Moreover, the risk of extinction is also affected by extrinsic factors (Table 1), such as precipitation, temperature, habitat loss and degradation, overexploitation, and human population density (Davies et al. 2006; Tingley et al. 2013; Böhm et al. 2016a; Chen et al. 2019b). Species that live in areas with high precipitation, higher number of predators, and higher human disturbance are predicted to be more prone to extinction (Sodhi et al. 2008; Tingley et al. 2013). In areas with high human population density, species have greater extinction risk because they are more susceptible to human threats, such as habitat loss and human overexploitation (Böhm et al. 2016b; Chen et al. 2019b). It is highlighted that intrinsic traits and extrinsic threats should be considered simultaneously to improve the study of extinction risk (Cardillo et al. 2004; Murray et al. 2011; Tingley et al. 2013; Böhm et al. 2016b).

China has a total of 188 lizard species by 2015 and is one of the countries with the richest lizard diversity in the world (MEP and CAS 2015; Cai et al. 2016). The threat status of the 188 Chinese lizard species was comprehensively evaluated for the first time by the China Biodiversity Red List in 2015 (MEP and CAS 2015). Among them, 38 species are assessed as threatened (Vulnerable [VU], Endangered [EN], and Critically Endangered [CR]), whereas 32 species are classified as Data Deficient (DD; Cai et al. 2016). However, studies on the extinction risk and biodiversity decline of Chinese lizards are far behind other taxa, such as birds, amphibians, snakes, and mammals (Wang et al. 2018; Chen et al. 2019a, 2019b; Shuai et al. 2021). To improve knowledge and facilitate conservation management, there is an urgent need to investigate the pattern and underlying processes of extinction and threat in Chinese lizards.

In this study, we conducted the first comparative phylogenetic analysis of extinction risk in Chinese lizards by considering both species intrinsic traits and extrinsic factors. We addressed the following 3 questions. First, what is the pattern of extinction and threat in Chinese lizards? Second, which species traits and extrinsic factors are correlated with extinction risk in Chinese lizards? Finally, how can we protect Chinese lizards based on our results?

Materials and Methods

Data collection
We obtained the species list and threat status of Chinese lizards from the China Biodiversity Red List released in 2015 (MEP and CAS 2015; Jiang et al. 2016). The information used in this Red List was mainly collected from museum specimens, available literature, and experts. It includes details on species distribution, new species discovery, ecology, conservation, threat factors, rates of population decline, and projected population trends (Cai et al. 2016). The China Biodiversity Red List evaluates the threat status of Chinese species mainly using *the IUCN Red List Categories and Criteria* (version 3.1) (IUCN 2012a) and *Guidelines for Application of IUCN Red List Criteria at Regional and National Levels* (version 4.0) (IUCN 2012b). Following the protocols used in previous studies (Purvis et al. 2000b; Jones et al. 2003; Wang et al. 2018), the extinction risk of Chinese lizard species was ranked as Least Concern (LC) = 0, Near Threatened (NT) = 1, VU = 2, EN = 3, and CR = 4 (Supplementary material, Appendix Table S1). No lizard species were classified as Extinct (EX) or Regionally Extinct (RE) = 5 in China.

We used the China Biodiversity Red List, rather than the IUCN Red List, to examine the extinction risk of Chinese lizards for 4 reasons. First, the China Biodiversity Red List includes the threat status of 54 species (28.72%) in China that are not assessed by the IUCN Red List (Cai et al. 2016). Second, the China Biodiversity Red List is the most appropriate scale and gives a better representation of the status of Chinese lizards than the IUCN Red List (Milner-Gulland et al. 2006). Third, data quality and availability for species at the national scale are more precise and reliable than those at the global scale (Milner-Gulland et al. 2006; Cai et al. 2016). Finally, the results from country-oriented studies are easier to be incorporated into effective conservation strategies because most conservation policies and actions are formulated at national scale (Verde Arregoitia 2016; Chen et al. 2019a).

We omitted 32 DD species of Chinese lizards from the analysis. These 32 DD species lack adequate information on population size, trends, distribution, and/or threats to assess them against the Red List criteria (Cai et al. 2016). Therefore, the remaining 156 lizard species were included in the following analyses. Based on the latest published phylogeny of global squamates (Tonini et al. 2016), we built a phylogenetic tree for these 156 Chinese lizards (Figure 1). Five species (*Japalura bapoensis*, *Phrynocephalus frontalis*, *Phrynocephalus grumgrzimailoi*, *Phrynocephalus guinanensis*, and *Gekko liboensis*) not present inside the global phylogeny were replaced by their phylogenetically sister species (*Pseudocalotes kingdonwardi*, *Phrynocephalus przewalskii*, *Phrynocephalus helioscopus*, *Phrynocephalus putjatai*, and *Gekko hokouensis*, respectively) (Gozdzik and Fu 2009; Rösler et al. 2011; Jin et al. 2018; Wang et al. 2019).

We collected data on 10 life-history and ecological traits that are commonly linked to extinction risk (Table 1) for each species following the methods of previous studies (e.g., Tingley et al. 2013; Böhm et al. 2016b; Todd et al. 2017; Meiri 2018). We used average body mass (g) of males and females to represent BS. For a few species lacking the data of body mass, we converted the snout–vent length (in mm) to body mass using taxon-specific allometric equations (Meiri 2010). Clutch size was defined as the number of eggs per clutch. We averaged the highest and lowest values of clutch size in case of multiple values (Meiri et al. 2020). Following Meiri (2018), habitat use was classified as semi-aquatic (1), terrestrial (2), saxicolous (3), and arboreal (4); activity time was quantified as nocturnal (a), diurnal (b), and cathemeral (c); leg development mode was categorized as 4-legged (1) and limbless (2). According to Meiri (2018), there was temporarily no species classified as reduced limbs in Chinese lizards. Reproductive mode was quantified as oviparous (1) and viviparous (2) (Meiri 2018). We considered ovoviviparous species and mixed modes as viviparous. We calculated HS by summing the number of habitat types inhabited by each species using the habitats classification scheme of IUCN Red List assessments (Böhm et al. 2016b). We used ArcGIS 10.2 to calculate the geographic range size (RS; km^2) in China for each species based on the recently published species range maps (Roll et al. 2017). We calculated the elevation range (ER) between the maximum and minimum elevation distribution for each species from Zhao (1998) and IUCN (2020) (http://www.iucnredlist.org/) including information just within China. There are a few species with missing values of ecological traits, that is, reproduction mode ($n = 9$), habitat use ($n = 4$), HS ($n = 4$), and clutch size ($n = 24$). For these species traits, we used the average value of their closest congeners, which is the protocol widely used by other studies (Wang et al. 2018; Chen et al. 2019a, 2019b).

Based on hypotheses and results of previous studies, we derived 7 extrinsic predictors (Table 1) within the geographic range of each species from published resources (Zhao 1998; Meiri 2018; Meiri et al. 2020; IUCN 2020; Uetz 2021) and related websites (https://xueshu.baidu.com; https://scholar.google.com; https://neo.sci.gsfc.nasa.gov/; https://chelsa-climate.org/; https://sedac.ciesin.columbia.edu/). Mean annual temperature and precipitation are generally used as proxies of climate conditions and reflect the primary environmental productivity (Böhm et al. 2016a). Mean human population density and human footprint represent the level of human impacts, which are viewed as direct threats to species (Cardillo et al. 2004; Böhm et al. 2016b; Marco et al. 2018). We obtained the information on human exploitation of lizard species from IUCN (2020) (http://www.iucnredlist.org/) and a variety of Chinese publications, such as *Medicinal Fauna of China* and *Identification atlas of common illegal trade wild animals and products* (Li et al. 2013; Yang and Hu 2016). We also conducted an extensive survey on a Chinese search engine (www.baidu.com) for reliable Chinese reports on hunting, trade, and smuggling of lizards. Based on the above
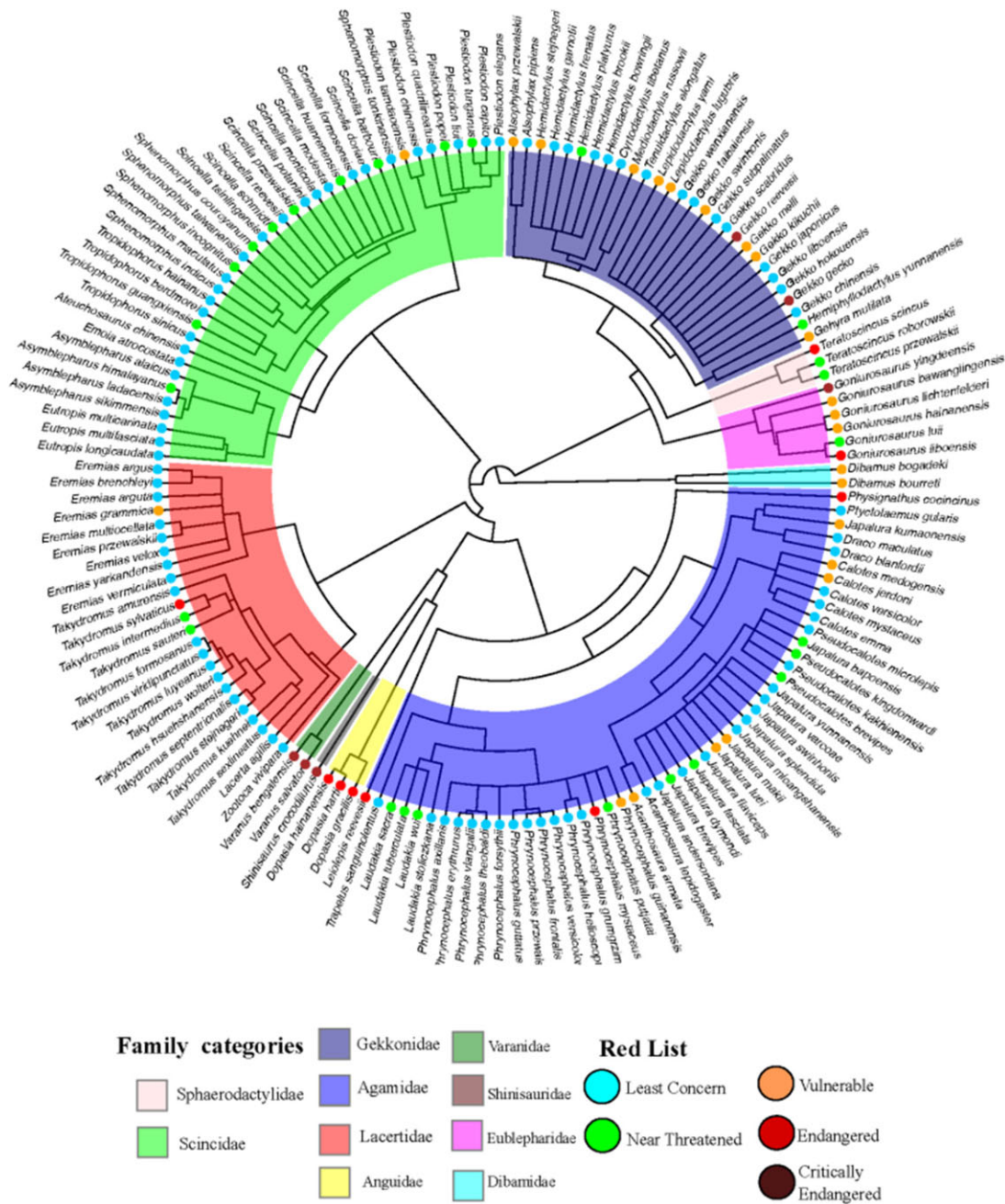
Figure 1. Phylogenetic tree of the 156 Chinese lizard species used in the comparative analysis. The phylogeny is built based on the global reptile phylogeny of Tonini et al. (2016). The color of tips represents the extinction risk category derived from the China BiodiversityRed List.

data, the human exploitation of each species was roughly set to 1 (reportedly utilized) or 0 (unutilized) (Shuai et al. 2021). Normalized difference vegetation index (NDVI) is a proxy for productive environmental energy, whereas mean annual solar insolation (SUN) has an impact on the activity period of lizards (Davies et al. 2006). NDVI and SUN across each species' range were calculated at 0.5° 0.5° resolution level. Moreover, the information on mean annual temperature and precipitation was extracted from the climate shapefiles at 1° 1° resolution level. Mean human footprint and human population density for each species were extracted in the same way. We used ArcGIS version 10.2 to obtain the above extrinsic variables across each species' range (Cardillo et al. 2008; Böhm et al. 2016b).

Statistical analyses

Correlates of extinction risk in Chinese lizards

We applied phylogenetic generalized least square (PGLS) analyses to control for the statistically phylogenetic non-independence between lizard species (Orme 2018). We used the maximum likelihood method to calculate Pagel's in each model (Table 2) and set and to the constant 1 to assume a Brownian motion model of evolution (Orme 2018). PGLS analyses were carried out using the "pgls" function in the R package "caper" (Orme 2018).

We built a set of relevant PGLS models in the following 4 steps to examine the relative role of intrinsic traits and external variables in determining extinction risk. First, we conducted univariate PGLS

analyses to regress species extinction risk with each of the ten species traits and 7 extrinsic factors separately (Purvis et al. 2000b; Chen et al. 2019a). Second, because strongly correlated variables (|r| 0.70) are likely to indicate similar underlying processes (Ducatez et al. 2014), we only retained variables presenting low correlation values with all other variables (Spearman < 0.70; Supplementary material, Appendix Table S2). Mean annual temperature was highly correlated with mean annual precipitation (MAP) and NDVI, and human population density was highly related to human footprint (Supplementary material, Appendix Table S2). Mean annual temperature and human population density were excluded from analyses because they had lower explanatory power in predicting extinction risk than their highly correlated variables (Table 2). Third, we selected potential important predictors ($P < 0.1$) identified in the first step and built a set of candidate models considering all possible combinations of these variables (Price and Gittleman 2007; Chen et al. 2019a). Fourth, we used the corrected Akaike information criterion (AICc) and the Akaike weight (w_i) to rank candidate models. The models with AICc < 2 are considered to have similarly substantial support (Burnham and Anderson 2002). Finally, we applied the model-average method to calculate weighted estimates of regression coefficients (), unconditional standard errors (SEs), and the relative importance (w_+) of each predictor for models in the 95% confidence set using the R package "MuMIn" (Barton 2020). Before performing the analysis, we log-transformed all continuous variables to normalize the distribution and equalize the residuals (Zar 2010). All data analyses were performed in R version 3.6.2 (R Core Team 2020).

Effects of range size on extinction risk

Assessments of extinction risk in reptiles were primarily based on restricted geographic range (IUCN criteria B and D2) (IUCN 2020). Therefore, the relationship between RS and extinction risk could be circular (Cooper et al. 2008; Böhm et al. 2016b). We performed 3 additional analyses to clarify the impact of RS on the extinction risk of Chinese lizards. First, we simply excluded species assessed as threatened based on the range criteria and repeated the above

analyses to test whether range size was still important in determining the extinction risk of Chinese lizards (Cooper et al. 2008; Wang et al. 2018; Shuai et al. 2021). Second, to evaluate the effect of RS on extinction risk, we compared the adjusted R^2 of the 2 best models that included and excluded the variable of RS (Böhm et al. 2016b; Chen et al. 2019a). Finally, we tested the synergistic interactions between RS and the other important variables (BS, HS, and MAP). The interaction analysis can test whether additional variables can increase the importance of determining threat level once a species is range restricted (Böhm et al. 2016b; Chen et al. 2019c).

Results

The pattern of extinction risk in Chinese lizards

According to the China Biodiversity Red List released in 2015, 92 species (48.94%) of Chinese lizards were classified as LC, 26 (13.83%) were NT, 23 (12.23%) were VU, 9 (4.79%) were EN, 6 (3.19%) were CR, whereas 32 species (17.02%) were DD (Figure 1; Supplementary material, Appendix Table S1). Therefore, 38 (24.36%) of the 156 non-data-deficient species were assessed as threatened (VU, EN, and CR) (Figure 1). Moreover, among the 38 threatened Chinese lizards, 31 species (81.58%) were assessed as threatened mainly due to their small geographic ranges (Supplementary material, Appendix Table S1).

Correlates of extinction risk in Chinese lizards

The univariate PGLS analyses showed that high extinction risk in Chinese lizards was significantly correlated with large BS, high MAP, high HS, small RS, small ER, and low level of sunlight (Table 2). The best multivariate model based on AICc accounted for 22.87% of the variance, suggesting that lizard species were at a greater risk of extinction if they had small range size, large BS, high MAP, and high HS (Table 3 and Figure 2). However, the w_i for the best model was only 0.2068 (Table 3), which suggests substantial model selection uncertainty. The relative variable importance (w_+) indicated that RS, MAP, HS, and BS were still important using model averaging in the 95% confidence set (Table 4).

Table 2. Results of univariate PGLS models predicting the extinction risk of Chinese lizards

Variables	λ	Slope	SE	t	P-value
Geographic range size	0.14	−0.12	0.02	−5.48	1.68E-07[***]
Body size	0.86[**]	1.99	0.67	2.97	0.003[**]
Habitat specialization	0.14	−0.18	0.06	−2.94	0.004[**]
Elevation range	0.16	−0.15	0.09	−1.66	0.099[+]
Reproductive mode	0.30[**]	−0.33	0.20	−1.60	0.112
Activity time	0.80[**]	0.35	0.24	1.44	0.152
Clutch size	0.31[**]	0.20	0.17	1.20	0.232
Maximum elevation	0.24[**]	−0.13	0.11	−1.20	0.233
Leg development	6.54[**]	0.56	0.96	0.58	0.565
Habitat use	0.69[**]	0.06	0.13	0.49	0.623
Mean annual precipitation	0.30[**]	0.19	0.08	2.36	0.019[*]
Mean annual solar insolation	0.31[**]	−0.10	0.08	−1.84	0.068[+]
Mean annual temperature	0.36[**]	−0.09	0.11	−0.86	0.393
Human exploitation	0.13	−0.22	0.15	−1.47	0.144
Human footprint	0.29[**]	0.01	0.02	0.83	0.408
Human population density	0.15	0.00	0.00	0.70	0.485
Normalized difference vegetation index (NDVI)	0.31[**]	0.01	0.53	−0.45	0.652

[+] $P < 0.1$, [*] $P < 0.05$, [**] $P < 0.01$, [***] $P < 0.001$.

Table 3. The performance of PGLS models predicting the extinction risk of Chinese lizards

Models	K	AICc	ΔAICc	w_i	Adjusted R^2
BS+HS+MAP+RS	5	385.73	0.00	0.2068	0.2287
BS+MAP+RS	4	386.45	0.72	0.1442	0.2205
BS+HS+MAP+RS+SUN	6	387.17	1.44	0.1006	0.2289
BS+HS+RS	4	387.21	1.49	0.0983	0.2149
BS+MAP+RS+SUN	5	387.76	2.03	0.0749	0.2208
BS+ER+HS+MAP+RS	6	387.89	2.16	0.0701	0.2233
BS+HS+RS+SUN	5	388.49	2.76	0.0519	0.2186
BS+ER+MAP+RS	5	388.55	2.82	0.0505	0.2155
BS+RS	3	388.65	2.92	0.0480	0.2031
BS+ER+HS+MAP+RS+SUN	7	389.34	3.61	0.0339	0.2244
BS+HS+MAP+SUN	5	401.27	15.54	0.0001	0.1353

The table shows models with ΔAICc ≤ 4, model rank, change in AICc from the top model (ΔAICc), model weight (w_i), and adjusted R^2. The 2 best models that included and excluded RS were highlighted in bold. All candidate models were listed in Supplementary material, Appendix Table S3. Abbreviations: BS, body size; HS, habitat specialization; MAP, mean annual precipitation; RS, geographic range size; SUN, mean annual solar insolation; ER, elevation range.
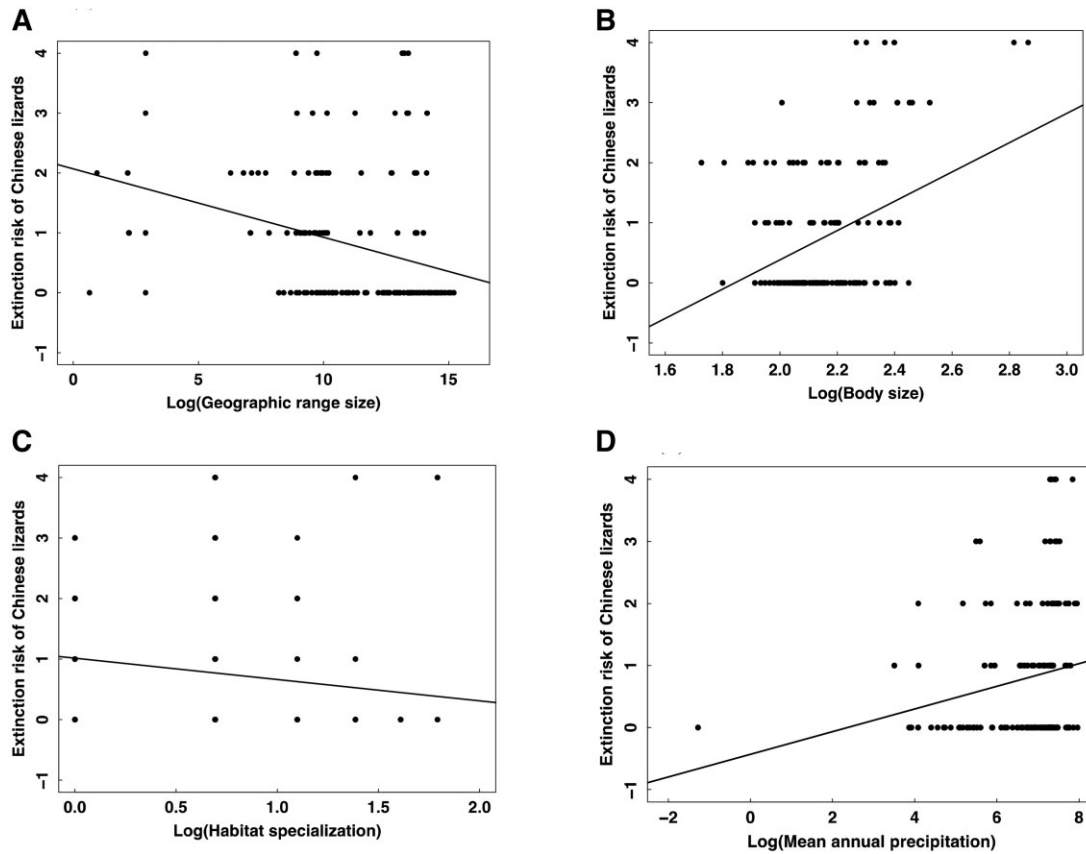
Figure 2. Relationships between extinction risk and RS (A), BS (B), HS (C), and MAP (D) for 156 lizard species in China.

Table 4. Model-averaged parameter estimates (θ), unconditional SEs and relative variable importance (w_+) for each variable in the 95% confidence set

	w_+	θ	SE	z-value	P-value
(Intercept)	—	−2.886	1.778	1.623	0.105
Geographic range size	1	−0.125	0.026	4.706	<0.001
Body size	0.98	2.269	0.720	3.149	0.002
Mean annual precipitation	0.72	0.148	0.077	1.933	0.053
Habitat specialization	0.59	−0.105	0.061	1.704	0.088
Mean annual solar insolation	0.35	0.001	0.002	0.886	0.375
Elevation range	0.23	−0.001	0.089	0.008	0.994

Table 5. The interaction models between RS and the other 3 important variables (BS, HS and MAP) for predicting the extinction risk of Chinese lizards

	Coefficient	SE	t	P-value
Range size × Body size	−0.050	0.0097	−5.1714	0.0000007
Range size × Habitat specialization	−0.0178	0.0042	−4.2442	0.00008
Range size × Mean annual precipitation	−0.0115	0.0031	−3.6823	0.00070

Effects of range size on extinction risk

When excluding lizard species that are assessed as threatened due to small geographic range, RS ($w_+ = 0.91$), along with BS ($w_+ = 1$) and HS ($w_+ = 0.88$), was still substantially important in predicting extinction risk in the 95% confidence set (Supplementary Appendix Table S2). Moreover, when excluding the variable of RS, the best multivariate model (AICc = 0) included BS, HS, MAP, and annual solar insolation (Table 3 and Supplementary material, Appendix Table S3). However, only 13.53% of the variance was explained by this model, which was much lower than the best model (22.87%) when RS was included (Table 3). Finally, RS interacted significantly with the other 3 important variables (BS, MAP, and HS; Table 5), indicating that they could increase the importance of deciding extinction risk once a species is range restricted.

Discussion

In this study, we conducted the first extensive analysis to systematically investigate the pattern and processes of extinction and threat in Chinese lizards. Nearly a quarter of Chinese lizards were assessed as threatened by the China Biodiversity Red List, which was mainly based on their restricted geographic ranges. Small RS, large BS, high MAP, and high HS were important predictors of high extinction risk in Chinese lizards.

Our results showed that 24.36% of non-data-deficient Chinese lizards were listed as threatened in the China Biodiversity Red List (MEP and CAS 2015; Cai et al. 2016). It should be noted that the estimated proportion of threatened lizards in China is conservative. Previous studies have shown that species classified as DD often have a higher extinction risk due to a lack of information on taxonomy, geographic distribution, population status, or threats (Bland et al. 2015; Jetz and Freckleton 2015; Gonzalez-del-Pliego et al. 2019; Gumbs et al. 2020). We thus speculate that if these DD species were

included and assessed using appropriate analysis methods (e.g., Bland et al. 2015; Jetz and Freckleton 2015), the true proportion of threatened lizards would be much higher.

We found that RS played an important role in determining the extinction risk of Chinese lizards. Generally, small range size is the most important predictor of extinction risk for many taxa, including amphibians, birds, reptiles, and mammals (Purvis et al. 2000b; Lee and Jetz 2011; Botts et al. 2013; Böhm et al. 2016b; Crooks et al. 2017; Chen et al. 2019a). In our study, regardless of which analysis methods were used, RS was always important in determining the extinction risk of Chinese lizards. Even if species assessed based on range criteria were excluded, lizards with smaller range size were still more prone to extinction. In general, species with small range usually imply small population size, which in turn are highly sensitive to demographic stochasticity, local catastrophes, and population inbreeding (Jones et al. 2003; Henle et al. 2004; Cooper et al. 2008). Moreover, species with restricted range often have smaller habitats, fewer food resources, lower population size, and inability to resettle in suitable habitats, which all increase the extinction risk (Purvis et al. 2000b; White and Bennett 2015; Li and Pimm 2016). Finally, species with small range sizes are more prone to be affected by habitat destruction, as any loss of their preferred habitat will result in population decline (Stuart et al. 2005; Botts et al. 2013).

BS was another important species trait for predicting the extinction risk of Chinese lizards. We found that larger lizards were more threatened than smaller ones, which is consistent with previous studies (Filippi and Luiselli 2000; Reed and Shine 2002; Tingley et al. 2013). Large BS is often associated with some extinction-prone characteristics, such as low population density and large home range, which may jointly promote the extinction risk of species (Henle et al. 2004; Collen et al. 2011). In addition, larger BS is usually associated with a higher probability of being hunted, as has been widely demonstrated for many human exploited taxa, such as birds, carnivores, primates, and snakes (Owens and Bennett 2000; Isaac and Cowlishaw 2004; Keane et al. 2005; Chen et al. 2019b). Finally, large-bodied lizards have high extinction risk probably because they have more difficulty in evading allochthonous predators (Tingley et al. 2013).

We also found that high HS was significantly related to the extinction risk of Chinese lizards. Previous studies have observed this relationship between HS and extinction risk in amphibians, lizards, birds, and mammals (Owens and Bennett 2000; Botts et al. 2013; Gonzalez-Suarez et al. 2013; Tingley et al. 2013). Compared with generalist species, specialists are less adaptable to environmental challenges (e.g., habitat loss and climate change) because they usually cannot survive outside their familiar habitats (Reed and Shine 2002; Fisher et al. 2003; Murray et al. 2011). Moreover, species with high HS only appear in a narrow range of environmental conditions (Ducatez et al. 2014). In addition, species with high HS are particularly vulnerable to habitat loss and fragmentation (Wang et al. 2015; Doherty et al. 2020). Therefore, high degree of HS renders Chinese lizards more susceptible to extinction (Murray and Hose 2005; Clavel et al. 2011).

Finally, lizard species living in regions with high MAP were more prone to extinction. Contemporary precipitation patterns can be used as a reflection of historical land-use changes (Tingley et al. 2013). In our study, there was a strong correlation between annual precipitation and temperature (Spearman = 0.78, Supplementary material, Appendix Table S2). Because 85% of reptiles are oviparous (Tinkle and Gibbons 1977), high temperature may affect the development of species and thus influence their hatching rates

(Hawkes et al. 2009; López-Luna et al. 2015). In addition, the positive effects of MAP on the extinction proneness of Chinese lizards may be caused by the higher number of predators in humid areas with high precipitation than that in dry areas (Tingley et al. 2013).

Comparative phylogenetic analyses can contribute to conservation prioritization by identifying species with extinction-promoting traits (Fisher and Owens 2004; Böhm et al. 2016b). We found that both intrinsic (RS, HS, and BS) and extrinsic (MAP) factors are important for predicting the extinction risk of Chinese lizards. Because most conservation policies and actions are formulated at national scale (Verde Arregoitia 2016; Chen et al. 2019a), our results have important implications for the protection of Chinese lizards. First, as small range size is an important predictor of extinction risk in Chinese lizards, such narrow-ranged species should be the focus of protection (Stuart et al. 2005; Cooper et al. 2008). Second, we should give conservation priority to lizards with large bodies and high HS because such species are extremely vulnerable to extinction. Moreover, our results also highlight the prior protection of lizards living in areas with high annual precipitation because these species have high extinction risk. Finally, it is important to prevent future habitat destruction because species with small range size and high HS are particularly vulnerable to habitat loss.

Authors' Contributions

Y.W. conceived the study. Y.Z. and C.C. collected the data. Y.Z. performed the analyses and wrote the first draft of the paper. Y.W. contributed substantially to the writing of the manuscript.

Conflicts of Interest Statement

We declare that we have no conflicts of interest.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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