

RESEARCH ARTICLE

Examining the Extinction Risk of Specialized Folivores: A Comparative Study of Colobine Monkeys

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Species extinctions are nonrandom with some taxa appearing to possess traits that increase their extinction risk. In this study, eight predictors of extinction risk were used as independent variables to predict the IUCN category of a subfamily of specialized folivorous primates, the Colobinae. All data were transformed into phylogenetically independent contrasts and were analyzed using bivariate regressions, multiple regression, and a maximum likelihood approach using Akaike's Information Criterion to assess model performance. Once an outlier was removed from the data set, species that devote a smaller proportion of their diet to mature leaf consumption appear to be at a greater risk of extinction. Also, as female body mass increases, so does extinction risk. In contrast, as maximum latitude and the number of habitat types increase, extinction risk appears to decrease. These findings emphasize the importance of examining detailed dietary variation for predicting extinction risk at a relatively fine taxonomic scale and, consequently, may help improve conservation management. *Am. J. Primatol.* 70:1–12, 2008. © 2008 Wiley-Liss, Inc.

Key words: primate; conservation; diet; folivory; threatened; taxonomic scale

INTRODUCTION

An increasing amount of attention has been devoted to the apparent nonrandom extinctions of various species [Cardillo et al., 2004; Ceballos et al., 2005; Harcourt & Schwartz, 2001; Isaac & Cowlishaw, 2004; Pimm & Raven, 2000; Purvis et al., 2000a]. The increasing rate of extinctions, largely owing to anthropogenic factors, has spurred research to determine the traits that contribute to extinction risk. Several broad-scale comparative studies have shown that extinction risk varies across time, space, and taxa, and that species' biological traits interplay with external factors to influence this variation [Cardillo & Bromham, 2001; Isaac & Cowlishaw, 2004]. In addition, many studies have illuminated the difficulty in identifying simple ecological correlates of overall extinction risk [Owens & Bennett, 2000].

Nonetheless, several variables have been found to be important predictors of extinction risk. For thousands of nonmarine mammals, species with large body sizes and small geographic ranges are vulnerable to extinction [Ceballos et al., 2005]. In particular, for species ≥ 3 kg, intrinsic biological traits and environmental factors are independent significant predictors of extinction risk. In contrast, for species < 3 kg, extrinsic factors appear to play a greater role in vulnerability to extinction [Cardillo et al., 2005].

Studies focusing on primate extinction risk have found similar patterns. For primates in general, four traits—large body size [Harcourt & Schwartz, 2001; Jernvall & Wright, 1998; Wright & Jernvall, 1999], high trophic level, small geographic range [although see Harcourt, 2000], and low population density [cf. Harcourt, 1998]—are significantly and independently associated with high risk [Purvis et al., 2000b]. Related studies on primate rarity found that rare and common primates are distinguished by just a single category of factors, degree of specialization, which includes dietary and habitat variety, as well as maximum latitude [Harcourt et al., 2002]. Taxa that had narrow dietary niches, habitat types, and maximum latitudes were at a greater risk than those taxa that had broader niches, habitats, and maximum latitudes. In addition, different primates appear to respond to multiple extinction threats in diverse ways. For example, taxa at risk from hunting

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have large body sizes [Isaac & Cowlshaw, 2004], whereas species at risk from logging exhibit low ecological flexibility and larger home ranges. Furthermore, primates vulnerable to agriculture are likely to be arboreal and have low-fruit diets [Harcourt, 1998; Isaac & Cowlshaw, 2004].

In addition, some folivores appear to maintain population levels in low to moderately disturbed habitats [Johns & Skorupa, 1987]. This probably is due to several factors including a greater number of potential food sources [Grassi, 2006], a more dense resource base [Grassi, 2006], and/or higher-quality resources in these habitats [Ganzhorn, 1992]. Several studies have demonstrated that leaf quality (as measured by protein/fiber ratio) is the best predictor of primate folivore biomass [Chapman & Chapman, 2002; Ganzhorn, 1992; Oates et al., 1990]. Leaf quality is related to several factors including the level of habitat disturbance, climatic seasonality, and/or the phenological stage of the leaf [Ganzhorn, 1995; van Schaik et al., 2005].

Although many folivorous primates are thought to be dietary specialists, they also may be considered ecological generalists because leaves are readily available in most habitats. Even though highly folivorous primates seem to be adept at surviving under various ecological scenarios, there still is variation in the levels of extinction risk and degree of folivory across taxa. Therefore, it is important to examine just how dietary variation within specialized folivores relates to extinction risk.

An additional factor to consider in analyses of susceptibility to extinction is the taxonomic breadth of the study. Analyses examining the extinction risk of several orders may produce confounding effects owing to the wide array of taxa considered [Harcourt, 2002]. Examining a smaller taxonomic unit may be advantageous to reduce potentially confounding variables due to phylogeny [Harvey & Pagel, 1991]. Also, comparing the results of small-scale analyses with broader-scaled studies may provide important information on the effects of taxonomic scale in extinction risk analyses.

Therefore, in this study, several potential correlates of extinction risk were examined in a single subfamily of specialized folivorous primates (Colobinae). Colobines exhibit several characteristics that are useful for a study of this nature. First, colobines represent a group of closely related species and, thus, some of the confounding effects of phylogeny can be reduced [Harvey & Pagel, 1991]. Second, the natural history of many of the species is known [Davies & Oates, 1994; Fashing, 2007; Kirkpatrick, 2007]. Third, colobines are considered specialized folivores, having morphological adaptations for leaf digestion [Chivers & Hladik, 1980], yet the degree of folivory varies across taxa. Colobine monkeys also differ in their degree of extinction risk [IUCN, 2006]. Finally, with the publication of the possible extinction of Miss

Waldron's red colobus [Oates et al., 2000] and the subsequent evidence of their potential existence [McGraw, 2005; McGraw & Oates, 2002], some recent attention has focused on colobine monkey extinction.

MATERIALS AND METHODS

Data Organization

Published data were gathered for 34 colobine species (Appendices A and B). Although data for Hanuman langurs (*Semnopithecus entellus*) were available, they were not included in the analyses because this species is either protected and/or provisioned throughout most of their range and this could affect their vulnerability to extinction [Koenig, personal communication; Koenig & Borries, 2001]. In addition, the number of species differed across analyses because all of the data were not available for all species. The IUCN [International Union for Conservation Nature, 2006] Red List extinction risk classification of each species was used as a proxy for extinction risk. For three of the species, *Presbytis siamensis*, *P. rubicunda*, and *Trachypithecus obscurus*, the IUCN classification data were obtained from Brandon-Jones et al. [2004]. The IUCN categorizes threatened species into three classes: vulnerable, endangered, and critically endangered, and less threatened species as either near threatened or least concern. This same classification scheme was used in this study. IUCN classifications are based on the population size, geographic range size, and the degree of population and/or geographic range size decline of taxa [IUCN, 2006].

We acknowledge that there are problems with using IUCN categories as a measure of extinction risk [Broderick et al., 2006; Harcourt, 2005; Mrosovsky, 1997]. One issue is that different people using the same criteria on the same species can vary in their assessment of threat from low risk to critically endangered [cf. Harcourt, personal communication; Regan et al., 2005]. In addition, lists produced for one goal but used for another can be misleading [Harcourt, personal communication; Possingham et al., 2002]. Notwithstanding, the IUCN Red List classification has been used as a proxy of extinction risk in numerous studies [Jones et al., 2003; Purvis et al., 2000b]. The fact that a particular method is commonly implemented does not justify its use [Harcourt, personal communication], yet precedence allows for comparisons with previous work. Thus, the use of IUCN categories maximizes our ability to place our results within the context of previous research. Following earlier research [e.g., Jones et al., 2003; Purvis et al., 2000b], IUCN categories were used in this study and treated as continuous variables: 1 = least concern, 2 = near threatened, 3 = vulnerable, 4 = endangered, and 5 = critically endangered.

Eight variables were used to predict extinction risk because of their: (1) relevance in affecting extinction vulnerability, (2) inclusion in previous analyses of extinction risk, and (3) availability in the published literature. The variables included seven intrinsic biological traits: (1) female body mass, (2) percent leaves in diet, (3) percent mature leaves in diet, (4) percent fruit/seeds in diet, (5) home range, (6) number of habitat types, and (7) absolute value of the maximum latitude of the species geographic range, and one extrinsic factor, (8) mean human population density (HPD) within the geographic range of a species. Body mass data were primarily utilized as a proxy for life history traits because quality life history data were unavailable for many species. Following previous studies, we expect that larger species displaying slower life histories are at a higher risk of extinction. Female body mass data were obtained from Smith and Jungers [1997], the number of habitat types was obtained from Jernvall and Wright [1998] and supplemented with data from Fashing [2007] for African colobines, and human population data were taken from Harcourt and Parks [2003]. For red colobus species (genus *Ptilocolobus*), the maximum latitude of geographic range size data were obtained from range maps from T. Struhsaker and N. Ting [personal communication]. Red colobus HPD data were extracted from the CIESIN online database [Tobler et al., 1995] using ArcGIS 9.0.

In addition to these predictor variables, previous studies of extinction risk often include population size and/or geographic range size as independent variables [Cardillo et al., 2004, 2005; Jones et al., 2003]. Because these variables also are used as criteria for assessing IUCN category, problems of circularity exist. Previous researchers have tried to solve this problem by only including taxa that have an IUCN category based on the reduction of population size and geographic range size, not the absolute value of these variables. We considered following this approach, yet this would reduce our already small data set. Therefore, these variables were not included in our study.

Data Analysis

Least-square regressions were used between each predictor variable and IUCN category. This method has the advantage of maximizing the sample size. However, it does not examine the independent effect of each variable. Therefore, multiple regressions also were employed to account for possible covariation among predictor variables. Stepwise techniques (either forward or backward) often are used with multiple regressions to find parsimonious sets of predictor variables from the most complex model. Several authors have shown that stepwise regression models are unstable, with the results

often affected by the order in which variables are entered into or removed from the model [Bronikowski & Altmann, 1996; Burnham & Anderson, 2003; Whittingham et al., 2006]. One remedy for this problem is to conduct an analysis using the most complex model (including all predictor variables), and then implement a maximum likelihood approach to find the most parsimonious models. Accordingly, a general linear model including all predictor variables was carried out. Next, Akaike's Information Criterion (AIC) was employed to determine which subset of variables best explained the IUCN categories of colobine monkeys. The AIC metric provides a measure of the likelihood of a model given a particular data set, while minimizing the model's assumptions (i.e., number of parameters in the model). With this approach, models within two AIC values of the "best" model are considered equally likely and deserve equal consideration [Burnham & Anderson, 2003; Towner & Luttbeg, 2007]. If several equally parsimonious models are found, the importance of the predictor variables is assessed by the frequency of occurrence in the total set of best models. The reasoning behind this is that a variable present in all of the best models should be considered a more important predictor compared with a variable that is present in only some of the best models.

All data were transformed into phylogenetically independent contrasts (PIC). This analytical method is a critical component of comparative analyses because species values are not independent due to shared evolutionary history [Felsenstein, 1985; Nunn & Barton, 2001]. Such nonindependence of data violates important assumptions of statistical tests. PIC techniques account for the nonindependence of data by calculating differences between species values and higher nodes. All PIC analyses were conducted with the software package CAIC [Purvis & Rambaut, 1995]. The best understood statistical assumption of PIC, that there should be no relationship between the contrast standard deviation and the age of the node, was tested as suggested by Nunn and Barton [2001]. We initially used the estimated divergence times between taxa, but using this method resulted in a failure to meet the previously mentioned assumption of PIC. Instead, we used equal branch lengths to better meet the statistical assumptions of the test [Garland et al., 1992].

The evolutionary relationships among colobines are not resolved, making it challenging to obtain sufficient phylogenetic data for the PIC analyses. Therefore, the phylogenetic hypotheses of several authors were combined into a single phylogeny (Fig. 1). In addition, some taxa were not present in any phylogeny. The evolutionary relationships of these taxa were based on their taxonomic history as stated by Rowe [1996] and Oates and Davies [1994] as previous research has shown good concordance between taxonomy and phylogeny [Garcia-Moreno

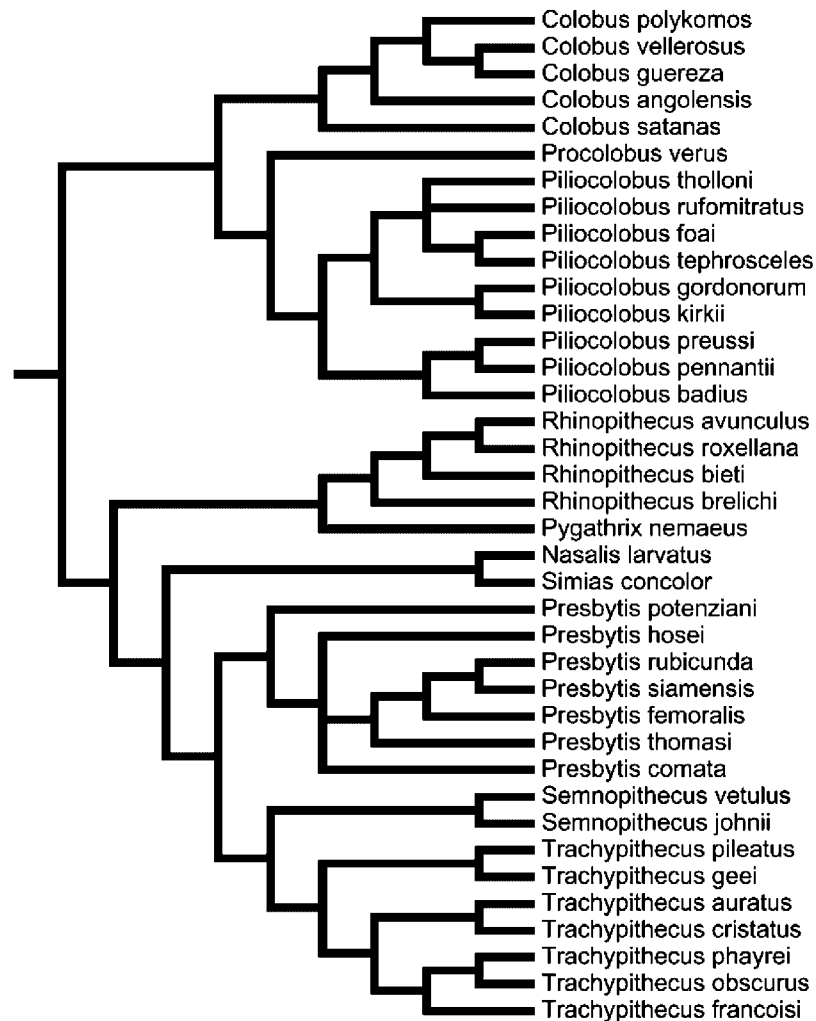


Fig. 1. Colobine phylogeny used in the phylogenetically independent contrasts analyses.

et al., 2003]. The basis of the phylogeny was from Purvis [1995] and Purvis and Webster [1999]. This included data for the genus-level relationships, as well as the species-level relationships of non-red colobus African colobines. The phylogenetic relationships of *Rhinopithecus* and the southeast Asian *Trachypithecus* species were based on the work of Roos and Nadler [2005]. The *Piliocolobus* species-level relationships were obtained from Struhsaker [1981] and the taxonomy presented in Grubb et al. [2003]. The tree typology of *Presbytis* species was obtained from Brandon-Jones [1996a,b]. As accurate divergence times were unavailable for many taxa, relative times of divergence were used based on the node level. This technique has been used in the past and yielded comparable results to known divergence times [Barraclough & Vogler, 2000]. As previous researchers have noted, minor errors in the phylogenetic hypothesis still are statistically superior to assuming a “star-like” phylogeny. Simulation studies demonstrated that PIC analyses are robust to

errors in the phylogenetic hypothesis used to calculate the contrasts [Martins, 1996]. All PIC regressions implemented a zero intercept model because when the predictor variable exhibits no change (a zero value contrast), no change is expected in the dependent variable [Garland et al., 1992].

All continuous data were log transformed before independent contrasts were calculated. In addition, the residuals from all regressions were examined for the presence of outliers. Residuals with a Cook’s distance >1.0 or a studentized residual ± 2.80 were considered outliers. Based on these criteria, a single outlier was found in many of the analyses, the contrast of *P. thomasi* vs. the clade containing *P. femoralis*, *P. rubicunda*, and *P. siamensis*. The data sets containing this outlier were subsequently reanalyzed with this sample removed.

We examined the relationships among variables in two ways. First, we conducted an exploratory analysis using a correlation table among all variables. Second, we examined the potential collinearity

among variables in the multiple regression analyses by calculating the variance inflation factor (VIF) for each predictor variable. We considered variables with a VIF value > 10 to have a high degree of collinearity [Hair et al., 2006]. With our data, one variable, percent of fruit in the diet, yielded a VIF of 10.18. With the outlier contrast removed from the data set, the variable with the highest VIF was percent of fruit in the diet, yet its value was only 6.78. Therefore, these results also demonstrate the importance of removing the outlier contrast to reduce the effects of collinearity. All analyses were conducted with Statistica 6.0.

RESULTS

As removing the outlier contrasts only had a minor effect on our results, we present our findings based on the data set without the outlier. The results of the exploratory analysis showed a significant relationship between the percent of fruit in the diet and two variables, female body mass (+) and the percent of leaves in the diet (–) (Table I). Based on the bivariate analyses, only one regression approached statistical significance, the relationship between maximum latitude and extinction risk. Species found at lower latitudes tended to display higher levels of extinction risk ($P = 0.05$) (Table II). The bivariate results are not necessarily surprising considering that many variables may interact to some extent, with the relationship between a predictor variable and extinction risk may be

obscured by another variable(s). Therefore, more weight should be placed on the results of the multiple regression analyses because this procedure examines the importance of each independent variable while accounting for the effects of the other predictor variables.

The multiple regression including all predictor variables produced a statistically significant model ($P = 0.011$; for further statistical values and results, see Table III). In this model, only two variables were significantly related to extinction risk maximum latitude (–) and number of habitats (–). In addition, female body mass ($P = 0.066$) and the percent of mature leaves in the diet ($P = 0.066$) were marginally

TABLE II. Least-Square Regressions Predicting IUCN Category Using Phylogenetically Independent Contrasts

Predictor variable	<i>F</i>	<i>r</i> ²	β	<i>P</i>	<i>N</i>
Female body mass	0.163	0.005	–0.074	0.689	31
% Leaves in diet ^a	0.219	0.008	–0.091	0.644	27
% Mature leaves in diet ^a	0.860	0.035	–0.186	0.363	25
% Fruit in diet ^a	0.456	0.018	0.134	0.506	26
Home range	1.637	0.055	–0.235	0.211	29
# of habitat types	0.905	0.028	–0.168	0.349	32
Maximum latitude ^a	4.181	0.122	–0.350	0.050	31
Human population density ^a	0.025	0.001	–0.029	0.876	31

^aThese analyses did not include the outlier contrast *P. thomasi* vs. the clade containing *P. femoralis*, *P. rubicunda*, and *P. siamensis*.

TABLE I. Correlation Matrix Between All Variables

Variable	IUCN category	Female mass	% Leaves	% Mature leaves	% Fruit	Home range	# Habitats	Maximum latitude	Human population density
IUCN category	–	0.271	–0.146	–0.196	0.240	–0.113	–0.256	–0.276	–0.095
	–	$P = 0.247$	$P = 0.538$	$P = 0.409$	$P = 0.309$	$P = 0.634$	$P = 0.276$	$P = 0.239$	$P = 0.691$
Female mass	0.271	–	–0.357	0.334	0.464	0.247	–0.146	0.184	–0.192
	$P = 0.247$	–	$P = 0.122$	$P = 0.151$	$P = 0.039$	$P = 0.294$	$P = 0.540$	$P = 0.438$	$P = 0.417$
% Leaves	–0.146	–0.357	–	0.158	–0.877	–0.137	0.065	0.116	0.053
	$P = 0.538$	$P = 0.122$	–	$P = 0.506$	$P = 0.00$	$P = 0.565$	$P = 0.785$	$P = 0.626$	$P = 0.824$
% Mature leaves	–0.196	0.334	0.158	–	–0.014	0.130	–0.072	0.178	–0.218
	$P = 0.409$	$P = 0.151$	$P = 0.506$	–	$P = 0.955$	$P = 0.584$	$P = 0.763$	$P = 0.454$	$P = 0.357$
% Fruit	0.240	0.464	–0.877	–0.014	–	0.084	–0.177	–0.059	–0.237
	$P = 0.309$	$P = 0.039$	$P = 0.00$	$P = 0.955$	–	$P = 0.724$	$P = 0.457$	$P = 0.806$	$P = 0.314$
Home range	–0.113	0.247	–0.137	0.130	0.084	–	0.163	0.319	–0.148
	$P = 0.634$	$P = 0.294$	$P = 0.565$	$P = 0.584$	$P = 0.724$	–	$P = 0.494$	$P = 0.171$	$P = 0.533$
# Habitats	–0.256	–0.146	0.065	–0.072	–0.177	0.163	–	–0.534	–0.217
	$P = 0.276$	$P = 0.540$	$P = 0.785$	$P = 0.763$	$P = 0.457$	$P = 0.494$	–	$P = 0.015$	$P = 0.359$
Maximum latitude	–0.276	0.184	0.116	0.178	–0.059	0.319	–0.534	–	0.387
	$P = 0.239$	$P = 0.438$	$P = 0.626$	$P = 0.454$	$P = 0.806$	$P = 0.171$	$P = 0.015$	–	$P = 0.092$
Human population density	–0.095	–0.192	0.053	–0.218	–0.237	–0.148	–0.217	0.387	–
	$P = 0.691$	$P = 0.417$	$P = 0.824$	$P = 0.357$	$P = 0.314$	$P = 0.533$	$P = 0.359$	$P = 0.092$	–

For each pair of variables, the first row indicates the correlation coefficient, and the second row lists the *P* value.

positively and negatively related to extinction risk, respectively.

The maximum likelihood analysis produced seven equally good models explaining extinction risk. The four variables that received the strongest support for predicting extinction risk were maximum latitude (–), number of habitats (–), female body mass (+), and the percent of mature leaves in the diet (–). These variables were the only factors that appeared in all seven of the best models (Table IV).

DISCUSSION

After removing an outlier from the data set, the maximum likelihood analyses identified four variables as being important predictors of colobine monkey extinction risk—female body mass, percent

TABLE III. Multiple Regression Model Predicting IUCN Category of Colobine Monkeys

Predictor variable	β	St. err. β	F	P value
Female mass	0.367	0.181	4.094	0.066
% Leaves	0.544	0.355	2.349	0.151
% Mature leaves	–0.336	0.166	4.080	0.066
% Fruit	0.356	0.378	0.886	0.365
Home range	0.298	0.182	2.689	0.127
# Habitats	–0.607	0.187	10.553	0.007
Maximum latitude	–0.746	0.220	11.447	0.005
Human population density	0.177	0.201	0.775	0.396
	r^2	F	P value	
Full model	0.747	4.425	0.011	

This analysis did not include the outlier contrast *P. thomasi* vs. the clade containing *P. femoralis*, *P. rubicunda*, and *P. siamensis*.

TABLE IV. Best Regression Models for Predicting Colobine Monkey Extinction Risk Based on Akaike's Information Criterion

Model #	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	Variable 6	Variable 7	df	AIC	Δ AIC	Log-likelihood ratio χ^2
Model 1	Female mass	% Leaves	% Mature leaves	Home range	# Habitats	Maximum latitude		6	15.813	0.000	23.225
Model 2	Female mass	% Leaves	% Mature leaves	# Habitats	Maximum latitude			5	16.552	0.739	20.487
Model 3	Female mass	% Mature leaves	# Habitats	Maximum latitude				4	16.652	0.838	18.387
Model 4	Female mass	% Mature leaves	Home range	# Habitats	Maximum latitude			5	16.812	0.998	20.227
Model 5	Female mass	% Leaves	% Mature leaves	% Fruit	Home range	# Habitats	Maximum latitude	7	17.237	1.424	23.802
Model 6	Female mass	% Leaves	% Mature leaves	Home range	# Habitats	Maximum latitude	Human population density	7	17.411	1.597	23.628
Model 7	Female mass	% Mature leaves	% Fruit	Home range	# Habitats	Maximum latitude		6	17.633	1.820	21.405

AIC, Akaike's Information Criterion. Models <2 AIC values from the "best" model are considered equivalent models. This analysis did not include the outlier contrast *P. thomasi* vs. the clade containing *P. femoralis*, *P. rubicunda*, and *P. siamensis*.

of mature leaves in the diet, number of habitats, and maximum latitude. The bivariate regressions only yielded one statistically significant predictor of extinction risk—maximum latitude. The discrepancy between the bivariate regressions and the maximum likelihood results is most likely due to confounding interactions between variables. Such problems are remedied by employing multiple regression analyses, which assess the effects of each predictor variable independent of other variables. Consequently, the maximum likelihood approach showed that several variables had important and independent effects on extinction risk.

Extinction Risk and Body Mass

Previous studies on nonhuman primate extinction risk have identified large body size as being significantly related to extinction risk [Isaac & Cowlshaw, 2004; Jernvall & Wright, 1998; Purvis et al., 2000b]. It is no surprise then that body mass was found to be an important predictor of colobine vulnerability in this study as well. The relationship between body mass and extinction risk probably is strong because body mass correlates with many crucial variables including interbirth interval, diet, group size, home range, population density, and maximum intrinsic rate of natural population increase [Clutton-Brock & Harvey, 1977; Harvey & Clutton-Brock, 1985].

Extinction Risk and Folivory

Previous research has shown that diet is an important factor in appraising rarity and extinction risk [Harcourt et al., 2002; Isaac & Cowlshaw,

2004; Purvis et al., 2000b]. Animals that can sustain themselves on leaves are at an advantage over animals that rely on more ephemeral resources such as fruits. For example, many workers have reported that frugivorous primate densities either declined after logging or were lower in logged than in unlogged forests [Bennett & Dahaban, 1995; Johns & Skorupa, 1987; Mathews & Mathews, 2002; Rosenbaum et al., 1998; Skorupa, 1986; White et al., 1995; Wilson & Wilson, 1975]. In a review of data from population censuses of 38 primate species in undisturbed or moderately disturbed forests (i.e., either selectively logged or a small amount of agricultural encroachment), Johns and Skorupa [1987] found that the degree of frugivory was significantly negatively correlated with species ability to survive in logged areas. Furthermore, only 35% of the species and subspecies of the highly folivorous *Alouatta* are threatened with extinction compared to the more frugivorous, large-bodied genera within the same family of which more than 75% include taxa threatened with extinction [Crockett, 1998]. Folivores seem to be better able to cope with the ever-increasing intrusions into their habitats.

In this study, diet also was found to be a significant predictor of extinction vulnerability. In particular, species that consumed more mature leaves exhibited lower extinction risk. Although colobines are considered to be the quintessential folivores of the primate world, they vary in their degree of folivory. For example, the diet of *Pygathrix nemaeus* includes over 80% leaves [Jablonski, 1998], whereas the diet of *Colobus satanas* is composed of less than 35% leaves [McKey et al., 1981]. In addition, there is variation in the quality of leaves depending on their stage of maturity. Young leaves, for example, tend to have more energy and a higher protein-to-fiber ratio [Chapman et al., 2002].

Why would the percent of mature leaves in the diet be related to extinction risk? In situations in which young leaves and other more easily digestible resources are not available, mature leaves can be used as a fallback resource by species that can efficiently digest them in relatively large quantities [Oates et al., 1990]. Although data are limited, morphological studies of colobine digestive anatomy suggest interspecific variability in relative gut size [Chivers, 1994]. This morphological variation may play a role in the efficiency of leaf digestion and, subsequently, food choice. In addition, in a preliminary analysis examining the factors correlated with mature leaf consumption, we found that body mass and latitude are positively correlated with mature leaf consumption in colobine species [Paciulli & Kamilar, 2007]. These results suggest that larger species may be better able to process the more fibrous mature leaves. Also, mature leaves at high latitudes may be of higher quality (all else being

equal) because of a shorter growing season [van Schaik et al., 2005].

The results of this study, in combination with additional research on colobines, have emphasized the importance of considering more detailed data when discussing the biology of folivorous primates. For instance, some socioecological models assumed that within-group feeding competition was low among folivorous primates [Sterck et al., 1997]. However, this assumption has been challenged. Some evidence for competition among colobines is the association between the quality of leaves in a forest and colobine biomass or density [Chapman et al., 2002; Oates et al., 1990]. In addition, there is increasing evidence suggesting that leaves may not be as evenly distributed or abundant as once thought. New data suggest that like frugivores, some folivores prefer patchily distributed and high-quality leaves. These primates experience within-group feeding competition and are food-limited [Koenig, 2002; Snaith & Chapman, 2007]. Thus, the new picture emerging is that variation among primate folivores is not only related to biology and physiology but also to behavioral ecology and extinction risk as well.

Extinction Risk and Number of Habitats

Species living in fewer habitat types exhibited higher IUCN extinction risk designations. Harcourt et al. [2002, 2005] showed that ecological specialization and habitat inflexibility are related to rarity in primates. Species adapted to a narrow ecological range may be more sensitive to habitat perturbations due to natural or anthropogenic causes.

Extinction Risk and Maximum Latitude

Species with geographic ranges at low absolute maximum latitudes exhibited higher IUCN extinction risk designations. This agrees with the study by Harcourt et al. [2002] on primate rarity. Rare primate species are found at lower latitudes and have small geographic ranges. Often, rarity is a precursor to extinction [Cowlshaw & Dunbar, 2000]. Low maximum latitudes somehow may be related to lower selection pressure for ecological flexibility (because these species live in narrowly defined latitudes). Correspondingly, Harcourt [2000] and Cowlshaw and Hacker [1997] found that species at higher latitudes tended to have wider distributions and, therefore, would be expected to face lower extinction risks. One reason for this could be that at higher latitudes individuals are exposed to a broader set of environmental conditions. In such habitats, ecologically flexible individuals would survive better than ecologically inflexible ones [Stevens, 1989].

Analyzing Extinction Risk at “Lower” Taxonomic Scales

One of the goals of this study was to examine the intrinsic and extrinsic factors related to extinction risk at a relatively fine taxonomic scale and to compare the results with previous broad-scale studies examining extinction risk in primates. This study demonstrates that categorizing species in general dietary categories such as frugivore or folivore may obscure details that could be critical for assigning levels of extinction risk. Even within the colobine diet-specialized clade, variation in the degree of folivory appears to play a significant role in predicting the evolutionary persistence of species. These findings emphasize the importance of examining correlates of extinction risk at various levels of analysis [cf. Harcourt et al., 2005]. “Broad-brush” comparisons are important for highlighting common patterns of extinction risk. Once the general “blueprint” of extinction vulnerability at a high taxonomic level has been exposed, examining it at a finer scale appears to be beneficial. Doing so may uncover patterns that are not apparent at higher levels [Harcourt, 2002].

In addition, revealing patterns of extinction risk at a lower taxonomic scale is important as it may help with conservation planning. For example, some conservation managers only know about the issues at their site and have the freedom to employ site-specific methods to alleviate the problems. Others use information from broad analyses to assist in conservation planning, yet the precise characteristics of the species of interest may be confounded by the inclusion of other taxa. Examining a closely related set of species should be more sensitive to the actual biological traits of the taxa and, consequently, the particular factors related to their extinction risk. If so, this information could be vital for conservation biologists who utilize such data to generate and implement conservation strategies that hopefully will improve a species chance of survival.

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APPENDIX A

Species list, predictor variables, and measures of extinction risk are given.

Species	Female body mass (kg)	% Total leaves	% Mature leaves	% Fruit/seed
<i>Colobus angolensis</i>	7.57	0.53	0.16	0.23
<i>Colobus guereza</i>	9.20	0.73	0.09	0.19
<i>Colobus polykomos</i>	8.30	0.54	0.23	0.42
<i>Colobus satanas</i>	7.42	0.34	0.08	0.56
<i>Colobus vellerosus</i>	6.90	–	–	–
<i>Nasalis larvatus</i>	9.82	0.56	0.05	0.36
<i>Ptilocolobus badius</i>	8.21	0.45	0.10	0.35
<i>Ptilocolobus gordonorum</i>	7.05	–	–	–
<i>Ptilocolobus kirkii</i>	5.46	0.65	0.08	0.21
<i>Ptilocolobus pennantii</i>	7.05	0.66	0.10	0.16
<i>Ptilocolobus preussi</i>	7.05	0.89	0.00	0.01
<i>Ptilocolobus rufomitratu</i>	7.21	0.58	0.05	0.24
<i>Presbytis comata</i>	6.71	0.65	0.06	0.14
<i>Presbytis femoralis</i>	6.19	0.29	0.03	0.58
<i>Presbytis hosei</i>	5.63	0.69	0.04	0.30
<i>Presbytis siamensis</i>	6.47	0.36	0.10	0.53
<i>Presbytis potenzi</i>	6.40	0.55	0.18	0.32
<i>Presbytis rubicunda</i>	6.17	0.37	0.01	0.49
<i>Presbytis thomasi</i>	6.69	0.48	0.15	0.36
<i>Procolobus verus</i>	4.20	0.80	0.06	0.14
<i>Pygathrix nema</i>	8.44	0.82	0.07	0.14
<i>Rhinopithecus avunculus</i>	8.50	0.38	0.01	0.62
<i>Rhinopithecus bieti</i>	9.96	0.06 (+0.86 lichen)	0.86 (lichen)	–
<i>Rhinopithecus brelichi</i>	–	0.7100	–	0.1500
<i>Rhinopithecus roxellana</i>	11.60	–	–	–
<i>Semnopithecus johnii</i>	11.20	0.52	0.27	0.25
<i>Semnopithecus vetulus</i>	5.90	0.60	0.40	0.28
<i>Simias concolor</i>	6.80	0.60	–	0.28
<i>Trachypithecus auratus</i>	5.76	0.47	0.01	0.32
<i>Trachypithecus francoisi</i>	7.35	0.53	0.14	0.3140
<i>Trachypithecus geei</i>	9.50	–	–	–

<i>Trachypithecus obscurus</i>	6.26	0.58	0.22	0.35
<i>Trachypithecus phayrei</i>	6.30	0.46	.1300	0.37
<i>Trachypithecus pileatus</i>	9.86	0.53	0.42	0.34

Home range (ha)	# Habitat types	Maximum latitude	Human population density (ind/km ²)	IUCN [2006] code
1,405.5	3	-12	21.00	1.00
33.5	3	14	69.00	1.00
50.5	2	14	33.51	2.00
316.5	2	5	9.01	3.00
28.5	3	10	79.55	3.00
373.0	2	6	31.85	4.00
34.0	1	8	37.72	4.00
-	2	-9	28.62	3.00
32.6	1	-6	251.42	4.00
73.0	2	3	51.49	4.00
-	1	6	64.94	4.00
11.3	1	-2	4.82	5.00
38.0	1	-8	928.97	4.00
22.0	2	3	42.00	2.00
34.0	1	7	12.42	3.00
24.0	1	13	81.24	1.00
23.5	2	-3	56.80	3.00
99.5	1	7	15.86	1.00
14.0	1	6	59.17	2.00
42.0	2	9	65.72	2.00
-	1	19	82.92	4.00
1,000.0	1	21	147.44	5.00
2,500.0	1	28	48.02	4.00
2,387.0	1	24	253.74	4.00
2,600.0	1	29	163.63	3.00
169.5	3	10	327.42	3.00
2.0	3	9	309.73	4.00
10.0	2	-3	56.80	4.00
5.5	1	-9	848.30	4.00
157.0	1	22	197.52	3.00
375.0	4	26	88.27	4.00
33.0	2	13	88.37	1.00
95.8	2	26	103.62	1.00
43.0	1	27	191.80	4.00

APPENDIX B

Data sources used in the study. Book chapters by Kirkpatrick [2007] and Fashing [2007] were used as additional sources of references and data.

Species	References
<i>Colobus angolensis</i>	Maisels et al. [1994], Groves [1973], Kanga [2001], Kanga and Heidi [1999/2000], Bocian [1997], Fimbel et al. [2001], and Fashing et al. [2007]
<i>Colobus guereza</i>	Groves [1973], Onderdonk and Chapman [2000], Suzuki [1979], Dunbar [1987], Grimes [2000], Bocian [1997], Krieger et al. [1998], Schenkel and Schenkel-Hulliger [1967], Oates [1974, 1977, 1994], Struhsaker [1997], Leskes and Acheson [1971], Fashing [2001], Fashing and Cords [2000], Rose [1978], Marler [1969], Wasserman and Chapman [2003], and Plumpré [unpublished data]

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<i>Colobus polykomos</i>	Dasilva [1989, 1994], Whitesides et al. [1988], Korstjens [2001], and Korstjens et al. [2007]
<i>Colobus satanas</i>	Harrison and Hladik [1986], M. Harrison [personal communication] cited in Dates [1994], White [1994], McKey [1978], McKey and Waterman [1982], Fleury and Gautier-Hion [1999], and Brugiere et al. [2002]
<i>Colobus vellerosus</i>	Saj et al. [2004], Olson in Dates [1994], Sicotte and Macintosh [2004], and Saj and Sicotte [2005]
<i>Nasalis larvatus</i>	Boonratana [1994], Yeager [1990], and Bennett and Sebastian [1988]
<i>Ptilocolobus badius</i>	Gatinot [1977], Starin [1991, personal communication], Whitesides et al. [1988], Davies [personal communication] cited in Dates [1994], Davies et al. [1999], Korstjens [2001], Wachter et al. [1997], Korstjens et al. [2007], and Holenweg et al.
<i>Ptilocolobus gordonorum</i>	Struhsaker and Leland [1987] and Struhsaker, [personal communication] cited in Dates [1994]
<i>Ptilocolobus kirkii</i>	Siex [2003] and Mturi [1991, 1993]
<i>Ptilocolobus pennantii</i>	Werre [2000]
<i>Ptilocolobus preussi</i>	Struhsaker [1975] and Usongo and Amubode [2001]
<i>Ptilocolobus rufomitratu</i>	Decker [1994] and Marsh [1979]
<i>Presbytis comata</i>	Ruhiyat [1983] and Rodman [1978]
<i>Presbytis femoralis</i>	Megantara [1989]
<i>Presbytis hosei</i>	Mitchell [1984]
<i>Presbytis siamensis</i>	Davies et al. [1988], Bennett [1983], Curtin [1976, 1980]
<i>Presbytis potenziani</i>	Fuentes [1994] and Watanabe [1981]
<i>Presbytis rubicunda</i>	Davies [1984, 1991], Davies et al. [1988], and Supriatna et al. [1986]
<i>Presbytis thomasi</i>	Gurmaya [1986], Steenbeek et al. [2000]
<i>Procolobus verus</i>	Korstjens [2001], Korstjens and Schippers [2003], Oates [1988], Whitesides et al. [1993], Davies et al. [1999], and Gates and Whitesides [1993]
<i>Pygathrix nemaesi</i>	Lippold [1977] and Jablonski [1998]
<i>Rhinopithecus avunculus</i>	Boonratana and Le [1998] and Jablonski [1998]
<i>Rhinopithecus bieti</i>	Kirkpatrick et al. [1998], Kirkpatrick [1996], and Jablonski [1998]
<i>Rhinopithecus brelichi</i>	Bleisch et al. [1993], Bleisch and Xie [1998], and Jablonski [1998]
<i>Rhinopithecus roxellana</i>	Su et al. [1998] and Ren et al. [1998]
<i>Semnopithecus johnii</i>	Poirier [1970]
<i>Semnopithecus vetulus</i>	Hladik [1977]
<i>Simias concolor</i>	Tenaza and Fuentes [1995] and Watanabe [1981]
<i>Trachypithecus auratus</i>	Kool [1992, 1993]
<i>Trachypithecus francoisi</i>	Zhou et al. [2006]
<i>Trachypithecus geei</i>	Srivastava et al. [2000, 2001] and Mukherjee [1978]
<i>Trachypithecus obscurus</i>	Curtin [1976, 1980]
<i>Trachypithecus phayrei</i>	Suarez [personal communication]
<i>Trachypithecus pileatus</i>	Stanford [1991] and Mukherjee [1978]

Please contact the authors for detailed information regarding the data references.