Explaining the primate extinction crisis: predictors of extinction risk and active threats

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ABSTRACT:

Explaining why some species are disproportionately impacted by the extinction crisis is of critical importance for conservation biology as a science and for proactively protecting species that are likely to become threatened in the future. Using the most current data on threat status, population trends, and threat types for 446 primate species, we advance previous research on the determinants of extinction risk by including a wider array of phenotypic traits as predictors, filling gaps in these trait data using multiple imputation, and considering more explicitly the mechanisms that connect organismal traits to extinction risk. Our Bayesian phylogenetically controlled analyses reveal that larger-bodied and insular species exhibit higher threat status, while those that are more omnivorous and live in larger groups have lower threat status. The same traits are not linked to risk when repeating our analyses with older IUCN data, suggesting that the traits that influence species risk are changing as anthropogenic effects continue to transform natural landscapes. We also show that larger-bodied and arboreal species are more susceptible to key threats responsible for primate population declines. Collectively, these results provide new insights to the determinants of primate extinction and identify the mechanisms (i.e., threats) that link traits to risk.

INTRODUCTION:

Anthropogenic activity is causing species to disappear at an alarming rate. However, not all species are affected equally: some species show no changes in abundance while others are increasing in abundance as human activity increases. Explaining why some species are more susceptible to extinction than others has become a major goal of conservation biologists as these contributions help to both explain current extinction patterns and allow for proactive protection of species possessing traits that could increase their probability of becoming imperiled. Previous studies have shown that phenotypic traits affect a species' susceptibility to extinction (Chichorro et al., 2019). Physical traits such as large body size and life history traits such as long generation lengths have been associated with increased risk of extinction (Purvis et al., 2000; Cardillo & Bromham, 2001; Cardillo et al., 2005; Lee & Jetz, 2011; Matthews et al., 2011). Behavioral traits have also been linked to increased extinction risk, including small group size and reduced innovativeness (Davidson et al., 2009; 2012; Ducatez et al., 2020).

While much effort has been put toward identifying how different traits covary with extinction risk, important knowledge gaps have limited the effectiveness of these analyses. First,

only a handful of studies have incorporated a broad range of traits in a single analysis. Chichorro et al. (2019) reviewed studies investigating the correlates of extinction risk and found significant variability in the traits that were investigated (or controlled for). In addition, some traits have only recently been linked to extinction risk, such as behavioral flexibility (Ducatez et al., 2020), and thus have not been widely investigated across clades.

Second, the relationship between the actual anthropogenic drivers of environmental change that are responsible for extinction and species traits are understudied in many clades (e.g., in primates; Estrada et al., 2017), limiting the impact of these comparative studies in applied conservation (Cardillo & Meijaard, 2012). Identifying which threats are most impactful to species with different trait types would enable actionable conservation steps. This could include mitigating key threats in susceptible species' ranges and identifying which species are most likely to be vulnerable to certain types of environmental change in the future. Despite this possible benefit of considering specific threats, previous studies have been mostly limited to linking traits and species' threat status, although a few exceptions have incorporated consideration of threats into these analyses (e.g., Purvis et al., 2005; González-Suárez et al., 2013; Murray et al., 2014).

Lastly, we lack information on relevant traits for many species, resulting in incomplete data. The species for which we lack data may be systematically biased towards those that are more difficult to study, such as arboreal or nocturnal species. In addition to reducing statistical power, removing these species from analyses has potential to bias observed relationships between variables (Nakagawa & Freckleton, 2008) and can result in a loss of real information when some traits included in an analysis have better data coverage than others.

Primates have been especially important in studies assessing predictors of extinction risk (Purvis et al., 2000; Purvis et al., 2005; Matthews et al., 2011; Machado et al., 2022). Primates are one of the most threatened animal clades, with ~65% of species at risk of extinction (IUCN, 2021). The number of threatened primate species is on the rise (up ~5% in approximately 5 years), yet the last comprehensive assessment of the major determinants of primate extinction risk was published over 20 years ago (Purvis et al., 2000). The number of recognized primate species has changed dramatically since earlier studies, having more than doubled from 180 to over 500 in the past few decades (Rylands & Mittermeier, 2014; Creighton et al. 2022). As a result of these taxonomic changes and limitations of older phylogenies, older studies focused on a relatively small number of currently recognized primate species. More speciose and up-to-date phylogenies have

recently become available (Upham et al., 2019) in addition to a greater quantity and quality of trait data for many species. These contributions create an opportunity for the inclusion of more described primate species in comparative analyses, bringing us closer to capturing the true scope of primate diversity. Primates are crucial components of tropical biodiversity, core players in the function of ecosystems, and central to many cultures and religions (Estrada et al., 2017). It is thus an urgent goal to determine which biological and behavioral traits contribute to primate extinction vulnerability and how these traits interact with anthropogenic impacts to contribute to population declines.

Here, we analyze the biological and behavioral determinants of primate extinction risk using a phylogenetic comparative approach. We investigate the relationship between multiple phenotypic traits and two measures of extinction risk reported by the International Union for Conservation of Nature (IUCN): threat status and population trend. We then assess how these same traits covary with vulnerability to the major threats facing primate species. This research addresses the gaps above by including multiple traits in the analysis and using imputation approaches based on phylogeny and phenotypic traits to fill in data for species with missing trait values. In addition, by investigating population trends and specific threats, we improve understanding of the connections between specific traits and the abundance of primates.

We focus on 10 key traits with proposed links to extinction risk (Table 1).

Table 1: The predicted direction of effect of biological and behavioral traits on extinction risk.

Trait:	**Expected risk high when:**	**Reason:**
Body mass (g)	Large body	Animals with large bodies have slow life histories and have been previously shown to be at increased extinction risk (Cardillo & Bromham, 2001; Cardillo et al., 2005).
Generation length (yrs)	Long generations	Slow life histories mean fewer generations to adapt to environmental changes (Purvis et al., 2000).
Home range size (ha)	Large home range size	Species that have individuals that maintain large home ranges are particularly vulnerable to habitat

		loss, degradation, and edge effects (Woodroffe & Ginsberg, 1998; Purvis et al., 2000).
Group size	Small group size	Small group size has been associated with heightened extinction risk, perhaps because large groups reduce predation and enhance foraging (Davidson et al., 2009; 2012).
Brain volume (cm^3)	Small brain volume	Large relative brain size is a proxy of general intelligence and behavioral flexibility (Reader et al., 2011; Navarrete et al., 2016), which have been associated with reduced extinction risk in birds (Ducatez et al., 2020).
Omnivory (true or false)	False	Animals with a large dietary breadth can rely on a wider range of food types when resources become limited (Boyles & Storm, 2007).
Social system	Polygynandry	Species characterized by complex social organization are hypothesized to have larger critical population sizes (i.e., more individuals must persist to maintain what is considered to be a healthy population) and may therefore go extinct more quickly than species in simpler social systems (Höglund, 1996).
Lifestyle	Arboreal	Strictly arboreal species are disproportionately affected from losing habitat via deforestation (Munstermann et al., 2022).
Insularity (true or false)	True	Island ecosystems are particularly vulnerable to anthropogenic change due to small population sizes, low habitat availability, and low functional redundancy (Biber, 2002; Blackburn et al., 2004; Leclerc et al., 2018).
Nocturnal (true or false)	Diurnal	Diurnal species are more likely to be disturbed by human activity (e.g., traffic) and diurnal activity

	has been connected to extinction risk (Purvis et al., 2000).

METHODS:

DATA:

We collected information on threat status (least concern = LC, near threatened = NT, vulnerable = VU, endangered = EN, critically endangered = CR, data deficient = DD, and not evaluated = NE) and population trend (increasing = I, stable = S, decreasing = D, and unknown = U), from the IUCN (2021) for 446 primate species present in the ultrametric primate phylogeny published by Upham et al. (2019) (Figure 1). We also collected a list of active threat types affecting each species in the IUCN (2021) as defined by the Salafsky et al. (2008) threat classification system: 1 = residential and commercial development, 2 = agriculture and aquaculture, 3 = energy production and mining, 4 = transportation and service corridors, 5 = biological resource use, 6 = human intrusions and disturbance, 7 = natural system modifications, 8 = invasive and other problematic species and genes, 9 = pollution, 10 = geological events, and 11 = climate change and severe weather.

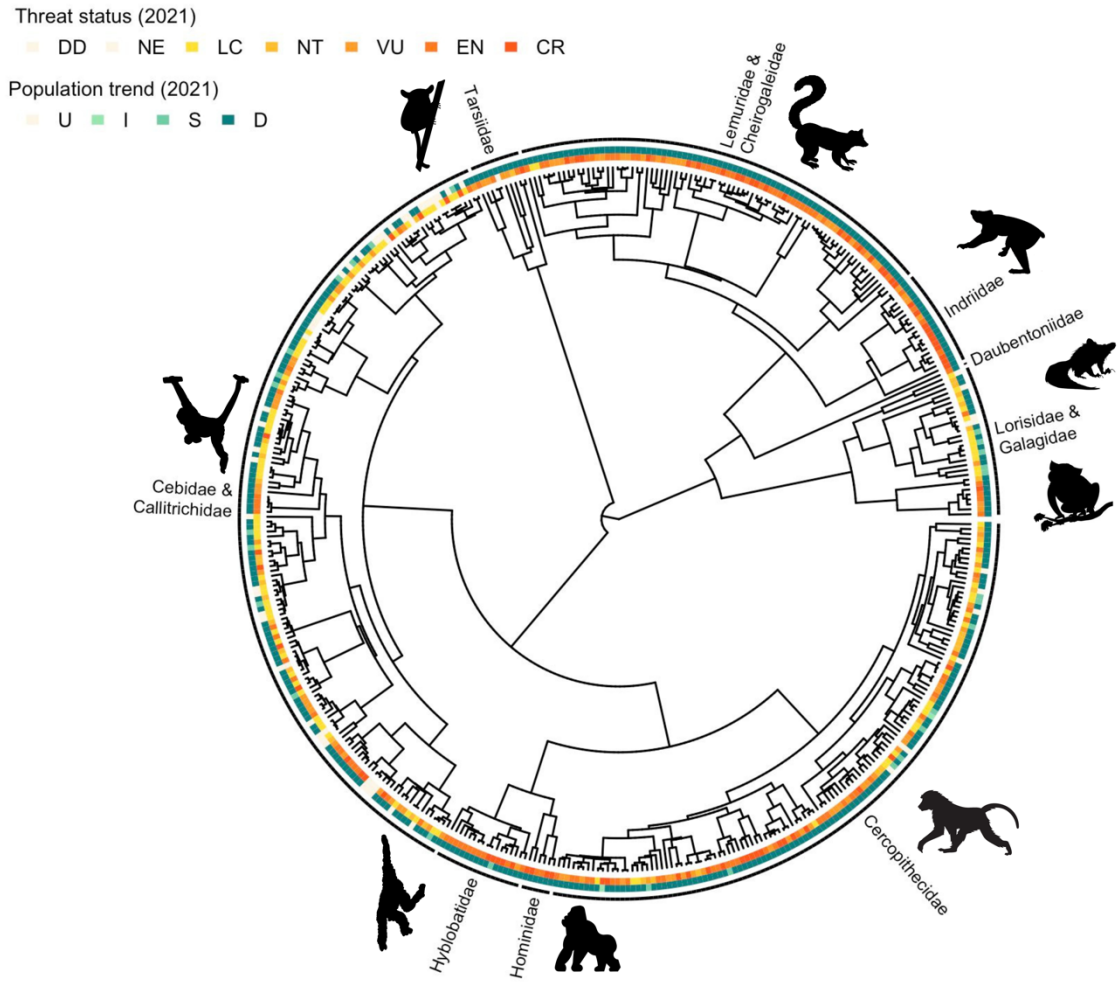


Figure 1: Phylogenetic distribution of threat status and population trends (IUCN, 2021) for 446 primate species in the Upham et al. (2019) phylogeny. Images of representative species are presented next to family labels. Codes for threat status: data deficient = DD, not evaluated = NE, least concern = LC, near threatened = NT, vulnerable = VU, endangered = EN, and critically endangered = CR. Codes for population trend: unknown = U, increasing = I, stable = S, and decreasing = D (IUCN, 2021).

For each of the 446 species in our dataset, we recorded data on 10 different biological and behavioral traits that have been proposed to be associated with extinction risk from various sources: body mass (g) (Galán-Acedo et al., 2019), generation length (yrs) (IUCN, 2021), home range size (ha) (Galán-Acedo et al., 2019), group size (Rowe & Myers, 2011), brain volume (Powell et al., 2017), omnivory (true or false), social system (solitary, pair-living, harem polygyny and polygynandry) (DeCasien et al., 2017; Rowe & Myers, 2011 and other sources), lifestyle

(arboreal, terrestrial, or both) (Rowe & Myers, 2011 and other sources), insular (true or false) (inferred from range data available in Rowe & Myers, 2011; IUCN, 2021), and nocturnal (true or false) (Estrada et al 2017; IUCN, 2021). The full list of references for trait values is available in the Supplementary Data. Table 1 summarizes how we expected each trait to be associated with primate extinction risk. Previous studies have included geographic range size as a covariate in similar analyses (e.g., Purvis et al., 2000; Machado et al., 2022). However, a species' geographic range size is one of the main criteria used by the IUCN to assign threat status: species with small population sizes that have small or restricted geographic ranges are considered to be more imperiled (IUCN, 2021) (i.e., threatened species have small geographic ranges by definition). Because we were interested in how biological and behavioral trait contribute to extinction risk, including effects on what geographic ranges they are able to occupy, we did not include geographic range size in our analysis. Notably, by including insularity in our analysis we controlled for the fact that species on small islands may not be able to maintain geographic ranges large enough to be considered healthy by the IUCN due to geographic barriers.

Following Powell et al. (2017), for sexually dimorphic clades (size difference > 10%) only brain volume and body mass data from adult females were used in analysis. For all other species, averages for all adults measured in the original source were used. Species found exclusively on Madagascar, Borneo, or Sumatra were not scored as insular since these islands are large enough to support large geographic ranges comparable to many mainland species. Further details on operational definitions and trait coding are provided in the Supplementary Materials, along with a correlation matrix of all traits and response variables (Figure S1), and a comparison of trait data from different sources (Figures S2, S3, and S4).

ANALYSIS:

Trait imputation

The availability of data varied across the species in our dataset. Percentages of species with missing trait data were: body mass (6%), omnivory (17%), generation length (23%), home range size (25%), group size (39%), and brain volume (46%). Restricting the analysis to only species with observed data on all traits reduced our sample size of species by over half (e.g., to from n=430 to n=151 in our analysis of threat status). We thus opted to use multiple imputation to avoid losing species from our analysis where one or more traits had missing observations. The main advantage

143 of imputation is that it avoids a loss of statistical power caused by reduced sample sizes due to
144 missing trait data and that it reduces potential biases in parameter estimates caused by eliminating
145 missing observations (see Nakagawa & Freckleton, 2008). For instance, if missing observations
146 are not missing completely at random, the relationship between two variables could change when
147 they are excluded from analysis (Nakagawa & Freckleton, 2008). In analyses with more than one
148 independent variable imputation also prevents the loss of real information if some variables have
149 better data coverage than others. For example, if an analysis has one independent variable with
150 100% data coverage and a second independent variable with only 80% data coverage, imputation
151 will allow all observations for the first trait to be kept in the analysis by substituting the 20% of
152 missing values for the second variable.

153 Multiple imputation was accomplished using phylogenetic information and data for other
154 traits. We started with phylogenetic multiple imputation using 100 randomly sampled trees
155 available from Upham et al. (2019). The imputation of traits was ordered so that imputed
156 information could be used to inform subsequent model fits along with phylogenetic information
157 (e.g., once body mass was imputed it was used to inform model fits for the imputation of other
158 variables). From each tree, we generated a variance-covariance matrix which we then dissolved
159 into 445 eigenvectors using the 'PVRdecomp' function from the R package PVR (Santos et al.,
160 2018). Using forward-backward model selection, we determined which phylogenetic eigenvectors
161 and traits had the best support for inclusion in models predicting each trait with missing data based
162 on Akaike information criterion (AICc) scores using the 'stepAIC' function from the MASS R
163 package (Ripley et al., 2013). We chose how many eigenvectors to include in model selection for
164 the imputation based on model performance in cross validation (Table S1). The top model for each
165 trait was used to impute values for each species missing data using the 'predict' function from the
166 car package in R (Fox et al., 2012). To propagate error, we then used the fits and standard
167 deviations associated with predicted values to take a randomly sampled trait value for each species
168 from the normal or binomial distribution (depending on whether traits were continuous or binary).

169 This imputation process was repeated once for each tree, resulting in 100 imputed datasets.
170 We performed a leave-one-out cross-validation of each imputation, where we removed observed
171 datapoints and used our imputation method to predict their value. When comparing these
172 predictions to the actual observed datapoints performance proved to be good in all cases (predictive
173 accuracy > 0.8 for continuous variables and area under the ROC curve > 0.8 for binary variables;

see Table S1).

Modelling threat status, population trends, and threat types

We ran multiple models to test predictors of three types of outcomes for primate populations. First, we tested which biological and behavioral traits are associated with the threat status of a species. Second, we tested the effects of species' behavioral and biological traits on population trends (i.e., population growth or decline). Third, we tested which traits were associated with species susceptibility to the most important threats that primate species face.

To determine which biological and behavioral traits are associated with threat status, we ran two phylogenetic generalized linear mixed models using Bayesian approximation as implemented in the MCMCglmm R package (Hadfield, 2010). The first model had an ordinal error structure, and the response variable was an ordinal measure of threat status scored as follows: LC=0, NT=1, VU=2, EN=3, and CR=4 (Butchart et al., 2007). We ran the second model with a threshold error structure; here the response variable was threat status scored as a binary outcome where species were scored as either being threatened (VU, EN, or CR) (scored as 1) or not threatened (NT or LC) (scored as 0).

To test the effects of traits on population trends we ran a third phylogenetic generalized linear mixed model with a threshold error structure (Hadfield, 2010). In this model, each species was assigned a binary outcome of either declining (scored as 1) or not declining (i.e., stable or increasing) (scored as 0).

Finally, to determine which biological and behavioral traits were associated with species' susceptibility to the most important threats that primate species face, we ran five phylogenetic generalized linear mixed models with threshold error structures (Hadfield, 2010), one for each of the top five threats to primates identified by the IUCN (2021). These top five threats identified for primate species were: 1 = residential and commercial development (35% of species), 2 = agriculture and aquaculture (80%), 3 = energy production and mining (22%), 5 = biological resource use (82%), and 7 = natural system modifications (23%). Here, each of our five models had a binary outcome of 1 (indicating that a species was affected by a particular threat) or 0 (indicating that a species was not affected by the threat).

Each model described above was run on 100 imputed datasets and phylogenies to account for uncertainty in phylogeny and trait estimates (Nakagawa & De Villemereuil, 2019). Models ran

205 a total of 550,001 iterations, with a thinning interval of 500 and a burn-in of 50,000 to ensure
206 convergence had occurred. We confirmed convergence had occurred by assessing trace plots after
207 analyses finished running (Hadfield, 2010). Species were dropped from analyses when the true
208 value of a response variable was unknown by the IUCN (2021) (e.g., if the threat status was DD
209 or NE). Traits were included as fixed effects and continuous variables were ln-transformed,
210 centered with respect to the mean, and scaled by 2 standard deviations in all models to make their
211 effect sizes comparable to those reported for binary variables (Gelman, 2008). We used a weakly
212 informative gelman prior for fixed effects.

213 We also tested the hypothesis that some traits previously shown to be associated with
214 primate extinction risk are losing signal as more species become imperiled, for example, if
215 anthropogenic threats are becoming so overwhelming that all species are beginning to suffer
216 regardless of their attributes. This analysis involved repeating our analyses of threat status using
217 an older IUCN threat status data and species list (obtained from Harcourt & Parks, 2003).

218 To interpret the output from our Bayesian analyses, we provide (i) the distribution of
219 posterior means for tests from all 100 imputed datasets in graphical form (Figures 2 and 3), (ii) the
220 89% credible intervals (per McElreath, 2018) from the full posterior distribution of estimates in
221 graphical form (Figures 2 and 3), and (iii) the percentage of iterations from each set of 100 models
222 that were consistently positive or negative (Tables S2 to S13). We focused on results that were
223 most supported based on these outcomes. For the purposes of providing an estimate of the
224 magnitude of an effect in the main text, posterior means were pooled across datasets using Rubin's
225 rules (Nakagawa & De Villemereuil, 2019) (hereafter, "pooled posterior mean").

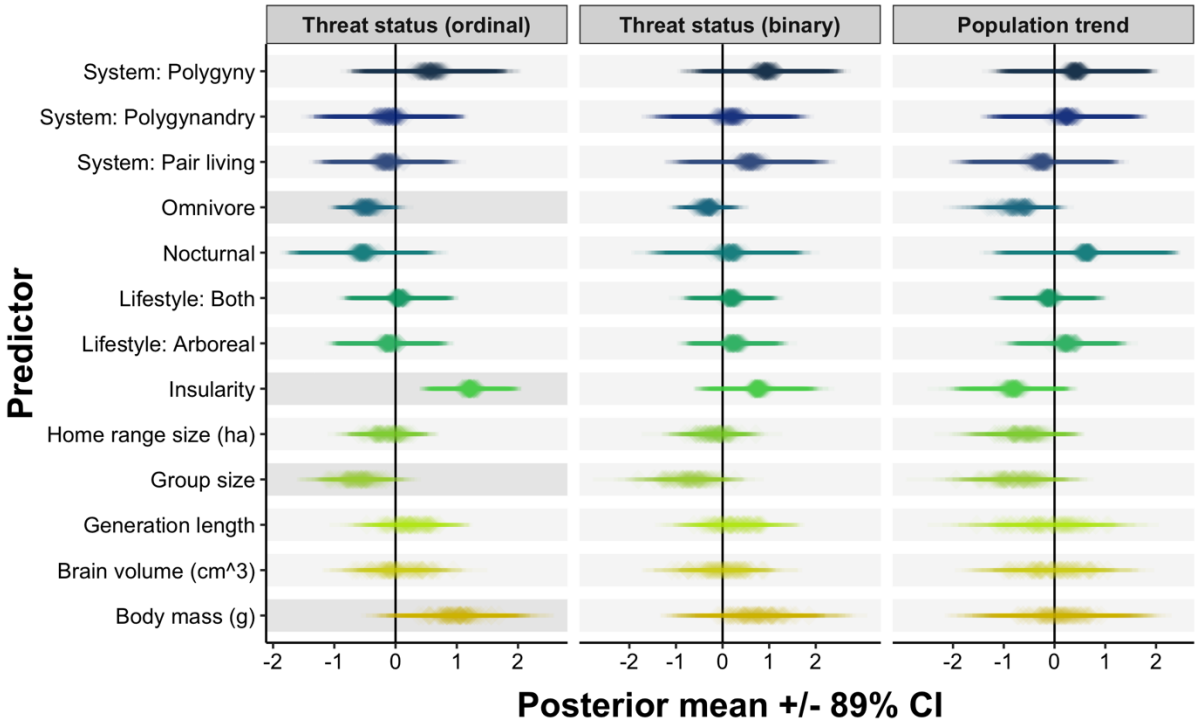
226

227 **RESULTS:**

228 *Predictors of threat status and population trends*

229 When scored as an ordinal outcome (LC=0, NT=1, VU=2, EN=3, and CR=4), threat status was
230 positively associated with insularity (pooled posterior mean = 1.217; 100% of 100,100 posterior
231 estimates > 0) and, albeit not as strongly, with body mass (pooled posterior mean = 0.995; 94%
232 estimates > 0) (Figure 2; Tables S2) across 430 species with known threat statuses. Ordinal threat
233 status was negatively associated with omnivory (pooled posterior mean = -0.475; 95% estimates
234 < 0) and group size (pooled posterior mean = -0.601; 95% estimates < 0) (Figure 2; Table S2). In
235 our analysis using older IUCN data, we found that only insularity (pooled posterior mean = 2.255;

236 100% estimates > 0) and home range size (pooled posterior mean = 1.532; 100% estimates > 0)
237 were associated with threat status (ordinal) in the predicted direction (Table S3).
238 Threat status was not strongly associated with any biological or behavioral traits when
239 scored as a binary response (Figure 2; Table S4). We repeated this analysis removing imputed
240 datapoints to see if their inclusion affected the lack of strong associations. We also ran three
241 separate models with body mass, generation length, and brain volume as sole predictors to
242 determine if correlations among these predictors (see Figure S1) in the full models affected the
243 results. Results from these additional analyses again consistently showed no strong effect of any
244 traits (Tables S5 and S6). In our analysis using older IUCN data, we found that insularity (pooled
245 posterior mean = 2.565; 100% estimates > 0) and home range size (pooled posterior mean = 1.116;
246 99% estimates > 0) were associated with threat status (binary) in the predicted direction (Table
247 S7). Population trend was not consistently associated with any biological or behavioral traits across
248 401 species with known population trends (Figure 2; Table S8).



249
250 Figure 2: Outcomes from three sets of models testing the relationship between traits and: threat
251 status scored as an ordinal variable (first panel), threat status scored as a binary variable (second
252 panel), and population trend scored as a binary variable (third panel). Each cell contains 100
253 posterior means (plotted as translucent diamonds) with their associated 89% credible intervals

(plotted as translucent horizontal lines) obtained from 100 MCMCglmm models run with 100 randomly sampled phylogenies across 100 trait datasets with missing datapoints obtained through multiple imputation. Darker shading behind effects interpreted in text. Continuous variables were ln-transformed, centered with respect to the mean, and scaled by 2 standard deviations.

Predictors of specific threat types

Our analyses of threat types included 404 species with known threats (Tables S9 to S13). Species with larger body masses were more likely to be affected by threat 1 = residential and commercial development (pooled posterior mean = 1.001; 96% estimates > 0; Table S9) and threat 3 = energy production and mining (pooled posterior mean = 1.267; 99% estimates > 0; Table S11) (Figure 3). Insularity was negatively associated with threat 1 = residential and commercial development (pooled posterior mean = -0.755; 98% estimates < 0; Table S9), threat 3 = energy production and mining (pooled posterior mean = -1.811; 100% estimates < 0; Table S11), and threat 7 = natural system modifications (pooled posterior mean = -1.312; 100% estimates < 0; Table S13) (Figure 3). Species living a strictly arboreal lifestyle were more likely to be affected by threat 1 = residential and commercial development than strictly terrestrial species (i.e., the baseline) (pooled posterior mean = 1.023; 97% estimates > 0; Table S9) (Figure 3).

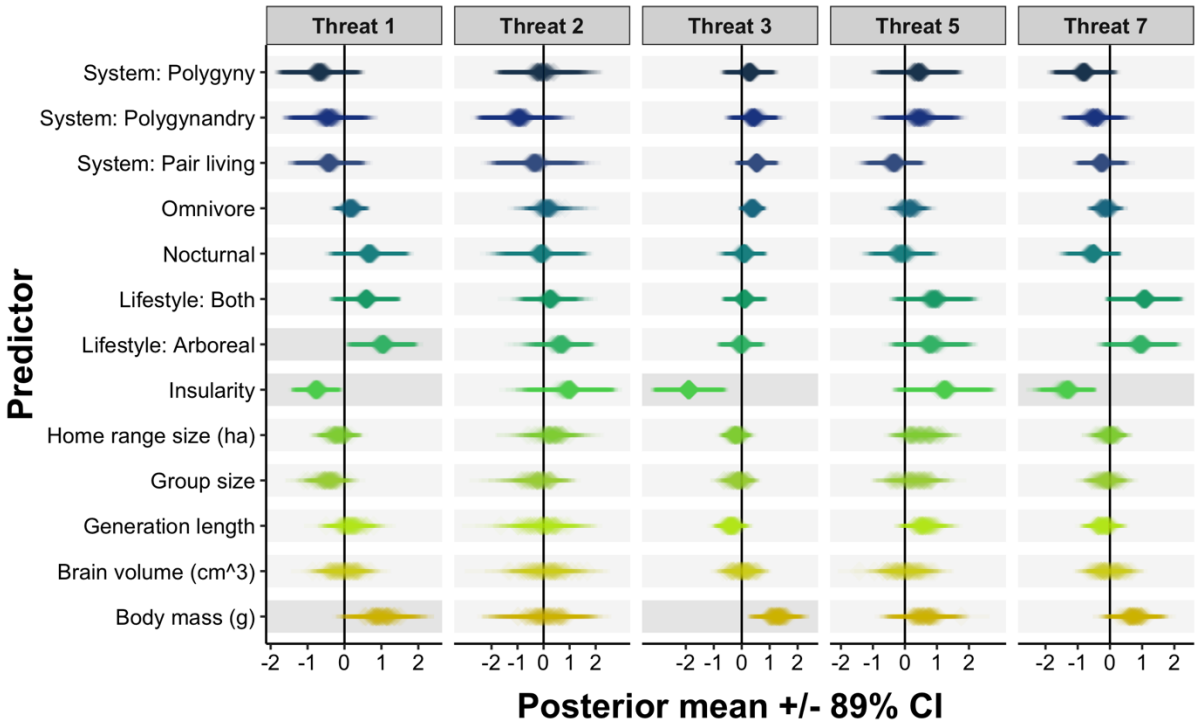


Figure 3: Outcomes from five sets of models testing the relationship between traits and species susceptibility to: threat 1 = residential and commercial development (first panel), threat 2 = agriculture and aquaculture (second panel), threat 3 = energy production and mining (third panel), threat 5 = biological resource use (fourth panel), and threat 7 = natural system modifications (fifth panel). Each cell contains 100 posterior means (plotted as translucent diamonds) with their associated 89% credible intervals (plotted as translucent horizontal lines) obtained from 100 MCMCglmm models run with 100 randomly sampled phylogenies across 100 trait datasets with missing datapoints obtained through multiple imputation. Darker shading behind effects interpreted in text. Continuous variables were ln-transformed, centered with respect to the mean, and scaled by 2 standard deviations.

DISCUSSION:

We investigated the correlates of extinction risk and threat susceptibility in primates using phylogenetic comparative methods to analyze the most complete and up-to-date set of trait data and IUCN data. One novelty of our approach involved the use of phylogenetic and trait-based imputation of missing data. Our analyses revealed that larger-bodied and more insular species exhibit higher threat status, while those that are more omnivorous or live in larger groups have lower threat status. When looking at specific threats, we found that larger-bodied and arboreal species are more vulnerable to key threats, while insular species are less vulnerable to these threats.

Our analyses with binary outcomes included threat status scored as threatened versus non-threatened and population trend scored as declining versus not declining. These analyses revealed that most traits are not strong predictors of whether a given primate species is considered threatened (contrary to findings in other taxonomic groups, such as birds; Lee & Jetz, 2011). When we scored threat status ordinally – with five ranked categories from least concern to critically endangered – higher threat status was associated with insularity, large body mass, omnivory, and small group size, consistent with our predictions for these traits. Therefore, primate species that are most imperiled, and thus score highest in ordinal threat status, do tend to be those with biological and behavioral predispositions to extinction.

We also considered how the effects of predictors changed over time. When applying the same methods to analyze a 1999 IUCN dataset, we found that insularity and home range size shared a positive relationship with both binary and ordinal threat status, but other traits were not

303 meaningfully associated with threat status. This pattern of results using newer versus older data
304 indicates that some traits (i.e., home range size) are becoming less important to extinction risk as
305 the effects of anthropogenic activity become increasingly overwhelming. The fact that traits
306 identified in our analysis of ordinal 2021 threat status (i.e., body mass, group size, and omnivory)
307 do not come out as strongly in our analysis with older data could indicate that these traits are
308 beginning to have a larger signal over time, or that the larger number of species in our 2021 dataset
309 (a consequence of taxonomic reevaluations in many clades; Creighton et al., 2022) enabled us to
310 more powerfully detect effects of these traits.

311 Previous studies have found an effect of variables not shown to explain meaningful
312 variation in our analysis. For example, Ducatez et al. (2020) investigated whether threat status
313 covaries with innovativeness, which is a known measure of behavioral flexibility associated with
314 general intelligence (Reader & Laland, 2002; Reader et al., 2011). We did not find an effect of
315 brain size, another known measure of behavioral flexibility and general intelligence (Reader et al.,
316 2011; Creighton et al. 2021), and correlate of innovativeness, in our analysis. The caveats
317 associated with each of these measures is discussed in Creighton et al. (2021), including the
318 difficultly of adequately controlling for literature effort when estimating innovativeness and the
319 small sample sizes used to estimate average brain sizes for many species. However, our difference
320 in results could point to the fact that different traits contribute to heightened extinction risk for
321 these two clades, and that the relationship between some traits and extinction risk may be far more
322 complicated than originally expected. Species with higher behavioral flexibility and general
323 intelligence may be less at risk of extinction because they are better equipped to find novel
324 solutions that allow them to overcome environmental challenges (Beever et al., 2017; Ducatez et
325 al., 2020). However, the relationship between behavioral flexibility and extinction may be more
326 complex, particularly in a clade like primates where innovations are frequent and human conflict
327 is common. Certain behavioral innovations can help species to avoid human conflict and endure
328 habitat modifications, such as novel approaches for accessing foods or shifting to new food
329 resources (Beever et al., 2017). However, other innovative behaviors can increase human-wildlife
330 conflict. In many primate species, crop-raiding and garbage eating have become common practice
331 and indicate their flexibility to survive in changing environments (e.g., chimpanzees and baboons;
332 Maples et al., 1976; Hahn et al., 2003; Hockings et al., 2009). These behaviors bring animals in
333 direct conflict with humans and, in some cases, attract them to lower quality habitats. Future

contributions should further address the paradox of how flexibility both helps and hinders survival, and what this means for species' persistence.

In analyses assessing predictors of direct threats, we found that strictly arboreal species were more likely to be threatened with residential and commercial development – a major driver of deforestation in many regions. We also found that species with large body masses were more likely to be affected by residential and commercial development and energy production and mining. Thus, the tendency of larger bodied species to be severely threatened is likely influenced by development and energy/mining activities. Finally, insular species were less likely to be vulnerable to multiple threats (residential and commercial development, energy production and mining, and natural system modifications) despite being more likely to be highly threatened. This indicates that the high threat statuses of insular species may not be driven by anthropogenic activity. Instead, their small geographic ranges enforced by geographic barriers could simply make it impossible to maintain healthy population sizes, despite not being subject to major threats.

There are some limitations to our analyses. One issue involves correlated predictor variables. Body mass, generation length, and brain volume were highly correlated in our dataset (correlation coefficients range between 0.6 and 0.9). We included these predictors in the same models to identify how they independently contributed to extinction risk and threat vulnerability (Freckleton, 2002). However, this creates the possibility of collinearity in model estimates for these variables. Increased uncertainty (i.e., wide credible intervals) around estimates for these three traits indeed point to some collinearity among estimates. We therefore investigated the effects of these variables individually in separate models, which yielded largely consistent results. Secondly, like most previous studies, response variables in our analysis come from IUCN assessments. While the IUCN maintains the largest global dataset on species extinction risk and threats useful for comparative analyses, these measures are vulnerable to errors in empirical data and in models used to estimate population declines and extinction risk (Rueda-Cediel et al., 2018). As a result, there is likely to be uncaptured uncertainty associated with the measures of extinction risk used in our analyses.

Information about how biological and behavioral traits contribute to species' susceptibility to direct threats has been a persistent knowledge gap in the conservation literature, particularly for primates (Estrada et al., 2017). We provide a first step in addressing this knowledge gap by linking traits to key threats responsible for population declines. This approach has potential to be expanded

365 to other clades. Understanding the biological and behavioral predictors of threat susceptibility in
366 broader range of taxa could help groups like the IUCN to identify which threats pose the most
367 imminent harm to species with shared characteristics. There is also an opportunity to apply the
368 knowledge contributed here to projections about which species are next to become threatened: we
369 propose that factoring in traits and threat information could provide more powerful inference and
370 will lead to more proactive monitoring of species that face the greatest risks in the future. For
371 instance, strictly arboreal species living in regions with residential development may be expected
372 to decline at a faster rate than other species without these characteristics.

373 In summary, by taking advantage of statistical approaches for dealing with missing data
374 and Bayesian inference, we have shown that multiple traits contribute to primate threat status. Our
375 findings suggest that the effects of some traits, such as home range size, have weakened over the
376 past 20 years, indicating that the traits that influence a species' threat status are changing as
377 anthropogenic effects continue to transform natural landscapes. Other characteristics shown to
378 affect extinction risk in other clades, such as behavioral flexibility, do not appear to affect primate
379 extinction risk, suggesting that different processes likely govern extinction in different clades.
380 Focusing on mitigating key threats, as identified here, from susceptible species' geographic ranges
381 will be an important and necessary step for future recovery.
382

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