

# Correlates of extinction risk and hunting pressure in gamebirds (Galliformes)

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## Abstract

The 284 species of Galliformes are a highly threatened group of birds subject to direct exploitation for food, sport and cultural practices. The impact of hunting is often assumed to contribute to the high percentage of species (26.4%) listed as threatened with extinction in the IUCN Red List. We take a macroecological approach to examine the anthropogenic and ecological correlates of extinction risk and hunting pressure using linear and stepwise regression. Independent contrasts are analysed, as well as raw species data, to control for the potential confounding influence of phylogenetic trends. Extinction risk is found to be predicted both by the ecological factors considered (e.g., latitudinal range, body mass, elevational range, habitat use) and secondarily by human factors (e.g., human population density, total calorie intake, composition of diet). Hunting pressure itself is also predicted well for the threatened species by several of the anthropogenic and ecological variables. The study demonstrates that human variables can be used successfully to predict extinction risk, and represent an improvement upon methods which examine ecological variables alone. Furthermore, we show that individual threats can be explored using similar techniques, providing a more detailed insight into the processes leading to extinction. As applied to the Galliformes, both approaches provide evidence supporting the hypothesis that hunting pressure has contributed to the high proportion of threatened species in this group, and thus reinforce the case for urgent measures to reduce the impacts of direct exploitation upon these birds.

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## 1. Introduction

### 1.1. The roots of the extinction crisis

Convincing evidence suggests that current extinction rates have been elevated by the actions of humans to a point many times the normal background level (e.g., Pimm et al., 1995; Mace and Kunin, 1994; Smith et al., 1993). This extinction ‘crisis’ appears to be ongoing

and intensifying (Lawton and May, 1995). Many factors have been identified which help to push a species towards extinction. Recently, attention has been directed at the potential effects of climate change on species’ distributions (Thomas et al., 2004). Similarly, pollutants and chemicals that are released into the environment by industry and agriculture affect a variety of species. For example, dramatic declines in the populations of vultures in the Indian subcontinent (Prakash et al., 2003) have been linked to the widespread use of a veterinary drug, diclofenac (Oaks et al., 2004). However, while climate change and pollution are relatively modern threats, humans have caused extinctions for much longer through what Diamond (1989) described as an ‘Evil

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Quartet' of processes, namely habitat destruction, overkill, the impact of alien species and chains of extinction. A recent assessment of the conservation status of globally threatened birds (GTBs) cited one of these – 'habitat destruction or degradation' – as a factor in 86% of cases (BirdLife International, 2004a). Nonetheless overkill, which was probably the most important factor driving prehistoric megafaunas to their extinction as humans first expanded their global range (Flannery, 2002), remains a very serious threat today. Overexploitation is now considered the second most prevalent anthropogenic threat to birds, affecting nearly 30% of GTBs (BirdLife International, 2004a). Despite the global impact of these factors, their importance relative to one another varies from place to place and between different groups of species.

### 1.2. *The Galliformes*

As a group particularly affected by direct exploitation, the Galliformes (game birds) provide a good illustration of this variation. The order comprises five families, with 284 species currently recognised (del Hoyo et al., 1994). These families are diverse and together occupy almost every terrestrial habitat on earth. The megapodes (Family = Megapodiidae) are found in South-East Asia and Australasia, including many small islands. They, in common with the cracids (Family = Cracidae), are thought to retain many ancestral features (Jones et al., 1995) but are probably best known for their unique breeding biology which usually involves constructing large, incubating mounds in which to lay their eggs. The cracids are found in tropical forests ranging from South America to Mexico (Delacour and Amadon, 1973). The third family, the New World quails (Family = Odontophoridae), also inhabits South American forests, although some species live as far north as southern Canada. They are generally smaller than the cracids. The fourth family, the Guineafowl (Family = Numididae), contains only five species, all of which are found in Africa. The last family (Family = Phasianidae) is the most diverse and includes the francolins, partridges, Old World quails, pheasants, and grouse. Phasianids are found in Africa, Asia, Europe and Northern America (Johnsgard, 1999), including many well-known species such as the Indian peafowl (*Pavo cristatus*), ring-necked pheasant (*Phasianus colchicus*) and the domestic chicken, whose wild ancestor is the red junglefowl (*Gallus gallus*).

The Galliformes are economically and socially important to humans the world over. In the United Kingdom pheasant shooting earns approximately £600 million per year and employs over 25,000 people in the rural economy (Game Conservancy Trust, 2004). Another hunted species is the helmeted guineafowl (*Numida melaegris*), Africa's most important game bird (Little and

Crowe, 2000). The global significance of the domestic chicken is enormous – over 65 million metric tons of chicken meat were produced worldwide in 2003 (FAO-Stat data, 2004). Even the tribal societies of Australasia used yolk from megapode eggs as a valuable source of protein (Dekker et al., 2000).

Thus economists and ecologists are likely to agree on the importance of the Galliformes, albeit from different standpoints. Despite this, Galliformes are one of the most threatened groups of birds. In 2004, 12.4% of all extant bird species were considered to be globally threatened (IUCN, 2004b). The equivalent figure for the Galliformes is much higher, at about 26.4% (BirdLife International, unpublished data). The difference may be explained by overexploitation but there is little hard evidence to confirm this supposition (McGowan, 2002).

### 1.3. *Identifying the threats*

In undertaking this study, our aims were to identify ecological and anthropogenic correlates of (1) extinction risk and (2) hunting pressure in the Galliformes, to understand better the processes which are jeopardising these species and to explore the perception that overexploitation is a key problem for the group as a whole.

Several approaches have been used to identify threatened and potentially threatened species, and the problems that confront them. The International Union for the Conservation of Nature and Natural Resources' (IUCN) Species Survival Commission (SSC) produces the Red List of Threatened Species (hereafter referred to as the Red List) which aims to assess species systematically and assign them to a threat category according to their perceived risk of extinction. The assessments for birds are carried out by BirdLife International according to the Red List Categories and Criteria (IUCN, 2001). BirdLife International also maintains the World Bird Database containing information on threatened and near-threatened species and the threats they face. The Red List is hugely influential, and has often been a useful catalyst for conservation action (Fuller et al., 2003) but, on its own, it tells us little about the factors underlying extinctions. Considerable effort has also been directed at elucidating factors which can predict extinction in species (e.g., Laurance, 1991; Harcourt, 1998; Purvis et al., 2000; Duncan and Lockwood, 2001; Norris and Harper, 2004). These studies have tested hypotheses about biological traits which might make a species more susceptible to human disturbance and extinction (see Simberloff, 1998). Similar hypotheses can be erected about the relationship between the anthropogenic variables associated with an area and the extinction risk faced by the species living there, and between ecological/anthropogenic variables and specific threats such as hunting. While this study follows other authors in modelling extinction risk, it gains

interest by using a combination of ecological traits and human variables to explain risk, and the results indicate which are the most important predictors of risk. Furthermore, it considers a measure of the perceived impact of hunting, which can be studied independent of risk of extinction. To our knowledge neither of these areas has been investigated previously.

We adopted an approach advocated by Purvis et al. (2000), using a variety of statistical techniques to model the relationships between predictor variables and extinction risk, or hunting pressure, including simple linear regression and multivariate stepwise regression, using either raw species data or independent contrasts. Each has its own strengths and weaknesses. Linear regression of species data allows the maximum number of points to be analysed and is thus more likely to produce significant relationships. Stepwise regression constructs models which include more than one significant predictor, controlling for covariance of predictors. Hence it can detect more complex relationships than linear regression alone, although it requires that the value of every predictor is known for each species analysed: therefore sample sizes are often reduced. The use of raw species data in either regression technique is subject to pseudoreplication if the traits under consideration follow a phylogenetic pattern (Harvey and Pagel, 1991), causing groups of closely related species sharing an ancestral trait to be given unwarranted weight in an analysis, leading to a greater likelihood of Type I error. This effect can be reduced if independent contrasts are first calculated from the raw data using a phylogeny of the groups involved (Felsenstein, 1985). Once again, this improvement has a cost in the form of loss of data – each independent contrast produced is usually a composite of data from multiple species. The accompanying reduction in sample size will be large if the phylogeny is incompletely resolved. Furthermore, a new source of potential error is introduced if the relationships between species are uncertain or incomplete.

Our analysis was based on Little and Crowe's (2000) phylogeny (but see Section 2) which draws upon information from a wide variety of traits (including anatomy, behaviour, chromosomal structure, eggs, digestive proteins and DNA). This is thought to be more accurate than relying on a single factor. In addition, it has been argued that, provided phylogenetic trends are present, even an incomplete phylogeny produces more accurate results within CAIC than analysis of raw species data alone (Purvis et al., 1994; Symonds, 2002). Given these drawbacks, a comparison of the results from each type of analysis may be the best way to ensure that real effects are detected. This is particularly true for our dataset that includes human variables whose influence on species may or may not show phylogenetic biases.

Together, a knowledge of the factors underpinning extinctions and the regions of the world where extinc-

tions seem imminent can be a powerful tool for directing effective conservation efforts, and such research may help to identify groups which are not given adequate consideration by current strategies.

## 2. Materials and methods

### 2.1. Data

#### 2.1.1. Extinction risk and hunting pressure

We modelled two separate response variables in Minitab 13.1. The first was IUCN Red List Category (IUCN, 2004b), the perceived risk of extinction at the species level. Species are assigned a threat status which are ranked from least concern (LC) to critically endangered (CR), in increasing order of relative risk. These discrete categories are easily ranked (from LC = 0 through near threatened, NT = 1, vulnerable, VU = 2 and endangered, EN = 3 to CR = 4) and, for the purposes of these analyses (Purvis et al., 2000), were treated as a continuous variable. The numbers of species falling into each of these five categories were respectively 175, 32, 51, 18 and 6. Species which have recently gone extinct (EX) or are thought to be extinct in the wild (EW) were excluded from the analyses. Species which have been evaluated but for which insufficient data are available to assign a threat status (data deficient, DD) were here excluded from the analysis.

The hunting impact score (HIS) was the second response variable analysed. For each threatened and near threatened species (but not Least Concern), BirdLife lists the threats believed by its global network of correspondents to be impacting the species. These threats are classified according to the IUCN Red List Authority Files (IUCN, 2004a). Each threat is given a score based on the timing (past or present), scope (the proportion of the population affected) and severity (how rapidly it is causing, or is likely to cause, a decline in the population) of the threat (BirdLife International, 2004b). When a threat is considered to be current and significant each of these factors is scored from 1 (lowest threat) to 3 (greatest threat), and the sum of them is the Impact Score for that threat. The scores ranged from 3 to 9 since species scoring zero in any one respect were not affected by hunting and automatically scored a total of zero. The HIS therefore indicates the perceived severity of the impact of hunting on a galliform species. Threatened species not considered to be affected by hunting were given an HIS of 0, and the species scoring 3–9 were re-scaled to 1–7. Species whose HIS was listed as 'unknown' were excluded from the analysis.

#### 2.1.2. Human and biological correlates

We initially considered 31 ecological and human variables (see Appendix A) for analysis. Some of these

factors trigger Red Listing, and therefore there is the risk of circularity. This is particularly the case for latitudinal range which is closely related to the area-based Red Listing Criteria, B1 and B2. To avoid this problem, we reclassified any species whose threat status depends on criteria B1 or B2 to a lower threat category which could be assigned using only criteria A and C–E (IUCN, 2001). In practise this re-classification affected only nine species. Five were ‘downlisted’ by one threat category, three by two categories (from vulnerable to least concern) and the remaining species by three categories, changing from endangered to least concern.

Since the use of strongly correlated variables in multivariate analyses can produce unreliable results, Pearson’s test for correlation was performed between each pair of variables, excluding any where the coefficient of correlation was found to be significant and greater than 0.5 (Appendix A). Where we had to choose one from a pair of correlated variables, we choose the variable where the data were more complete and reliable. One exception to this rule of using only one of a pair of correlated variables was made in the case of human population density and mammals (see following descriptions), where, although a strong correlation was found at a global scale (Pearson’s coefficient = 0.628), the correlation was weaker at the regional level. Mean clutch size was also excluded because the data were too patchy and unreliable. Thus we arrived at 11 suitable predictors, six ecological and five human. Non-habitat variables (i.e., 1–4, 7–11) were logarithmically transformed so that they more closely approximated a normal distribution. The Pearson’s correlation coefficients between these variables are shown in Table 1. Each predictor’s importance to this study and the primary sources for our dataset are described below.

1. *Mean body mass* (BMASS): in grams (Dunning, 1993). Where more than one estimate was given, the mean value was calculated, weighted according

to sample size. Male and female data were included. Large body size is predicted to be associated with an increased likelihood both of extinction and of hunting, because larger species are less able to cope with human perturbations (McKinney, 1997) and are more visible and attractive to hunters.

2. *Minimum elevation* (MINELEV): in metres (del Hoyo et al., 1994; Delacour and Amadon, 1973; Johnsgard, 1983, 1988, 1999; Jones et al., 1995). Species limited to upland areas may be more prone to extinction because of restricted distributions and small populations (Gaston, 1994). Alternatively, species living in lowlands may face more habitat destruction than upland species (Manne et al., 1999), increasing the risk of extinction. Low minimum elevation may bring species into contact with humans more frequently, thereby increasing hunting pressure.
3. *Elevational range* (ELEV R): in metres (del Hoyo et al., 1994; Delacour and Amadon, 1973; Johnsgard, 1983, 1988, 1999; Jones et al., 1995). Large elevational range raises the chance that species will have a large, continuous distribution, is more likely to provide refuges from the impacts of humans and thus should correlate with lower risk of extinction and hunting impact.
4. *Latitudinal range* (LATR): in degrees of latitude, estimated from range maps (del Hoyo et al., 1994; Delacour and Amadon, 1973; Johnsgard, 1983, 1988, 1999; Jones et al., 1995). This factor is strongly correlated with global range size. Thus, large latitudinal ranges are predicted to reduce risk of extinction (Gaston, 1994). There is no clear basis for predicting the effect of latitudinal range on hunting pressure.

We designed a simple system for classifying habitat usage. Habitats were grouped into eight broad types (forest, scrub, savannah, wetlands, grasslands, rocky, coastline and desert) which were

Table 1  
Pearson correlation coefficients between the 11 variables used in this study – for a description of each, see Section 2

	BMASS	MINELEV	ELEV R	LATR	HDIV	MAXHCOM	PDENS00	TOTCAL	%MEAT	%FISH
MINELEV	0.095									
ELEV R	0.022	0.010								
LATR	-0.154*	-0.385***	0.415***							
HDIV	-0.035	-0.018	0.291***	0.280***						
MAXHCOM	0.283***	-0.037	-0.149*	-0.241***	-0.116					
PDENS00	-0.084	0.080	-0.078	-0.205***	0.151*	0.057				
TOTCAL	0.096	0.013	0.011	0.058	-0.105	0.060	0.033			
%MEAT	0.143*	0.107	0.078	0.142	-0.161**	-0.076	-0.417***	0.437***		
%FISH	0.026	0.024	-0.043	-0.038	0.006	0.007	0.237***	0.103	0.067	
MAMMALS	0.070	0.096	-0.057	-0.210***	0.085	0.016	0.628***	0.133*	-0.189**	0.386***

All variables except for HDIV and MAXHCOM were logarithmically transformed.  $N = 226$ .

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

given a score according to their complexity. Eight types of habitat were sufficiently distinct from one another to require separate categories but some were considered to be equally complex so the complexity scores range from 1 to 5. Forests, the most complex habitat, scored 5 while deserts, the least complex, scored 1. Individual species were considered present or not present in each habitat. The primary sources for the data are listed under the description of each variable.

5. *Habitat diversity* (HDIV): Total number of habitat types that a species uses, inferred from published descriptions (del Hoyo et al., 1994; BirdLife International, 2004b; Delacour and Amadon, 1973; Johnsgard, 1983, 1988, 1999; Jones et al., 1995). In most cases the more habitats a species is able to use, the less threatened it will be by hunting and extinction because it will be more able to find refuge from the effects of humans. However, relationships were carefully examined as some species depend upon a variety of different habitats, or transitional ecotones between habitats, so are threatened by loss of any of them.
6. *Maximum habitat complexity* (MAXHCOM): The score given to the most complex habitat a species uses. This score, intended to reflect the number of vertical levels into which a habitat could be sensibly divided, was inferred from published descriptions (del Hoyo et al., 1994; BirdLife International, 2004b; Delacour and Amadon, 1973; Johnsgard, 1983, 1988, 1999; Jones et al., 1995). The relationship between habitat complexity and hunting pressure is difficult to predict, and may be non-linear: most hunting occurring in moderately open habitats near human settlements, less in forested or desert habitats. However, forest species may be most severely affected by loss of habitat overall (BirdLife International, 2004a), so extinction risk should be positively correlated with habitat complexity.
 

The following demographic and human variables (7–11) were only available at the country scale. To estimate a value for each gamebird species we calculated the sum of the values for each range country weighted according to the proportion of the species' range occurring in each country. Data on species' ranges were estimated by digitising maps of their global distribution (WPA, unpublished data).
7. *Population density in 2000* (PDENS00): human population per square kilometre within a species' range countries (United Nations Population Division, 2002). The greater the number of people in a given area, the greater their likely effect on other species, therefore extinction risk and hunting are both predicted to increase with human population density.
8. *Total caloric intake* (TOTCAL): number of calories consumed by humans per capita per day within a species' range countries (FAOStat data, 2004). Galliformes are more likely to be hunted if other sources of food are scarce, as is the case in many poor areas of the developing world. Total caloric intake also correlates strongly with several other measures of human well-being and development. One of these is purchasing power parity (PPP), an index used to compare income and standard of living between countries. Thus, low caloric intake should be associated with higher hunting pressure, especially if larger galliform species are available to make hunting viable.
9. *Proportion of meat in diet* (%MEAT): the proportion of the caloric intake of humans per capita per day from meat within the species' range countries (FAOStat data, 2004). If other sources of protein are scarce people may resort to hunting Galliformes or harvesting their eggs so a low proportion of meat in the human diet may be associated with increased hunting and extinction risk.
10. *Proportion of fish in diet* (%FISH): the proportion of the caloric intake of humans per capita per day from freshwater fish and seafood within the species' range countries (FAOStat data, 2004). The proportion of the human diet coming from fish in an area is expected to be negatively correlated with both hunting pressure and extinction risk because Galliformes may provide protein when other sources are unavailable.
11. *Mammals available for hunting* (MAMMALS): the proportion of mammalian species over four kilograms in weight (Walker, 1999) listed as threatened or data deficient (IUCN, 2001). If mammalian quarry larger than four kilograms, roughly the size of the largest galliforms, are available, hunting galliforms will be less attractive. Since the ideal data, on the biomass of large mammals categorised according to body mass, are not available for each country, we developed an alternative measure of mammal availability. We assumed that threatened mammals will be relatively scarce, and thus less available to hunters. Therefore, so our argument runs, the proportion of threatened larger mammal species in an area will correlate positively with the hunting pressure on galliforms. The prediction is that the proportion of threatened mammals (MAMMALS) will correlate positively with hunting impact scores on galliforms. Furthermore, many other threats to mammals (e.g., habitat destruction) also affect the Galliformes, so extinction risk should also show a positive relationship.

### 2.1.3. Species

Using the above variables we compiled two databases. The first contained the 268 species for which data were available (from a total of 284): it could also be split by family for the purposes of analysis. The second was for analyses at the continental level (regions were defined following the Major Areas from the [United Nations Population Division, 2002](#)). This separation was necessary because only species which are endemic or near-endemic (defined as having 85% or more of their global range within the region) could be included in continental analyses due to the need to weight human variables according to the distribution of the species' range.

Where analyses required a phylogeny we used that of [Little and Crowe \(2000\)](#), modified to include several genera of Phasianidae which were not explicitly placed. Their positions were based on [Johnsgard \(1988, 1999\)](#). See [Appendix B](#) for the full phylogeny used.

## 2.2. Correlates of extinction risk

Regression analyses were used to test hypotheses about the relationship between Red List status ([IUCN, 2004b](#)) and the predictor variables. Raw species data and independent contrasts, generated using comparative analysis by independent contrasts, CAIC 2.6.9 ([Purvis and Rambaut, 1995](#)), were examined separately because it was not clear whether the impact of human variables on extinction risk would be related to phylogeny. In an attempt to isolate effects due to phylogeny we include only contrasts generated at branching points at or above the genus level. Not only does this produce stronger patterns in many cases (e.g., [Purvis and Harvey, 1995](#)), but also the amount of useful sub-generic phylogenetic information is very limited.

Following an approach taken by several authors (e.g., [Laurance, 1991](#); [Harcourt, 1998](#); [Purvis et al., 2000](#)) we first performed linear regressions to investigate the significance of each predictor separately. This was done for the global dataset, comprising the 225 species with information available for all predictors, then separately for two families (Cracidae and Phasianidae) and three continental regions (Africa, Asia and Latin America, and the Caribbean). These subsets were included to determine whether patterns were dependent upon the scale of investigation chosen. The sample sizes of subsets for other families and regions were insufficient to permit analysis. We then repeated the analysis using independent contrasts.

Next we performed stepwise regressions to produce minimum adequate models (MAM) predicting risk of extinction ([Zar, 1999](#)). This technique sequentially adds significant ( $p \leq 0.15$ ) predictor variables to a

model, controlling at each step for variables already included. It also removes any predictors in the model which, with the addition of new predictors, fall below the chosen level of significance (in Section 3, 'significant' effects are reported at the familiar  $p < 0.05$  level). As a precaution against 'overfitting', if the number of predictors included in a model was close to, or higher than, the sample size divided by ten we discriminated between alternatives based upon their  $R^2(\text{pred})$  scores (a measure of the predictive power of the model). Raw species data for the global, family and continental region datasets were analysed separately. The reduction in sample size associated with independent contrasts meant that, along with the global dataset, only the Asian and Phasianidae subsets could be modelled separately.

## 2.3. Correlates of hunting pressure

An identical method was used to investigate the relationship between predictor variables and HIS, looking first at individual predictors and then producing MAMs by stepwise regression. HIS are only available for species listed as threatened (CR, EN or VU) and near-threatened so sample sizes were smaller than in the previous analysis. Raw species data were analysed at the global scale but only two family subsets (Cracidae and Phasianidae), and two continental regions (Asia and Latin America) were large enough for analysis. Independent contrasts were also analysed at the global level but, due to the reduction in sample size, the only subsets modelled were for the Phasianidae and Asia.

## 3. Results

### 3.1. Correlates of extinction risk

The results of linear regression of extinction risk against each of the 11 predictor variables are shown in [Table 2](#). In the global dataset linear regression slopes were significantly different from zero for all of ecological predictors considered. By contrast, none of the human predictors was found to be significant. The strongest relationship was found for latitudinal range ( $t = -8.85$ ,  $p < 0.001$ ), followed by elevational range ( $t = -7.05$ ,  $p < 0.001$ ), habitat diversity ( $t = -4.19$ ,  $p < 0.001$ ) and mean body mass ( $t = 3.96$ ,  $p = 0.001$ ). The direction of all significant relationships was as predicted.

In the family subsets ecological variables were again the only significant predictors, with variation between the Cracidae and the Phasianidae as to which was most important (body mass and latitudinal range,

Table 2

Results of linear regression of Red List category against 11 predictors using the raw species data for the global dataset and family and regional subsets

Predictor	All ( $n = 225$ )	Cracidae ( $n = 39$ )	Phasianidae ( $n = 144$ )	Africa ( $n = 28$ )	Asia ( $n = 99$ )	Latin America and the Caribbean ( $n = 65$ )
BMASS	3.96***	2.82**	2.45*	1.60	1.75	3.43***
MINLEV	2.02*	0.60	1.88	1.46	0.55	0.45
ELEV	-7.05***	-2.30*	-6.61***	-2.68*	-4.94***	-2.97**
LATR	-8.85***	-2.54*	-8.99***	-6.61***	-2.68**	-2.22*
HDI	-4.19***	0.92	-5.42***	-3.47**	-4.24***	-0.42
MAXHCOM	2.79**	–	2.96**	2.19*	2.07*	0.82
PDENS00	1.79	-0.06	1.89	-1.51	0.74	-0.87
TOTCAL	0.59	0.74	0.59	-0.50	1.25	0.63
%MEAT	-0.70	-0.91	0.23	0.07	0.31	-0.78
%FISH	0.77	-0.63	1.26	-0.01	1.07	-0.40
MAMMALS	1.50	0.93	0.97	-0.08	1.32	2.51*

Values shown are  $t$  statistics. – indicates that there was insufficient variation within a variable for it to be included in this subset of the data.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

respectively). Similar patterns were seen in the three continental regions, although one anthropogenic variable – mammals – is significant in Latin America ( $t = 2.51$ ,  $p = 0.014$ ).

Fewer significant relationships were found when linear regressions were performed using independent contrasts, but the remaining predictors were generally the most significant predictors in the models produced from raw species data (Table 3). An exception was seen in Asia, where latitudinal and elevational range were no longer significant, leaving only the two habitat variables as significant.

Stepwise analyses of the raw data produced models which broadly follow the same patterns as linear regression, usually with fewer significant predictors in each analysis (Table 4). The MAM for the global dataset included three highly significant ( $p < 0.001$ ) variables: lat-

itudinal range ( $t = -6.27$ ), elevational range ( $t = -4.91$ ) and body mass ( $t = -3.97$ ), explaining 36.1% of the variance in the data.

Details of family and regional models varied, although latitudinal range was significant or near significant in every model. Human variables appeared in few of the global, family or regional models, the notable exception being in Latin American where mammals ( $t = 3.34$ ,  $p \leq 0.001$ ), percentage of meat ( $t = -2.42$ ,  $p = 0.019$ ) and percentage of fish ( $t = -2.54$ ,  $p = 0.014$ ) in the human diet were all significant. All relationships were as hypothesised except for human population density in Africa ( $t = -1.98$ ,  $p = 0.059$ ). This may be due to the continent's relatively low proportion of threatened galliform species, which gives individual threatened species a disproportionately strong influence on the direction of relationships. For example, threatened species

Table 3

Results of linear regression of Red List status against 11 predictors using independent contrasts

Predictor	All ( $n = 28$ )	Asia ( $n = 17$ )	Phasianidae ( $n = 22$ )
BMASS	2.37*	1.16	1.62
MINLEV	1.57	0.66	1.33
ELEV	-3.87***	-1.50	-2.89**
LATR	-3.41**	-0.86	-3.00**
HDI	-2.69*	-3.57**	-2.55*
MAXHCOM	2.08*	2.94**	2.11*
PDENS00	-0.33	0.21	-0.39
TOTCAL	1.53	1.32	-1.70
%MEAT	-1.70	-0.64	-1.86
%FISH	0.77	0.93	0.87
MAMMALS	-1.89	0.94	-1.89

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Only supra-generic contrasts are included in this analysis. Values shown are  $t$  statistics.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

Table 4  
Results of multivariate regression of Red List status against 11 predictors using raw species data at global, family and regional levels

Predictor	All ( <i>n</i> = 225), <i>R</i> <sup>2</sup> (adj) = 36.1, <i>R</i> <sup>2</sup> (pred) = 34.3	Cracidae ( <i>n</i> = 39), <i>R</i> <sup>2</sup> (adj) = 30.5, <i>R</i> <sup>2</sup> (pred) = 23.4	Phasianidae ( <i>n</i> = 144), <i>R</i> <sup>2</sup> (adj) = 48.5, <i>R</i> <sup>2</sup> (pred) = 45.7	Africa ( <i>n</i> = 28), <i>R</i> <sup>2</sup> (adj) = 65.2, <i>R</i> <sup>2</sup> (pred) = 54.8	Asia ( <i>n</i> = 99), <i>R</i> <sup>2</sup> (adj) = 33.2, <i>R</i> <sup>2</sup> (pred) = 29.6	Latin America and the Caribbean ( <i>n</i> = 65), <i>R</i> <sup>2</sup> (adj) = 44.1, <i>R</i> <sup>2</sup> (pred) = 27.8
BM <sub>ASS</sub>	3.97***	3.25**	3.09**		3.08**	4.58***
MIN <sub>ELEV</sub>			−1.94 ( <i>p</i> = 0.054)			
ELEV <sub>R</sub>	−4.91***		−4.08***		−4.28***	
LAT <sub>R</sub>	−6.27***	−3.01**	−5.59***	−6.80***	−1.94 ( <i>p</i> = 0.055)	−2.82**
HD <sub>IV</sub>			−2.91**		−2.65**	
MAX <sub>HCOM</sub>		–				
PD <sub>ENS00</sub>				−1.98 ( <i>p</i> = 0.059)		
TOT <sub>CAL</sub>	1.48 ( <i>p</i> = 0.139)					1.71 ( <i>p</i> = 0.093)
% <sub>MEAT</sub>						−2.42*
% <sub>FISH</sub>						−2.54*
M <sub>AMMALS</sub>						3.34***

Values shown are *t* statistics. – indicates that there was insufficient variation within a variable for it to be included in this subset of the data.

Actual *p* values are included if they are close to significance.

\* *p* ≤ 0.05.

\*\* *p* ≤ 0.01.

\*\*\* *p* ≤ 0.001.

such as the Djibouti francolin (*Francolinus ochropectus*) and Swierstrai’s francolin (*Francolinus swierstrai*), living in areas with relatively low population densities, may not be representative of other African galliforms. The amount of variation explained by the models was 30.5% for the Cracidae and 48.5% for the Phasianidae, and ranged from 33.2% in Asia to 65.2% in Africa.

Throughout the linear and stepwise regressions using raw data, latitudinal and elevational range proved to be good predictors of extinction risk. To explore their ef-

fects on the models we repeated the stepwise analyses above without these two factors. If both were excluded the importance of other predictors generally increased, and new predictors often entered the models, particularly human variables (Table 5). A good example is seen in the Cracidae. When latitudinal and elevational ranges were allowed to enter the model, the percentage of meat in the human diet did not. However, when these ecological factors were excluded the availability of meat became a significant predictor of extinction risk (*t* = −2.43, *p* = 0.020).

Table 5  
Results of multivariate regression of Red List status against nine predictors using raw species data at global, family and regional levels – latitudinal and elevational ranges are excluded

Predictor	All ( <i>n</i> = 232), <i>R</i> <sup>2</sup> (adj) = 18.4, <i>R</i> <sup>2</sup> (pred) = 16.5	Cracidae ( <i>n</i> = 41), <i>R</i> <sup>2</sup> (adj) = 24.3, <i>R</i> <sup>2</sup> (pred) = 12.9	Phasianidae ( <i>n</i> = 148), <i>R</i> <sup>2</sup> (adj) = 27.6, <i>R</i> <sup>2</sup> (pred) = 24.9	Africa ( <i>n</i> = 31), <i>R</i> <sup>2</sup> (adj) = 44.9, <i>R</i> <sup>2</sup> (pred) = 35.6	Asia ( <i>n</i> = 99), <i>R</i> <sup>2</sup> (adj) = 21.5, <i>R</i> <sup>2</sup> (pred) = 17.8	Latin America and the Caribbean ( <i>n</i> = 65), <i>R</i> <sup>2</sup> (adj) = 38.4, <i>R</i> <sup>2</sup> (pred) = 20.8
BM <sub>ASS</sub>	4.38***	3.43***	3.02**		2.29*	4.07***
MIN <sub>ELEV</sub>	1.71 ( <i>p</i> = 0.088)					
ELEV <sub>R</sub>						
LAT <sub>R</sub>						
HD <sub>IV</sub>	−5.20***		−6.37***	−3.69***	−4.66***	
MAX <sub>HCOM</sub>		–	2.34*	2.62*	1.66 ( <i>p</i> = 0.101)	
PD <sub>ENS00</sub>	3.66***		1.88 ( <i>p</i> = 0.062)	−2.19*	1.72 ( <i>p</i> = 0.089)	
TOT <sub>CAL</sub>		1.87 ( <i>p</i> = 0.070)				1.72 ( <i>p</i> = 0.90)
% <sub>MEAT</sub>		−2.43*				−3.09**
% <sub>FISH</sub>						−2.32*
M <sub>AMMALS</sub>						3.31**

Values shown are *t* statistics. – indicates that there was insufficient variation within a variable for it to be included in this subset of the data.

Actual *p* values are included if they are close to significance.

\* *p* ≤ 0.05.

\*\* *p* ≤ 0.01.

\*\*\* *p* ≤ 0.001.

Table 6  
Results of multivariate regression of Red List status against 11 predictors using independent contrasts

Predictor	All ( $n = 28$ ), $R^2(\text{adj}) = 53.7$ , $R^2(\text{pred}) = 38.5$	Asia ( $n = 17$ ), $R^2(\text{adj}) = 55.2$ , $R^2(\text{pred}) = 38.6$	Phasianidae ( $n = 22$ ), $R^2(\text{adj}) = 54.8$ , $R^2(\text{pred}) = 34.1$
BMASS	1.50 ( $p = 0.147$ )		
MINLEV			1.61 ( $p = 0.125$ )
ELEV	-2.19*		
LATR		-2.31*	
HDI	-3.38**	-4.48***	-4.49***
MAXHCOM			
PDENS00			
TOTCAL			
%MEAT	-1.71 ( $p = 0.101$ )		-3.19**
%FISH			
MAMMALS			

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Only supra-generic contrasts are included in this analysis. Values shown are  $t$  statistics.

Actual  $p$  values are included if they are close to significance.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

The results from analysis of independent contrasts differed from models using the raw data (Table 6). The poorly resolved phylogeny for several families restricted the modelling of subsets to the Phasianidae and Asia. Each model contained two significant predictors – habitat diversity and one other. Despite having occurred in every model when raw data were used, latitudinal range ( $t = -2.31$ ,  $p = 0.037$ ) was significant only for the Asian subset using independent contrasts. Another interesting result was that the amount of meat in the human diet was negatively correlated with extinction risk among Phasianidae ( $t = -3.19$ ,  $p = 0.005$ ). This factor, acting in the predicted direction, was absent when raw data were examined.

### 3.2. Correlates of hunting pressure

When hunting impact scores, available only for threatened and near-threatened species, were analysed, the trends that emerged from linear regressions (Table 7) were different to those produced in the analyses of extinction risk. There were fewer significant relationships between the predictors and HIS, partly due to reduced sample sizes. Furthermore, significant relationships were found for human variables more often than for ecological traits, a contrast with the extinction risk analyses. From the global dataset body mass ( $t = 2.39$ ,  $p = 0.020$ ) and %fish ( $t = -2.37$ ,  $p = 0.021$ ) were the only significant predictors. The Phasianidae

Table 7  
Results of linear regression of HIS against 11 predictors using raw species data

Predictor	All ( $n = 70$ )	Cracidae ( $n = 15$ )	Phasianidae ( $n = 45$ )	Asia ( $n = 40$ )	Latin America and the Caribbean ( $n = 20$ )
BMASS	2.39*	0.45	1.32	1.23	1.31
MINLEV	-0.41	-2.32*	0.68	0.49	-2.16*
ELEV	-0.00	-1.41	0.57	1.23	-1.46
LATR	-0.57	1.47	-1.67	-0.85	1.41
HDI	0.68	-0.08	0.91	1.45	-0.06
MAXHCOM	1.17	-	0.71	0.08	-
PDENS00	-0.75	-0.30	0.76	2.00	-0.28
TOTCAL	-1.27	1.75	-2.24*	-1.86	2.22*
%MEAT	-0.16	0.66	-0.33	-0.70	0.71
%FISH	-2.37*	-0.75	-0.40	-0.36	-2.15*
MAMMALS	-1.45	0.53	-0.31	0.04	0.21

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Values shown are  $t$  statistics. – indicates that there was insufficient variation within a variable for it to be included in this subset of the data.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

Table 8  
Results of linear regression of HIS against 11 predictors using independent contrasts at the global and regional level

Predictor	All ( <i>n</i> = 19)	Asia ( <i>n</i> = 10)	Phasianidae ( <i>n</i> = 13)
BMASS	−0.25	−1.08	−0.06
MINELEV	−0.36	−1.90	−0.05
ELEVR	1.12	1.72	0.56
LATR	−0.16	0.46	−0.49
HDIV	2.44*	3.24*	1.96
MAXHCOM	0.70	−0.81	0.65
PDENS00	−0.73	1.36	−0.60
TOTCAL	−1.07	−0.87	−1.16
%MEAT	−1.62	−1.79	−1.70
%FISH	−1.17	−1.32	−1.13
MAMMALS	−0.97	1.26	−0.67

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Only supra-generic contrasts are included in this analysis. Values shown are *t* statistics.

- \*  $p \leq 0.05$ .
- \*\*  $p \leq 0.01$ .
- \*\*\*  $p \leq 0.001$ .

showed a significant relationship only with total calories ( $t = -2.24, p = 0.030$ ), and the Cracidae with minimum elevation ( $t = -2.32, p = 0.037$ ). At the regional level the results were different again. No factors were significant in Asia, although population density ( $t = 2.00, p = 0.053$ ) and total calories ( $t = -1.86, p = 0.071$ ) were close to significance. In Latin America three variables were significant: total calories ( $t = 2.22, p = 0.039$ ), minimum elevation ( $t = -2.16, p = 0.045$ ) and % fish ( $t = -2.15, p = 0.046$ ). Linear regressions using independent contrasts found very few significant relationships – only habitat diversity predicted hunting pressure in the global and Asian datasets, and there

were no significant relationships in the Phasianidae (Table 8).

Stepwise analysis was limited to the global dataset and subsets for two families (Cracidae and Phasianidae) and two regions (Asia and Latin America) by sample sizes. Contrary to the findings for extinction risk, the number of significant relationships revealed by stepwise regression was generally greater than for linear regression of individual predictors. In keeping with the results of linear regression, human predictors are significant in the MAMs more often than ecological traits, and the details vary between regions and families (Table 9). The global MAM included two significant factors, body

Table 9  
Results of multivariate regression of HIS against 11 predictors using raw species data at the global, family and regional levels

Predictor	All ( <i>n</i> = 70), $R^2(\text{adj}) = 12.4$ , $R^2(\text{pred}) = 4.8$	Cracidae ( <i>n</i> = 15), $R^2(\text{adj}) = 23.9$ , $R^2(\text{pred}) = 6.5$	Phasianidae ( <i>n</i> = 45), $R^2(\text{adj}) = 12.6$ , $R^2(\text{pred}) = 1.4$	Asia ( <i>n</i> = 40), $R^2(\text{adj}) = 11.8$ , $R^2(\text{pred}) = 0$	Latin America and Caribbean ( <i>n</i> = 20), $R^2(\text{adj}) = 23.5$ , $R^2(\text{pred}) = 1.19$
BMASS	2.19*		1.75 ( $p = 0.087$ )		
MINELEV		−2.32*			
ELEVR				1.88 ( $p = 0.068$ )	
LATR					1.58 ( $p = 0.133$ )
HDIV					
MAXHCOM		–			
PDENS00					
TOTCAL	−1.50 ( $p = 0.140$ )		−2.53**	−2.35*	2.32*
%MEAT					
%FISH	−2.13*				
MAMMALS					

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Values shown are *t* statistics. – indicates that there was insufficient variation within a variable for it to be included in this subset of the data. Actual *p* values are included if they are close to significance.

- \*  $p \leq 0.05$ .
- \*\*  $p \leq 0.01$ .
- \*\*\*  $p \leq 0.001$ .

Table 10  
Results of multivariate regression of HIS against 11 predictors using independent contrasts at the global and regional levels

Predictor	All ( $n = 19$ ), $R^2(\text{adj}) = 53.6$ , $R^2(\text{pred}) = 34.1$	Asia ( $n = 10$ ), $R^2(\text{adj}) = 51.3$ , $R^2(\text{pred}) = 11.6$	Phasianidae ( $n = 13$ ), $R^2(\text{adj}) = 58.2$ , $R^2(\text{pred}) = 31.7$
BMASS			
MINELEV			
ELEV R			
LATR			
HDI V	4.51***	3.24*	3.95**
MAXHCOM			
PDENS00			
TOTCAL	-3.57**		-3.36**
%MEAT			
%FISH			
MAMMALS			

Sample sizes are too small to permit analysis of subsets of the data for regions and families not included in this table. Only supra-generic contrasts are included in this analysis. Values shown are  $t$  statistics.

- \*  $p \leq 0.05$ .  
 \*\*  $p \leq 0.01$ .  
 \*\*\*  $p \leq 0.001$ .

mass ( $t = 2.19$ ,  $p = 0.032$ ) and %fish ( $t = -2.13$ ,  $p = 0.037$ ), which were the only variables to show a significant relationship in linear regressions using this dataset. This model explained 12.4% of the variance in the data. The MAMs for Asia and Latin America, explaining 11.8% and 23.5% of variation, respectively, include total calories as their only significant predictor but in Latin America, the direction of relationship was contrary to our prediction. It is noteworthy that total calories was not revealed as a significant predictor in Asia by simple linear regression. Turning to the family analyses, the phasianid species experienced more severe hunting impact where total calorie intake was lower, and cracids where they dwelt at lower minimum elevations.

When independent contrasts were analysed (Table 10) the composition of the models changed. Once again, poor phylogenetic resolution of several families restricted analysis to the Phasianidae and Asia. In each model habitat diversity was positively correlated with hunting pressure: global ( $t = 4.51$ ,  $p \leq 0.001$ ), Asia ( $t = 3.24$ ,  $p = 0.012$ ) and Phasianidae ( $t = 3.95$ ,  $p = 0.003$ ). In the global and Phasianidae models hunting pressure decreased as the total human calorie intake increased. The variance explained by each model was over 50%, a dramatic increase in every case over the models derived from raw data.

## 4. Discussion

### 4.1. Correlates of extinction risk

As has been found in studies of other taxa (Owens and Bennett, 2000; Gage et al., 2004), the extinction risk of galliforms is positively correlated with body

size and negatively correlated with latitudinal range. Human variables are very poorly represented in the linear and stepwise models of extinction risk produced using raw data, appearing only in the Latin America MAM. This is particularly surprising given the enormous body of evidence implicating human actions in the extinction process (Harcourt and Parks, 2003), and the high proportion of Galliformes thought to be threatened by overexploitation. A possible explanation might be that the crudity of the data used for human predictors, caused by the need to derive values for species whose ranges occupy parts of several countries from country-scale data, renders these predictors relatively insensitive. However, the observation that these same human predictors model HIS fairly well, producing models with several significant relationships, largely supporting our a priori hypotheses (see Section 4.2), and explaining a substantial percentage of the variance in the datasets studied, suggests that this is not the case. Furthermore, when latitudinal and elevational range, two of the most powerful ecological predictors are excluded the significance of human variables increases and they are included in MAMs more often. This result may be attributed to two separate effects working together. Firstly, the significance of human predictors appears to depend in many cases on interactions between several variables. This is to be expected, given the diversity of motivations causing humans to hunt and shaping their choices of prey, and explains the lack of significant relationships in linear regressions against human predictors which cannot reflect such complexity. The second effect becomes apparent when latitudinal and elevational range are excluded from multivariate models. It seems likely that latitudinal and elevational

range explain such a large proportion of the variance alone that, when included in a model, they drastically reduce the amount of variance available to be explained by other predictors, and thus reduce the significance of the relationships with other predictors. When they are excluded, this statistical ‘smothering’ is removed and the effects of human predictors become more apparent. The subtlety of effects revealed by these manipulations of our models suggest that our human variables are sensitive enough to reflect human impact in the range of the species concerned.

Variation in the composition of models constructed for different families and regions points, as might be expected, to possible heterogeneities in the responses of the several families to threats and in the processes which threaten Galliformes. For example, a striking contrast is observed between the raw data models for Asia and Latin America. The prominence of human variables in South America might be explained in several ways. Firstly, it could be that hunting contributes to extinction risk to a greater degree here than in Asia. Peres (2000) has documented massive numbers of cracid species being removed from the Amazon by hunters, and direct exploitation is regarded as one of the principal threats to this family (Brooks and Strahl, 2000). However, the Asian Galliformes are also thought to be seriously threatened by hunting, and the presence of body mass in the model for Asia lends the hypothesis some support. The lack of a clear relationship with human variables might be explained if threats vary over a much finer spatial scale in this region.

Unfortunately, our current understanding of the phylogenetic relationships within most galliform families is insufficient to allow us to compare different families or regions using independent contrasts. Only the Phasianidae, whose ancestry has received more attention than the other families, and Asia (where the majority of species are from this family) can be analysed in this way. Such imbalances in our understanding will also tend to bias the results of analyses of independent contrasts, giving more weight to taxa whose phylogenies are more complete. Thus, it is likely that our global model does not adequately reflect the situation for the cracids, megapodes, guinea-fowl and New World quails. Within the Phasianidae, however, it seems that taxa that are able to utilise a greater variety of habitats have a lower risk of extinction; similarly, taxa inhabiting areas where the human diet contains a high proportion of meat (most of which is likely supplied from domesticated animals) are less threatened. It is reassuring that the two most important predictors seem to reflect the principle threats of habitat degradation and direct exploitation.

#### 4.2. Correlates of hunting pressure

Throughout the analyses of HIS human predictors showed a significant relationship more often than ecological variables, in contrast to the findings for extinction risk. Smaller samples doubtless contributed to there being fewer significant relationships. The lack of overlap between predictors of extinction risk and hunting pressure for the basic analyses may be partly due to the ‘smothering’ of human factors in models of extinction risk (see Section 4.1).

The variance explained by models derived from raw species data is generally lower for more diverse groupings (Table 9). For example, the Latin American MAM have  $R^2(\text{adj})$  values of approximately 23.9% and 23.5%, respectively. Much lower  $R^2(\text{adj})$  values are found in Asia (11.8%), which includes a very diverse assemblage of Galliformes, and the global analysis (12.4%), where all species are considered together. The higher  $R^2$  values in the less taxonomically diverse analyses are consistent with the existence of phylogenetic trends, but does not prove the point since the pattern could be also explained by purely spatial variation in human factors.

Variation between models (Table 9) suggests that factors influencing hunting impact differ from region to region. This may be partly due to the nature of hunting. Factors motivating people to hunt Galliformes might vary at a very fine scale (both temporally and spatially), and be further complicated by opportunistic hunting. It is still unclear whether phylogenetic trends are seen in the impact of anthropogenic variables associated with hunting, so the use of independent contrasts cannot be automatically presumed to give the ‘best’ model.

Two variables were significant or near significant in more than one of the MAMs produced (Table 9): body mass and total calories consumed. In each case the relationship was as predicted a priori. The presence of total calories, a good proxy for many different measures of development, emphasises once again how important the improvement of human opportunities and welfare is to effective conservation. The importance of the proportion of fish in the human diet shown in the global model suggests that the use of fish as an alternative protein source might reduce hunting pressure on threatened Galliformes, a suggestion supported by the finding that, in West Africa, hunting of bushmeat increases in years of poor fish supply (Bra-shares et al., 2004). An unexpected relationship was found in Latin America for total calories ( $t = 2.32$ ,  $p = 0.033$ ). A possible explanation is that in South America, where all the species under consideration are forest dwellers, increasing total calories is correlated with the opening up of the forest, and thus increased opportunity to hunt Galliformes. This scenario seems

plausible since many projects which bring wealth to forested areas (raising total calories), such as mining, forestry or agriculture, require the construction of access roads. In other continents, a proportion of the galliforms are open-country species on which subsistence hunting impact may decline as human prosperity increases.

The models derived from independent contrasts again show that hunting pressure decreases as the total number of calories consumed increases. Surprisingly, they also show that higher level taxa (above the level of genera) which use a wider range of habitat types tend to suffer a greater level of hunting. This might be explained if the more hunted groups make use of edges and transitional habitats, increasing both the frequency of encounters with humans and the number of habitats in which they are observed.

HIS are not a perfectly objective measure of hunting impact. The processes used to determine the scope, severity and timing of exploitation rely heavily on inference and anecdotal evidence. However, the relationships found here with factors likely to influence hunting lend these HIS scores credibility. With further refinement it may be possible to develop a reliable method for predicting the intensity of hunting that poorly known species in a region are likely to face. However, any such approaches must take account of geographic scale (Gage et al., 2004, this study), and should attempt to determine whether or not phylogenetic biases can occur in anthropogenic variables.

#### 4.3. Conclusions

The IUCN Red Listing process has produced many successes, and is a valuable tool for conservationists. However, it does not, and is not intended to, tell us anything about the factors which threaten species. Thus, there is a pressing need to continue refining and improving the mechanisms that exist for predicting where, and in which groups, extinctions are most likely to occur. Previous studies have demonstrated that ecological variables can be used to predict the risk of extinction in various groups of animals (e.g., Laurance, 1991; Harcourt, 1998; Purvis et al., 2000; Norris and Harper, 2004). Despite their successes, this approach clearly only considers one aspect of a complex problem. There is already a huge amount of evidence linking the actions of humans with threats to species' survival. As Cardillo et al. (2004) have recently shown for the world's carnivores, our work demonstrates that human variables can be successfully included in statistical modelling approaches predicting extinction risk, better reflecting the complexity of

threat involved and thereby increasing the predictive power of such models. We have also shown that individual threats to species (in this case hunting pressure) can be modelled in a similar way, bringing a further degree of sophistication.

There are several issues which should be taken into account when using human data to predict extinction risk or specific threats to species. Obviously there are some facets of human nature which do not lend themselves well to this sort of modelling approach. For example, cultural traditions, taboos, religion and the like affect the attitudes of humans towards other species, and thus change the balance of threats that species face between different areas. These important factors must not be ignored, but this should not prevent the use of other, more tractable variables in predicting threat. We have shown that even relatively crude data can produce useful, meaningful results. However, this study has also illustrated that interactions between the variables in models are important. It seems likely, at least for human factors, such interactions will be common, reflecting the complexity of human activities.

The Galliformes, a very threatened group of birds, urgently need effective conservation actions to ensure their survival. However, the reasons which have caused, and are still causing, them to be so threatened remain unclear. The established belief that hunting and other forms of direct exploitation contribute to the high proportion of threatened Galliformes is supported by little hard evidence. Many studies have looked at the number or combined weight of individuals killed in an area without exploring the effects of such losses on population dynamics. Our findings suggest that hunting does help to 'tip the balance' of threat against the Galliformes, but future work should aim, where possible, to quantify the effects of exploitation on population numbers and stability.

We hope that studies such as this, by increasing our understanding of the different factors driving extinctions, the interactions between them, and the spatial scales over which they operate, will help to direct and inform future conservation efforts dedicated to saving these species.

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**Appendix A. Predictor variable correlation matrix**

	LGRRange	LBMass	LClutch	LMinElev	LMaxElev	LElevR	MinLat	MaxLat	LLatR	LPPP	LTotCal
LBMass	-0.075										
LClutch	0.230	-0.195									
LMinElev	-0.303	0.095	0.030								
LMaxElev	0.214	0.069	0.282	<b>0.536</b>							
LElevR	0.448	0.022	0.304	0.010	<b>0.773</b>						
MinLat	-0.083	0.115	0.230	0.301	0.261	0.161					
MaxLat	0.390	-0.018	0.386	0.075	0.350	0.398	<b>0.775</b>				
LLatR	<b>0.865</b>	-0.154	0.222	-0.385	0.128	0.415	-0.238	0.306			
LPPP	0.193	0.039	0.185	-0.095	-0.016	0.109	0.217	0.325	0.216		
LTotCal	0.088	0.096	0.136	0.013	-0.017	0.011	0.322	0.331	0.058	<b>0.687</b>	
LMeat	0.219	0.148	0.142	0.098	0.110	0.072	0.223	0.275	0.138	<b>0.687</b>	<b>0.601</b>
LFWFish	0.059	0.069	0.151	0.122	0.088	0.000	0.295	0.313	-0.018	-0.161	0.172
LSeafood	-0.015	0.041	0.136	-0.020	-0.070	-0.040	0.204	0.188	-0.013	0.294	0.389
LTotFish	-0.005	0.050	0.158	0.026	-0.028	-0.038	0.244	0.229	-0.021	0.193	0.353
L%Meat	0.225	0.143	0.128	0.107	0.127	0.078	0.173	0.230	0.142	<b>0.609</b>	0.437
L%Fish	-0.029	0.026	0.130	0.024	-0.025	-0.043	0.172	0.154	-0.038	0.018	0.103
L%AnimPr	0.260	0.096	0.134	0.060	0.112	0.118	0.281	0.375	0.183	<b>0.766</b>	0.507
L%Eggs	0.134	0.114	0.081	0.115	0.131	0.103	0.413	0.434	0.080	<b>0.689</b>	<b>0.691</b>
L%Poultry	0.166	0.115	-0.106	-0.045	-0.047	0.030	0.035	0.079	0.153	<b>0.786</b>	<b>0.508</b>
LMammals	-0.170	0.070	0.015	0.096	0.008	-0.057	0.357	0.240	-0.210	-0.236	0.133
LTVs	0.170	0.121	0.115	-0.019	0.059	0.146	0.328	0.382	0.118	<b>0.877</b>	<b>0.729</b>
LRadio	0.226	0.091	0.145	-0.009	0.085	0.148	0.150	0.257	0.201	<b>0.784</b>	<b>0.523</b>
LInternet	0.246	0.010	0.137	-0.096	-0.020	0.092	0.134	0.288	0.272	<b>0.948</b>	<b>0.662</b>
LPopn00	0.145	0.066	0.191	0.107	0.123	0.057	0.441	0.470	0.069	0.135	<b>0.521</b>
LPDens00	-0.229	-0.084	-0.036	0.080	-0.006	-0.078	0.348	0.250	-0.205	-0.352	0.033
L%Urban00	0.137	0.106	-0.088	-0.096	-0.086	0.021	-0.081	-0.031	0.099	<b>0.657</b>	0.332
AvgHCom	-0.353	0.276	-0.414	-0.014	-0.259	-0.261	-0.100	-0.340	-0.342	0.026	0.112
MinHCom	-0.334	0.237	-0.412	0.001	-0.267	-0.277	-0.106	-0.343	-0.345	0.081	0.106
MaxHCom	-0.283	0.271	-0.293	-0.037	-0.162	-0.149	-0.066	-0.257	-0.241	-0.086	0.060
HDiv	0.288	-0.035	0.309	-0.018	0.266	0.291	0.087	0.266	0.280	-0.165	-0.105

	LMeat	LFWFish	LSeafood	LTotFish	L%Meat	L%Fish	L%AnimPr	L%Eggs	%Poultry	LMammals
LBMass										
LClutch										
LMinElev										
LMaxElev										
LElevR										
MinLat										
MaxLat										
LLatR										
LPPP										
LTotCal										
LMeat										
LFWFish	0.099									
LSeafood	0.255	<b>0.523</b>								
LTotFish	0.230	<b>0.682</b>	<b>0.977</b>							
L%Meat	<b>0.982</b>	0.070	0.194	0.175						
L%Fish	0.082	<b>0.676</b>	<b>0.932</b>	<b>0.967</b>	0.067					
L%AnimPr	<b>0.873</b>	-0.079	0.064	0.024	<b>0.862</b>	-0.113				
L%Eggs	<b>0.777</b>	0.187	0.405	0.381	<b>0.710</b>	0.217	<b>0.723</b>			
L%Poultry	<b>0.794</b>	-0.207	0.244	0.145	<b>0.772</b>	0.016	<b>0.762</b>	<b>0.737</b>		
LMammals	-0.140	<b>0.508</b>	0.327	0.396	-0.189	0.386	-0.196	0.153	-0.258	
LTVs	<b>0.720</b>	0.060	0.353	0.290	<b>0.636</b>	0.110	<b>0.742</b>	<b>0.806</b>	<b>0.766</b>	-0.056
LRadio	<b>0.657</b>	-0.083	0.148	0.093	<b>0.615</b>	-0.044	<b>0.693</b>	<b>0.532</b>	<b>0.688</b>	-0.405
LInternet	<b>0.692</b>	-0.141	0.316	0.215	<b>0.621</b>	0.049	<b>0.769</b>	<b>0.727</b>	<b>0.826</b>	-0.257
LPopn00	0.223	<b>0.531</b>	0.187	0.289	0.126	0.166	0.176	0.481	0.018	<b>0.597</b>
LPDens00	-0.363	0.429	0.133	0.231	-0.417	0.237	-0.389	0.006	-0.415	<b>0.628</b>
L%Urban00	0.476	-0.371	0.030	-0.094	0.456	-0.190	<b>0.547</b>	0.347	<b>0.672</b>	-0.525
AvgHCom	0.088	-0.055	0.079	0.036	0.073	0.008	-0.005	0.077	0.216	-0.052
MinHCom	0.148	-0.062	0.072	0.028	0.142	0.001	0.064	0.094	0.272	-0.095
MaxHCom	-0.054	-0.037	0.050	0.022	-0.076	0.007	-0.135	0.004	0.050	0.016
HDiv	-0.166	0.111	-0.073	-0.021	-0.161	0.006	-0.113	-0.097	-0.283	0.085

(continued on next page)

## Appendix A (continued)

	LTVs	LRadio	LInternet	LPopn00	PDens00	L%Urban00	AvgHCom	MinHCom	MaxHCom
LBMass									
LClutch									
LMinElev									
LMaxElev									
LElevR									
MinLat									
MaxLat									
LLatR									
LPPP									
LTotCal									
LMeat									
LFWFFish									
LSeafood									
LTotFish									
L%Meat									
L%Fish									
L%AnimPr									
L%Eggs									
L%Poultry									
LMammals									
LTVs									
LRadio	<b>0.804</b>								
LInternet	<b>0.835</b>	<b>0.774</b>							
LPopn00	0.293	-0.007	0.106						
LPDens00	-0.213	-0.477	-0.368	<b>0.529</b>					
L%Urban00	<b>0.661</b>	<b>0.746</b>	<b>0.642</b>	-0.303	<b>-0.631</b>				
AvgHCom	0.103	0.083	0.050	-0.140	-0.059	0.234			
MinHCom	0.146	0.140	0.102	-0.172	-0.123	0.303	<b>0.936</b>		
MaxHCom	-0.018	-0.057	-0.068	-0.066	0.057	0.039	<b>0.811</b>	<b>0.563</b>	
HDiv	-0.190	-0.182	-0.169	0.162	0.151	-0.347	<b>-0.620</b>	<b>-0.799</b>	-0.116

N.B. The values in bold indicate a correlation coefficient greater than the chosen cut-off of 0.5.

The abbreviations used in the correlation matrix are explained below. The prefix 'L' on an abbreviation indicates that the log<sub>10</sub> of this variable was used. A full list of sources for the data is available from the authors.

LGRange = Global range size (km<sup>2</sup>)

LBMass = Mean body mass (g)

LClutch = Clutch size

LMinElev = Minimum elevation at which species occurs (m above sea level)

LMaxElev = Maximum elevation at which species occurs (m above sea level)

LElevR = MaxE – MinE (m)

MinLat = Most southerly latitude at which species has been recorded

MaxLat = Most northerly latitude at which the species has been recorded

LLatR = The number of degrees of latitude over which the species has been recorded

MinHCom = The score given to the least complex habitat occupied by the species (see 'Section 2' for further information)

MaxHCom = The score given to the most complex habitat occupied by the species (see 'Section 2' for further information)

AvgHCom = The mean of the complexity scores for each habitat occupied by the species (see 'Section 2' for further information)

HDiv = The number of different habitat types a species uses (see 'Section 2' for further information)

The following human variables have been recalculated from the country scale to apply to individual species. This was achieved by taking an average of the values for each range country weighted by the proportion of the species' range that lies within each country.

LPPP = Purchasing power parity (US\$)

LTotCal = Total number of calories consumed by humans (calories per capita per day)

LMeat = Number of calories in the human diet coming from meat (calories per capita per day)

LFWFFish = Number of calories in the human diet coming from freshwater fish (calories per capita per day)

LSeafood = Number of calories in the human diet coming from seafood (calories per capita per day)

LTotFish = Number of calories in the human diet coming from freshwater fish and seafood together (calories per capita per day)

L%Meat = Percentage of calories in the human diet coming from meat

L%Fish = Percentage of calories in the human diet coming from freshwater fish and seafood together

L%AnimPr = Percentage of calories in the human diet coming from all animal products

L%Eggs = Percentage of calories in the human diet coming from eggs

L%Poultry = Percentage of calories in the human diet coming from poultry

LMammals = An index of the availability of wild mammals for hunters (see 'Section 2' for full description)

LTVs = Number of television sets per 1000 people

LRadio = Number radios per 1000 people

LInternet = Number of internet users per 10,000 people

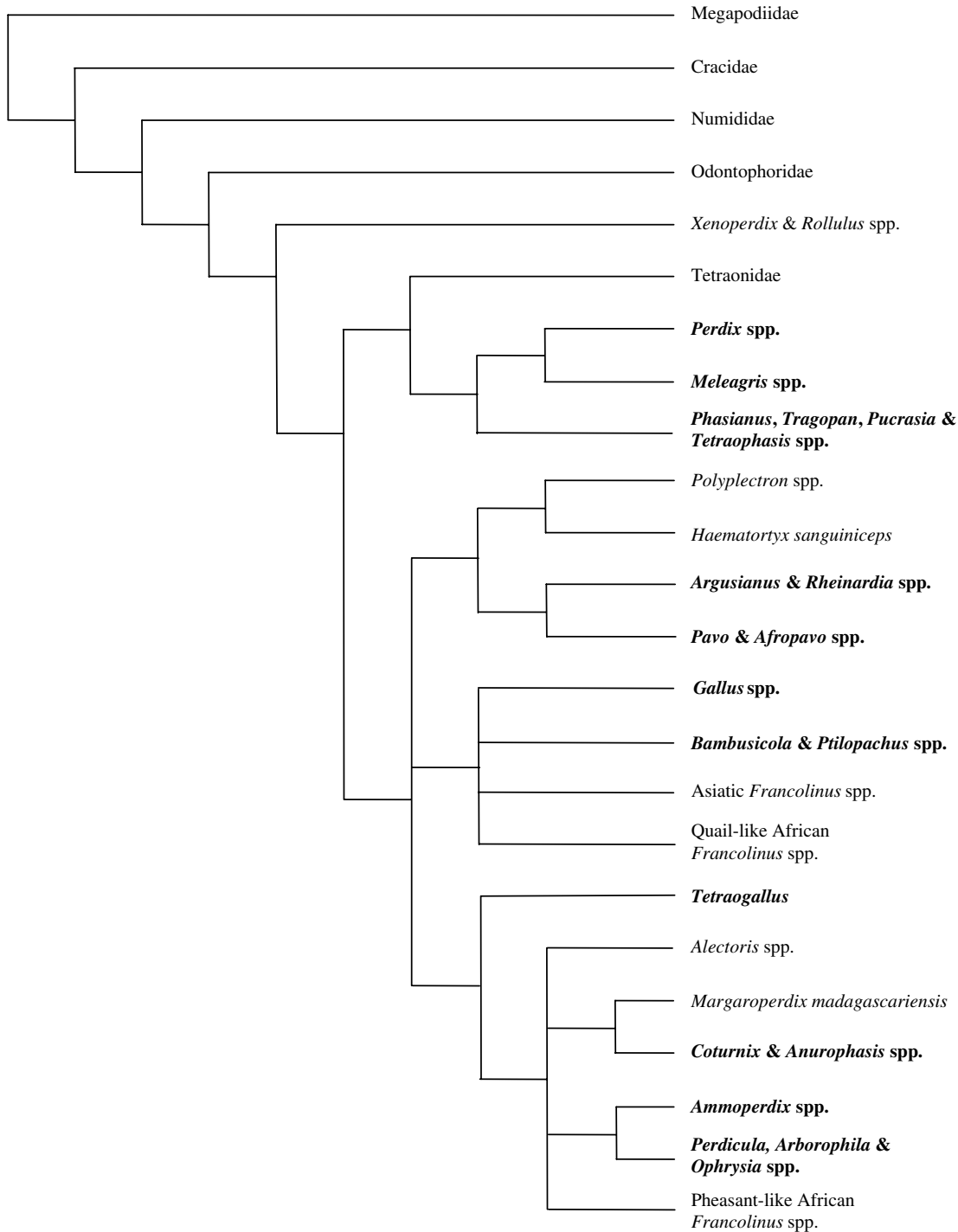
LPopn00 = Human population in the year 2000

LPDens00 = Human population density in the year 2000

L%Urban00 = Percentage of human population residing in urban areas in the year 2000

## Appendix B

Phylogeny of the Galliformes used in this study. Branch lengths are not drawn to scale. Branches which have been modified from Little and Crowe (2000) are indicated in bold type



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