

Engines of speciation: a comparative study in birds of prey

O. KRÜGER

Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK

Keywords:

comparative analysis;
MacroCAIC;
raptors;
sexual conflict;
species richness.

Abstract

Sexual selection as a promoter of speciation has received much attention in recent years, but has produced highly equivocal evidence. Here, I test whether sexual conflict is related to species richness among genera in accipitrid birds of prey using phylogenetically controlled comparative analyses. Increased species richness was associated with both 'male-win' as well as 'female-win' situations, i.e. males being able to promote gene flow through mating or females being able to restrict gene flow through female choice. Species richness was higher when plumage differed between males and females and in polygynous breeding systems compared with monogamous ones. To assess the relative importance of sexual conflict and natural selection as correlates of species richness simultaneously, I also performed a multivariate analysis of correlates of species richness. Population density, plumage polymorphism, geographic range size and breeding latitude were predictors of species richness for birds of prey. These results stress the importance of both sexual and natural selection in determining species richness but with a clear overall emphasis on natural selection in birds of prey.

Introduction

The question why some lineages of organisms contain so many more species than others is far from trivial. Although Darwin recognized that both natural selection (Darwin, 1859) and sexual selection (Darwin, 1871) can drive speciation, natural selection has traditionally been considered the dominant force (Mayr, 1942; Dobzhansky, 1946; Kiliias *et al.*, 1980; Schluter, 1998, 2001). However, theoretical and empirical studies have shown that sexual selection is a process which might also be important in determining speciation rates (Lande, 1981; West-Eberhard, 1983; Rice & Hostert, 1993; Andersson, 1994; Seehausen *et al.*, 1997; Kirkpatrick & Ravigne, 2002). There is a growing emphasis on sexual conflict as a promoter of speciation (Chapman *et al.*, 1995, 2003; Rice, 1996; Holland & Rice, 1999; Gavrillets, 2000; Panhuis *et al.*, 2001; see Parker, 2006 for a review), because it can lead to antagonistic coevolution (Parker & Partridge, 1998; Arnqvist *et al.*, 2000; Gage *et al.*, 2002) and hence reproductive isolation (Rice, 1998). Two

opposing hypotheses have been formulated (Parker & Partridge, 1998; Gavrillets, 2000) that relate the scope for sexual conflict to species richness (see Parker, 2006 for a detailed review).

In Parker & Partridge's (1998) so-called *outcome-moderated* hypothesis, speciation should be higher in a 'female-win' scenario, where females do not face the risk of forced copulations, harassment or punishment and can exert female choice unconstrained by males. In this scenario, females restrict male gene flow through their mating preferences and hence enhance premating isolation. Although it is difficult to define exactly what constitutes such a scenario, Parker & Partridge (1998) made three predictions: (1) where size dimorphism varies, clades in which females are larger than males should be more species rich than those in which males are larger or of the same size; (2) as sexual plumage dimorphism might be an indicator of female choice (but see Dunn *et al.*, 2001), dimorphic clades should be more species rich than monomorphic ones; and (3) species richness should be higher in monogamous mating systems compared with polygynous ones.

By sharp contrast, Gavrillets (2000) championed the idea of an *engine of speciation* hypothesis. It predicts that

Correspondence: Oliver Krüger, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.
Tel.: +44 1223 336610; fax: +44 1223 336676; e-mail: ok212@cam.ac.uk

high potential for sexual conflict will generally result in high species richness, as female preferences and coevolutionary male counter-strategies lead to high sexual conflict, generating rapid evolutionary change as well as isolating mechanisms. As sexual conflict is related to mating systems, the prediction can be formulated that especially polygyny and maybe also polyandry should be associated with high species richness, but monogamy with low species richness.

So far, studies testing the predictions of Parker & Partridge (1998) and Gavrilets (2000) have yielded highly equivocal results (Parker, 2006). Most of these studies have used a very broad taxonomic assemblage, whereas Parker & Partridge (1998) emphasized that a comparative test should focus on an assemblage not differing grossly in ecology. In addition, no study has examined the importance of sexual conflict relative to natural selection: it might be that the equivocal results obtained so far indicate that in those groups tested sexual conflict is of minor importance compared with ecological or life-history variables as correlates of species richness.

The family Accipitridae (true hawks) is ideally suited to test the importance of sexual conflict because they match Parker & Partridge's ideal test assemblage. In this taxon, there is a wide variety of sexual size dimorphism, ranging from males being the same size as females to males being only half the size of females and there is great variation in sexual plumage dimorphism. Most importantly, species richness, which can be used as a surrogate measure for the outcome of the speciation process (Gittleman & Purvis, 1998), varies greatly between genera, with many genera comprising one species only to the goshawks and sparrowhawks of the genus *Accipiter* with 47 species. Species number can be a source of error in comparative analyses (Isaac *et al.*, 2004), but the true hawks are comparatively well studied and so taxonomic uncertainty at the species level is very likely to be low. Furthermore, breeding systems, life history and ecology are well known (Table 1), rendering it possible to test many hypotheses simultaneously (Barraclough *et al.*, 1998; Panhuis *et al.*, 2001) and produce a multivariate model explaining differences in species richness between genera. Such a multivariate approach has recently been used in comparative abundance in other taxa (Gittleman & Purvis, 1998; Stuart-Fox & Owens, 2003; Isaac *et al.*, 2005). However, all of these studies have only explained a small proportion of the variation in species richness (10–25%, but see Phillimore *et al.*, 2006). This could be because of the broad taxonomic scale of these analyses. Six major hypotheses have been formulated that try to explain differences in species richness between taxa on the basis of natural selection.

The body size hypothesis. Species richness might be correlated with a measure of body size as small-bodied species might be less prone to extinction and require fewer resources (Purvis *et al.*, 2003; Stuart-Fox & Owens,

Table 1 Variables included in the analysis, their description and sources.

Variable	Description
Body weight	Body weight (g) ^{a,b,c}
Body size	Body size from tip of bill to tip of tail (cm) ^{a,b,c}
Wingspan	Wingspan (cm) ^{a,b,c}
Wing length	Wing length (cm) ^{a,b,c}
Tail length	Tail length (cm) ^{a,b,c}
Relative male size	Male wing length over female wing length, then cubed ^b
Sex plumage dimorphism	Scored from 0 = no difference to 4 = completely different plumage, categories adopted from Krüger & Davies (2002) ^{a,b}
Plumage polymorphism	Number of described plumage morphs ^{a,b}
Population density	Number of breeding pairs/100 km ^{2a,b}
Population size	World population estimate in breeding pairs ^{a,b}
Breeding system	-1 = polygyny, 0 = monogamy, 1 = polyandry ^{a,b}
Display behaviour	1 = ground display, 2 = aerial nonacrobatic display, 3 = aerial acrobatic display, 4 = very acrobatic display ^{a,b}
Egg volume	Estimated egg volume (ml) ^{a,b}
Clutch size	Mean clutch size ^{a,b}
Clutch volume	Egg volume × mean clutch size
Incubation time	Mean incubation time (days) ^{a,b}
Fledging time	Mean fledging time (days) ^{a,b}
Reproduction rate	Mean number of chicks fledged/pair and year ^{a,b}
Prey size	1 = fruits, 2 = insects, 3 = snails, 4 = frogs, 5 = lizards, 6 = snakes, 7 = fish, 8 = rodents, 9 = birds, 10 = small carrion, 11 = mammals, 12 = large carrion ^{a,b}
Prey specialization	Scored from 1 to 4, categories adopted from Krüger (2000) ^{a,b}
Hunting method	Scored from 1 to 4, categories adopted from Krüger (2000) ^{a,b}
Habitat preference	1 = tropical forest, 2 = subtropical & temperate forest, 3 = woodland, 4 = freshwater habitats, 5 = coastline, 6 = marsh, 7 = savannah, 8 = grassland, 9 = mountain, 10 = semi-desert ^{a,b}
Habitat productivity	Productivity of the breeding habitat in g carbon m ⁻² per year ^d
Niche breadth	Number of different habitats a species breeds in ^{a,b}
Breeding altitude	Median breeding altitude above sea level (m) ^{a,b}
Breeding latitude	Median breeding latitude (degrees), 90° S = -90° and 90° N = 90° ^{a,b}
Migration pattern	Scored from 0 to 4, categories adopted from Krüger & Davies (2002) ^{a,b}
Range size	Global breeding range size (km ^{2a,b})

^aThiollay (1994).

^bFerguson-Lees & Christie (2001).

^cKrüger (2000).

^dReichle (1970).

2003). Support for the body size hypothesis is highly equivocal (Isaac *et al.*, 2005; Phillimore *et al.*, 2006). Under this scenario, I expect species richness to be

negatively correlated with body size, body weight or wing length.

The life-history hypothesis. Taxa with 'fast' life histories may be less prone to extinction because of their ability to bounce back from population crashes (Krüger & Radford, 2008) and to adapt more quickly to environmental change because of higher rates of evolutionary change (Marzluff & Dial, 1991; Isaac *et al.*, 2005). Under this hypothesis, I expect species richness to be positively correlated with clutch size, clutch volume and reproduction rate and negatively with egg volume, incubation and fledging period.

The population abundance hypothesis. Species with higher local abundance and/or larger global population sizes have lower extinction risk, thereby increasing species richness of the corresponding higher taxon (Rosenzweig, 1995). Second, the foundation of peripheral isolate populations might be facilitated by density-dependent migration (Brown, 1958) and Hubbell (2001) proposed a model in which speciation rate is proportional to global population size. In addition, Gavrillets (2000) model shows that reproductive isolation by sexual conflict is higher at high population density. Under this hypothesis, I expect species richness to be positively correlated with population density and global population size.

The ecological specialization hypothesis. Species which are less specialized might be less prone to extinction as they can tolerate environmental change and might be more widespread (Rosenzweig, 1995). Habitat generalists might also be more likely to colonize new habitats and ultimately speciate (Stuart-Fox & Owens, 2003). However, highly specialized species might be at high risk of extinction, but they could also be a signal of an adaptive radiation. Whatever version of the hypothesis applies, I expect species richness to be correlated with niche breadth, habitat preference, prey specialization, prey size and hunting method. The occurrence of plumage polymorphism within populations, very common among raptor species, might also indicate that different morphs are adapted to slightly different niches, thereby increasing the total usable niche space of a species (Fowlie & Krüger, 2003). Hence, I predict a positive correlation between the number of plumage morphs and species richness.

The range size hypothesis. Species with large ranges are less prone to extinction as they commonly have higher population sizes (Gaston, 1994), and the probability of allopatric speciation might increase with range size (Rosenzweig, 1995). This would give rise to a positive correlation between mean geographic range size per genus and species richness. On the other hand, species with small ranges might live in archipelagos or have undergone a higher rate of cladogenesis (Jablonski & Roy, 2003). This would give rise to a negative correlation between mean geographic range size per genus and species richness. In addition, as range size

commonly increases from the equator to the poles (Rosenzweig, 1995), breeding latitude might be a correlate of species richness, being highest at the equator (Rosenzweig, 1995). Under this hypothesis, I expect species richness to be correlated with geographical range size and median breeding latitude.

The dispersal hypothesis. Higher levels of dispersal may increase the opportunity for speciation by increasing the rate at which novel habitats are encountered (Rosenzweig, 1995). By the same argument, migration should also lead to higher speciation rates. Under this hypothesis, I expect species richness to be positively correlated with migration pattern and wingspan, as it signals the capability for long-distance flying (Calmaestra & Moreno, 2001). Although the capability for long-distance flying might also promote gene flow between population, there are some likely examples in raptors where migration has led to speciation (forest buzzard *Buteo oreophilus*) or is likely to do so in future (Southern African population of booted eagle *Hieraetus pennatus*).

Only by using a multivariate model selection approach can the relative importance of all these hypotheses be tested (Stuart-Fox & Owens, 2003). Hence, the aims in this paper were twofold:

- 1 I test whether species-richness differences are associated with sexual conflict and sexual selection. Does species richness increase under a 'female-win' or 'male-win' scenario?
- 2 I use a multivariate model selection approach, based on an information criterion, to assess the relative importance of sexual and natural selection as promoters of species richness. In addition, can explanatory power be increased by focusing on a small, clearly monophyletic assemblage?

Material and methods

I collected data on the 241 species recognized by Ferguson-Lees & Christie (2001) in the family Accipitridae (true hawks) from the literature (mainly Thiollay, 1994; Krüger, 2000; Ferguson-Lees & Christie, 2001; see Appendix 1 for summary data). The dependent variable, species richness, was measured as the number of described species in a genus (Owens *et al.*, 1999; Arnqvist *et al.*, 2000). I started with 28 predictor variables (Table 1). This large number of potential predictor variables controls for confounding effects and assesses the relative importance of allometry, life history and ecology as correlates of species richness. Relative male size was measured as the ratio of wing length of males to that of females and this ratio was then cubed. Data on wing length are available for more species than body weight and the cubed index gives an estimate of both differences in bulk as well as flight performance (Ferguson-Lees & Christie, 2001). The amount of reversed size dimorphism was used as a

surrogate for a 'female-win' situation because it is related to female dominance (Mueller & Meyer, 1985). However, I also acknowledge that size dimorphism might have evolved because of ecological factors, rather than sexual selection (Krüger, 2005). Plumage dimorphism was scored as 0 (no difference), 1 (difference in eye colour or eye ring), 2 (less than 25% of plumage differs between the sexes), 3 (more than 25% of plumage differs) or 4 (entirely different plumage). Plumage polymorphism refers to the number of plumage morphs described for the same sex of a species and was taken from Ferguson-Lees & Christie (2001). The variable breeding system was coded as -1 = polygyny, 0 = monogamy and 1 = polyandry. I also looked at the species-specific literature in cases where departures from monogamy were described as 'rare' or 'common', using again mainly Thiollay (1994) and especially Ferguson-Lees & Christie (2001). Hence, I also assigned numerical values between the three categories. A world population estimate for each bird of prey species was obtained from Ferguson-Lees & Christie (2001). Egg volumes were estimated from egg length and breadth measurements in Schönwetter (1967–1992) and the approximation for egg volume provided by Hoyt (1979). Prey size categories generally differed by an order of magnitude in weight. The variable hunting method was included to reflect the energetic cost of hunting and the aerial skill level needed. The habitat-preference variable was ranked from closed-canopy habitat to increasingly more open and less productive habitat; hence, there is some overlap with the habitat-productivity variable. Global breeding range size was calculated for each species from information in Ferguson-Lees & Christie (2001). As I used the mean range size of all species within a genus, my range-size estimate takes into account that some genera have successfully colonized archipelagos; so, it includes an island factor.

I calculated phylogenetically independent contrasts using Felsenstein's (1985) method as implemented in MacroCAIC (Agapow & Isaac, 2002). MacroCAIC generates Felsenstein-independent contrasts for the explanatory variables, but uses the proportional difference in species numbers as a contrast in species richness between sister taxa (PDI). This measure of species richness is least prone to error and most conservative (Isaac *et al.*, 2003). The comparative analysis was based on a genus-level composite phylogeny combining several published phylogenies (Holdaway, 1994; Wink & Sauer-Gürth, 2000, 2004; Gamauf & Haring, 2004; Helbig *et al.*, 2005). This composite phylogeny (Appendix 2) contained 61 of 65 genera and 235 of 241 species. The four missing genera are very poorly known (Thiollay, 1994) and phenotypically resemble kites (genera *Chondrohierax*, *Rostrhamus* and *Ictinia*) and true eagles (genus *Ictinaetus*). Raw contrasts were standardized by dividing them through the square root of their variance

(i.e. sum of branch lengths) prior to analysis (Agapow & Isaac, 2002).

I developed multiple regression models in SPSS (SPSS Inc., Chicago, IL, USA). The models did not include an intercept, as recommended by Garland *et al.* (1992). To select the model fitting the data best, I used an information theory approach, the small-sample version of the Akaike information criterion (AICc) which penalizes a model for every additional parameter used and hence avoids overfitting (Burnham & Anderson, 2002). I started with models containing one variable and then added more variables one by one with all possible variable combinations. I checked for variable redundancy by including collinearity statistics and 0.1 was used as a lower threshold, as recommended by Hair *et al.* (1995). Differences in AICc between models above unity suggest less support (Burnham & Anderson, 2002). This model selection approach seems preferable to stepwise regression models (Whittingham *et al.*, 2006).

Results

To test the predictions of Parker & Partridge (1998) and Gavrilets (2000), I first examined the relationship between the three variables describing sexual conflict (relative male size, sexual plumage dimorphism and breeding system) and species richness (Fig. 1a–c). Contrasts in species richness were positively correlated with contrasts in sexual plumage dimorphism ($r_{52} = 0.298$, $P = 0.028$). Removing the one data point with high leverage (contrast between the highly dimorphic harriers *Circus* and the crane hawk *Geranospiza*) from the data turned the significant correlation into a strong trend ($r_{51} = 0.247$, $P = 0.071$). Contrasts in species richness were negatively correlated with contrasts in breeding system ($r_{52} = -0.348$, $P = 0.010$), indicating that species richness was higher in polygynous breeding systems and lower in monogamous and more polyandrous breeding systems. Again removing the one data point with high leverage (contrast between the monogamous buzzards *Buteo* and the often polyandrous Harris hawk *Parabuteo*) from the data did not affect the significance of the correlation ($r_{50} = -0.273$, $P = 0.048$). There was no evidence for a correlation between contrasts in species richness and contrasts in relative male size ($r_{52} = 0.058$, $P = 0.676$).

To see which variables predicted differences in species richness between genera in general, multiple regression models were developed for the independent contrasts and compared using AICc. Of all possible models, the 10 with lowest AICc values are shown in Table 2a. Population density occurred in all 10 of the best models, breeding latitude in nine, breeding system in eight, plumage polymorphism and range size in seven and plumage dimorphism in five of the 10 best models. The most likely model contained four variables: population density, median breeding latitude,

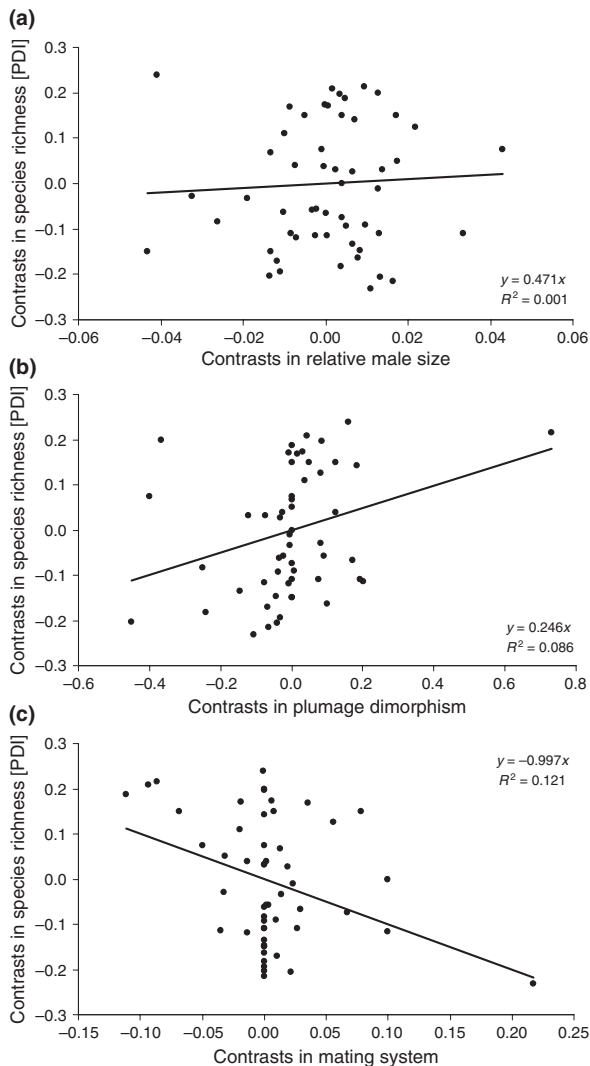


Fig. 1 Scatter plots between contrasts in species richness and contrasts in (a) relative male size, (b) sexual plumage-dimorphism and (c) breeding system.

plumage polymorphism and geographic range size. Species richness increased with increasing population density, plumage polymorphism and increasing breeding latitude, whereas species richness decreased with increasing range size (Table 2b). This model was highly significant ($F_{4,50} = 7.860$, $P < 0.001$) and explained 38.6% of the variation around the origin in species richness between accipitrid genera. The second-best model was almost as likely to fit the data ($\Delta\text{AICc} = 0.74$) and contained an additional variable: breeding system. Averaging slopes for the six variables within the 10 best models showed that both population density and breeding latitude had a significant average slope ($P = 0.003$ and 0.048 respectively) and plumage polymorphism had a strong trend towards significance

($P = 0.063$), range size a weak trend ($P = 0.092$) and both breeding system and plumage dimorphism were not significant on average ($P = 0.130$ and 0.205 respectively). Hence, species richness was more related to ecological forces than sexual selection.

Discussion

In accipitrid birds of prey, sexual size dimorphism was not related to species richness, thus not supporting the prediction of Parker & Partridge (1998). So far, not a single study found support for the prediction; so, it might be that variation in size dimorphism alone is a poor predictor of sexual conflict resolution (Parker, 2006) or that sexual conflict does not affect speciation. Sexual size dimorphism has also rarely been found to be a correlate of species richness (Parker, 2006) with the exception of agamid lizards (Stuart-Fox & Owens, 2003).

However, sexual plumage dimorphism was positively correlated with species richness: high sexual plumage dimorphism is generally associated with female choice (Barraclough *et al.*, 1995) and thus I found higher species richness in a 'female-win' scenario (see also Møller & Cuervo, 1998). The data point with high leverage (contrast between harriers *Circus* and the crane hawk *Geranospiza*) is well supported by several phylogenies (Holdaway, 1994; Wink & Sauer-Gürth, 2004); so, it is likely that the contrast depicts rapid evolutionary change rather than phylogenetic uncertainty.

By contrast, the negative correlation between breeding system and species richness supports the prediction of Gavrillets (2000). A polygynous breeding system is often, not always (i.e. leks) more likely a 'male-win' scenario as males are more likely to enforce matings and a monogamous breeding system is more likely a 'female-win' scenario where females can exert female choice more freely (Parker & Partridge, 1998), and I found a higher species richness in more polygynous breeding systems and a lower species richness in more monogamous ones. Again, the contrast with high leverage (buzzards *Buteo* and Harris hawk *Parabuteo*) is very robust phylogenetically (Holdaway, 1994; Wink & Sauer-Gürth, 2004); so, a rapid change in the breeding system is the most likely explanation for the large contrast.

As emphasized by Parker & Partridge (1998), comparative studies on the importance of sexual conflict should focus on groups which do not differ grossly in ecology. Many studies have found highly equivocal support for the predictions relating sexual conflict to speciation (Gage *et al.*, 2002; Morrow *et al.*, 2003; Phillimore *et al.*, 2006), and this might not solely be because of the broad sweep analyses on wide ranging groups of taxa. The birds of prey studied here are clearly monophyletic, they do not differ grossly in ecology, and although they have produced some evidence for sexual conflict influencing

Table 2 Results of the Akaike information criterion modelling approach.

Model	Parameter	AICc	Δ AICc		
(a)					
Density + latitude + polymorphism + range	5	-236.63	0.00		
Density + latitude + polymorphism + range + breeding	6	-235.90	0.74		
Density + latitude + polymorphism + range + plumage	6	-235.63	1.00		
Density + latitude + polymorphism + range + breeding + plumage	7	-235.28	1.36		
Density + latitude + range + breeding + plumage	6	-234.49	2.14		
Density + latitude + polymorphism + breeding	5	-234.31	2.32		
Density + latitude + polymorphism + breeding + plumage	6	-234.14	2.49		
Density + latitude + breeding + plumage	5	-234.06	2.58		
Density + polymorphism + range + breeding	5	-233.81	2.83		
Density + latitude + range + breeding	5	-233.72	2.91		
Variable	β	SE	t	P	Collinearity
(b)					
Population density	0.602	0.184	3.266	0.002	0.875
Breeding latitude	0.012	0.006	2.024	0.048	0.753
Plumage polymorphism	0.491	0.195	2.524	0.015	0.905
Range size	-0.262	0.126	2.076	0.043	0.900
Variable	Mean β	Mean SE	t		
(c)					
Population density	0.615	0.186	3.301		
Breeding latitude	0.012	0.006	2.074		
Plumage polymorphism	0.420	0.217	1.937		
Range size	-0.225	0.131	1.717		
Breeding system	-0.561	0.375	1.496		
Plumage dimorphism	0.114	0.099	1.147		

(a) The 10 best models are shown, (b) the details of the most likely model and (c) the model-averaged slopes and standard errors for variables among the best 10 models.

patterns of species richness, the evidence for both Parker & Partridge (1998) and Gavrilets (2000) hypotheses is clearly not unambiguous and even where correlations are significant, there is enormous scatter in the data (Fig. 1). It is very plausible that either the surrogate variables for sexual conflict do not capture it very well; that they are themselves correlated with other variables of greater importance or that sexual conflict does indeed not play a prominent role in birds of prey when compared with natural selection.

My analysis of species richness indicated the potential importance of sexual conflict (Mitra *et al.*, 1996; Panhuis *et al.*, 2001), but especially emphasized ecological factors (Schluter, 2001) as promoters of species richness. The predictive power of the most likely model (39% of variance explained) was higher than the spectrum reported which commonly ranges from 10% to 25% (Phillimore *et al.*, 2006), but see Arnqvist *et al.* (2000) and Phillimore *et al.* (2006).

Species richness increased with population density, thus supporting the *population abundance* hypothesis. Higher population abundance might increase the chance of genotypic variation arising and decrease the chance of local extinction (Marzluff & Dial, 1991; Frankham,

1996). Isaac *et al.* (2005) also reported population density to be positively correlated with species richness in marsupials and primates, but they found this correlation not to be very robust. In addition, density-dependent dispersal is common in the highly territorial and aggressive birds of prey (Thiollay, 1994); so, it might be plausible that Brown's (1958) hypothesis of covariation between dispersal strategy, encounter rate of novel environments and speciation rate could explain the importance of population density as a correlate of species richness in birds of prey.

Species richness also increased with increasing plumage polymorphism, indicating that phenotypic variation might be an initial precursor of speciation events (Lode, 2001; Proulx, 2001; Kai *et al.*, 2002). Different morphs can also be better adapted to different environments or climates, providing a mechanistic explanation for both allopatric and sympatric speciation (Galeotti & Cesaris, 1996; Brommer *et al.*, 2005). Polymorphic populations can comprise distinct genetic populations; so, reproductive isolation might have occurred (Kai *et al.*, 2002).

Geographic range size was negatively related to species richness, supporting one variant of the *range*

size hypothesis. Although range size has been repeatedly documented as a correlate of taxonomic diversity, the direction of this relationship is debated. Rosenzweig (1995) predicted a positive relationship between range size and species richness because of allopatric speciation, but Jablonski & Roy (2003) predicted a negative relationship because of correlations with abundance and dispersal. Although my finding fits the prediction that smaller ranges should be associated with higher species richness, this is not because of a correlation with population abundance which is not significant ($r_{52} = 0.048$, $P = 0.730$). Phillimore *et al.* (2006) have proposed that higher rates of allopatric speciation lead to an increased dissection of ranges so that taxa that have speciated at a faster rate contain species with smaller ranges, fitting to the result presented here. However, smaller ranges can also lead to higher extinction rates (Jones *et al.*, 2003; Krüger & Radford, 2008).

Finally, species richness increased with higher breeding latitudes. As the median breeding latitude across genera was exactly on the equator, but species richness was highest around 10° north of the equator, this means that moving from the southern hemisphere to the equator and slightly further north was associated with an increase in species richness. Range sizes were also smallest around the equator which might be a potential mechanistic explanation for breeding latitude as a correlate of species richness, but as latitude had an independent effect on species richness, it could be that it simply reflects speciation in tropical archipelagos such as South-East Asia, where some species-rich genera such as the goshawks and sparrowhawks *Accipiter* and serpent-eagles *Spilornis* have evolved different species on neighbouring islands (Thiollay, 1994; Ferguson-Lees & Christie, 2001).

In line with a number of other recent studies (Owens *et al.*, 1999; Stuart-Fox & Owens, 2003; Phillimore *et al.*, 2006; but see Isaac *et al.*, 2005), I found no evidence for the *body size* and *life-history* hypotheses explaining differences in species richness. Although earlier work (i.e. Marzluff & Dial, 1991), focussing on very large taxonomic assemblages, found these two hypotheses to be commonly supported, they might not have equally high explanatory power at a finer taxonomic scale (Nee *et al.*, 1992; Owens *et al.*, 1999).

There was also no support for the *ecological specialization* hypothesis, if plumage polymorphism is excluded. Whereas Owens *et al.* (1999) found higher species richness in avian clades consisting of habitat generalists and Phillimore *et al.* (2006) reported feeding generalization to be a correlate of species richness, none of the variables in this study describing the degree of habitat or feeding specialization was an important predictor of species richness. It could well be that either the variables were measured too crudely or

that the shared predatory habit of birds of prey narrows the variation in feeding specialization and hence the explanatory power.

The aforementioned arguments have highlighted that current species richness can be viewed as the differential outcome of speciation and extinction events (Owens *et al.*, 1999), so ideally the same variables that are found to be predictors of species richness should also be important predictors of extinction risk (Coyne & Orr, 2004). In a multivariate analysis of extinction risk in accipitrid birds of prey species (Krüger & Radford, 2008), the strongest correlate of extinction risk (measured as either IUCN threat status, small range size or small population size) was indeed plumage polymorphism. This indicates that at least one correlate identified here seems to be especially meaningful in birds of prey.

In conclusion, this study has highlighted that the level of analysis should be appropriate for the predictions tested. It also showed that both sexual selection as well as ecology influence species richness in birds of prey, with a more prominent role overall for ecology. This is not entirely surprising, given that birds of prey are among the most monogamous taxa, both socially and genetically (Thiollay, 1994). Finally, results also showed that, besides using a clearly defined monophyletic group, explanatory power of comparative models of speciation is not particularly high (but see Phillimore *et al.*, 2006). Possible reasons in this analysis could be uncertainties in the phylogeny, data limitations or chance events (Ricklefs, 2003). However, my finding that there are robust predictors of species richness in birds of prey, such as population density, plumage polymorphism, geographical range size and breeding latitude, does not support the idea that chance plays the most dominant role.

Acknowledgments

I am indebted to L. Birch for help with data acquisition and to M. Brooke, N. Davies, R. Johnstone, G. Parker, A. Radford and three anonymous referees for comments on the manuscript. This study was funded by a Royal Society Research Fellowship.

References

- Agapow, P.M. & Isaac, N.J.B. 2002. MacroCAIC: revealing correlates of species richness by comparative analysis. *Divers. Distrib.* **8**: 41–43.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Arnqvist, G., Edvardsson, M., Friberg, U. & Nilsson, T. 2000. Sexual conflict promotes speciation in insects. *Proc. Natl Acad. Sci. USA* **97**: 10460–10464.
- Barraclough, T.G., Harvey, P.H. & Nee, S. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond. B* **259**: 211–215.

- Barracough, T.G., Vogler, A.P. & Harvey, P.H. 1998. Revealing the factors that promote speciation. *Phil. Trans. R. Soc. Lond. B* **353**: 241–249.
- Brommer, J.E., Ahola, K. & Karstinen, T. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proc. R. Soc. Lond. B* **272**: 935–940.
- Brown, W.L.J. 1958. General adaptation and evolution. *Syst. Zool.* **7**: 157–168.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Inference: A Practical Information-theoretic Approach*, 2nd edn. Springer-Verlag, Berlin.
- Calmaestra, R.G. & Moreno, E. 2001. A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. *Ardea* **89**: 407–416.
- Chapman, T., Liddle, L., Kalb, J.M., Wolfner, M.F. & Partridge, L. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**: 241–244.
- Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. 2003. Sexual conflict. *Trends Ecol. Evol.* **18**: 41–47.
- Coyne, J.A. & Orr, H.A. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Darwin, C. 1859. *The Origin of Species by Means of Natural Selection*. John Murray, London.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- Dobzhansky, T. 1946. Complete reproductive isolation between two morphologically similar species of *Drosophila*. *Ecology* **27**: 205–211.
- Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**: 161–175.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Ferguson-Lees, J. & Christie, D.A. 2001. *Raptors of the World*. Christopher Helm, London.
- Fowlie, M.K. & Krüger, O. 2003. The evolution of plumage polymorphism in birds of prey and owls: the apostatic selection hypothesis revisited. *J. Evol. Biol.* **16**: 577–583.
- Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. *Conserv. Biol.* **10**: 1500–1508.
- Gage, M.J.G., Parker, G.A., Nylin, S. & Wiklund, C. 2002. Sexual selection and speciation in mammals, butterflies and spiders. *Proc. R. Soc. Lond. B* **269**: 2309–2316.
- Galeotti, P. & Cesaris, C. 1996. Rufous and grey colour morphs in the Italian Tawny Owl: geographical and environmental influences. *J. Avian Biol.* **27**: 15–20.
- Gamauf, A. & Haring, E. 2004. Molecular phylogeny and biogeography of Honey-buzzards (genera *Pernis* and *Henicopernis*). *J. Zool. Syst. Evol. Res.* **42**: 145–153.
- Garland, T., Harvey, P.H. & Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.
- Gaston, K.J. 1994. *Rarity*. Chapman & Hall, London.
- Gavrilets, S. 2000. Rapid evolution of reproductive isolation driven by sexual conflict. *Nature* **403**: 886–889.
- Gittleman, J.L. & Purvis, A. 1998. Body size and species-richness in carnivores and primates. *Proc. R. Soc. Lond. B* **265**: 113–119.
- Hair, J.F., Anderson, R.E., Tatham, R.L. & Black, W.C. 1995. *Multivariate Data Analysis with Readings*, 4th edn. Prentice-Hall Int., Englewood Cliffs, NJ.
- Helbig, A.J., Kocum, A., Seibold, I. & Braun, M.J. 2005. A multi-gene phylogeny of aquiline eagles (Aves: Accipitriformes) reveals extensive paraphyly at the genus level. *Mol. Phylogenet. Evol.* **35**: 147–164.
- Holdaway, R.N. 1994. An exploratory phylogenetic analysis of the genera of the Accipitridae, with notes on the biogeography of the family. In: *Raptor Conservation Today* (B. U. Meyburg & R. D. Chancellor, eds), pp. 601–647. Pica Press, Berlin.
- Holland, B. & Rice, W.R. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**: 5083–5088.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73–77.
- Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography. Monographs in Population Biology*. Princeton University Press, Princeton, NJ.
- Isaac, N.J.B., Agapow, P.M., Harvey, P.H. & Purvis, A. 2003. Phylogenetically nested comparisons for testing correlates of species richness: a simulation study of continuous variables. *Evolution* **57**: 18–26.
- Isaac, N.J.B., Jones, K.E., Gittleman, J.L. & Purvis, A. 2005. Correlates of species richness in mammals: body size, life history, and ecology. *Am. Nat.* **165**: 600–607.
- Isaac, N.J.B., Mallet, J. & Mace, G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* **19**: 464–469.
- Jablonski, D. & Roy, K. 2003. Geographic range and speciation in fossils and living mollusks. *Proc. R. Soc. Lond. B* **270**: 401–406.
- Jones, K.E., Purvis, A. & Gittleman, J.L. 2003. Biological correlates of extinction risk in bats. *Am. Nat.* **161**: 601–614.
- Kai, Y., Nakayama, K. & Nakabo, T. 2002. Genetic differences among three colour morphotypes of the black rockfish, *Sebastes inermis*, inferred from mtDNA and AFLP analyses. *Mol. Ecol.* **11**: 2591–2598.
- Kiliias, G., Alahiotis, S.N. & Pelecanos, M. 1980. A multifactorial genetic investigation of speciation theory using *Drosophila melanogaster*. *Evolution* **34**: 730–737.
- Kirkpatrick, M. & Ravigne, V. 2002. Speciation by natural and sexual selection: models and experiments. *Am. Nat.* **159**: S22–S35.
- Krüger, O. 2000. Correlates of population density and body weight of raptors in the family Accipitridae: a comparative study. *J. Zool. Lond.* **250**: 185–192.
- Krüger, O. 2005. The evolution of reversed size dimorphism in hawks, falcons and owls: a comparative analysis. *Evol. Ecol.* **19**: 467–486.
- Krüger, O. & Davies, N.B. 2002. The evolution of cuckoo parasitism: a comparative analysis. *Proc. R. Soc. Lond. B* **269**: 375–381.
- Krüger, O. & Radford, A.N. 2008. Doomed to die? Predicting extinction risk in the true hawks Accipitridae. *Anim. Conserv.* doi:10.1111/j.1469-1795.2007.00155.x.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**: 3721–3725.
- Lode, T. 2001. Genetic divergence without spatial isolation in polecat *Mustela putorius* populations. *J. Evol. Biol.* **14**: 228–236.
- Marzluff, J.M. & Dial, K.P. 1991. Life history correlates of taxonomic diversity. *Ecology* **72**: 428–439.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.

- Mitra, S., Landel, H. & Pruett-Jones, S. 1996. Species richness covaries with mating system in birds. *Auk* **113**: 544–551.
- Møller, A.P. & Cuervo, J.J. 1998. Speciation and feather ornamentation in birds. *Evolution* **52**: 859–869.
- Morrow, E.H., Pitcher, T.E. & Arnqvist, G. 2003. No evidence that sexual selection is an 'engine of speciation' in birds. *Ecol. Lett.* **6**: 228–234.
- Mueller, H.C. & Meyer, K. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the Western Palearctic. *Curr. Ornithol.* **2**: 65–101.
- Nee, S., Mooers, A.O. & Harvey, P.H. 1992. Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl Acad. Sci. USA* **89**: 8322–8326.
- Owens, I.P.F., Bennett, P.M. & Harvey, P.H. 1999. Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond. B* **266**: 933–939.
- Panhuis, T.M., Butlin, R., Zuk, M. & Tregenza, T. 2001. Sexual selection and speciation. *Trends Ecol. Evol.* **16**: 364–371.
- Parker, G.A. 2006. Sexual conflict over mating and fertilization: an overview. *Phil. Trans. R. Soc. Lond. B* **361**: 235–259.
- Parker, G.A. & Partridge, L. 1998. Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond. B* **353**: 261–274.
- Phillimore, A.B., Freckleton, R.P., Orme, C.D.L. & Owens, I.P.F. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.* **168**: 220–229.
- Proulx, S.R. 2001. Female choice via indicator traits easily evolves in the face of recombination and migration. *Evolution* **55**: 2401–2411.
- Purvis, A., Orme, C.D.L. & Dolphin, K. 2003. Why are most species small-bodied? A phylogenetic view. In: *Macroecology: Concepts and Consequences* (K. J. Gaston & T. M. Blackburn, eds), pp. 155–173. Blackwell Scientific, Oxford.
- Reichle, D.E. 1970. *Analysis of Temperate Forest Ecosystems*. Springer-Verlag, New York.
- Rice, W.R. 1996. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**: 232–234.
- Rice, W.R. 1998. Intergenomic conflict, interlocus antagonistic coevolution, and the evolution of reproductive isolation. In: *Endless Forms: Species and Speciation* (D. Howard & S. Berlocher, eds), pp. 261–270. Oxford University Press, Oxford.
- Rice, W.R. & Hostert, E.E. 1993. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**: 1637–1653.
- Ricklefs, R.E. 2003. Global diversification rates of passerine birds. *Proc. R. Soc. Lond. B* **270**: 2285–2291.
- Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Schluter, D. 1998. Ecological causes of speciation. In: *Endless Forms: Species and Speciation* (D. Howard & S. Berlocher, eds), pp. 114–129. Oxford University Press, Oxford.
- Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.
- Schönwetter, M. 1967–1992. *Handbuch der Oologie*. Akademie-Verlag, Berlin.
- Seehausen, O., van Alphen, J.J.M. & Witte, F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**: 1808–1811.
- Stuart-Fox, D. & Owens, I.P.F. 2003. Species richness in agamid lizards: chance, body size, sexual selection or ecology? *J. Evol. Biol.* **16**: 659–669.
- Thiollay, J.M. 1994. Family Accipitridae. In: *Handbook of the Birds of the World, Vol. 2* (J. del Hoyo, A. Elliott & J. Sargatal, eds), pp. 52–205. Lynx Edicions, Barcelona.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**: 15–183.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.P. & Freckleton, R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* **75**: 1182–1189.
- Wink, M. & Sauer-Gürth, H. 2000. Advances in the molecular systematics of African raptors. In: *Raptors at Risk* (R. D. Chancellor & B. U. Meyburg, eds), pp. 135–147. Hancock House Publishers, Surrey, BC.
- Wink, M. & Sauer-Gürth, H. 2004. Phylogenetic relationships in diurnal raptors based on nucleotide sequences of mitochondrial and nuclear marker genes. In: *Raptors Worldwide* (R. D. Chancellor & B. U. Meyburg, eds), pp. 483–498. WGBP, Berlin.

Received 9 August 2007; revised 6 January 2008; accepted 8 January 2008

Appendix 1. Data for the genera used in the study. Abbreviations: SR, species richness; BW, body weight; BS, body size; WS, wingspan; WL, wing length; TL, tail length; SD, size dimorphism; SPD, Sexual plumage dimorphism; PP, plumage polymorphism; PD, population density; PS, population size; BrS, breeding system; DB, display behaviour; EV, egg volume; CS, clutch size; CV, clutch volume; IT, incubation time; FT, fledging time; RR, reproduction rate; PrS, prey size; PSp, prey specialization; HM, hunting method; HP, habitat preference; CS, habitat productivity; NB, niche breadth; BA, breeding altitude; BL, breeding latitude; M, migration; RS, range size.

Genus	SR	BW	BS	WS	WL	TL	SD	SPD	PP	PD	PS	BaS	DB	EV	CS	CV	IT	FT	RR	PrS	PSp	HM	HP	HPr	NB	BA	BL	M	RS
<i>Accipiter</i>	47	2.46	1.56	1.82	1.33	1.22	0.68	0.64	1.39	0.92	4.16	0.00	2.73	1.42	2.99	1.90	1.52	1.52	1.89	7.30	1.80	2.11	1.51	2.77	2.18	2.87	-0.32	0.48	5.89
<i>Aegypius</i>	1	3.99	2.01	2.44	1.90	1.57	0.93	0.00	1.00	0.08	3.93	-0.50	3.50	2.35	1.01	2.36	1.74	2.03	0.57	11.25	1.75	0.50	3.00	2.24	6.00	3.00	38.00	1.00	6.85
<i>Aquila</i>	9	3.46	1.87	2.26	1.75	1.47	0.86	0.18	1.59	0.44	4.31	0.00	3.05	2.05	2.06	2.37	1.64	1.86	0.73	8.39	1.61	2.27	4.41	2.53	3.55	3.02	19.45	1.86	6.66
<i>Aviceda</i>	5	2.46	1.60	1.97	1.48	1.29	0.93	0.80	1.60	0.44	4.00	0.00	2.60	1.41	2.35	1.78	1.50	1.54	0.85	3.50	1.05	1.40	1.20	2.78	2.20	2.92	-3.40	0.80	6.14
<i>Busarellus</i>	1	2.87	1.68	2.11	1.58	1.27	0.84	0.00	1.00	0.74	5.40	0.00	3.00	1.78	1.50	1.95	1.54	1.66	0.74	5.75	1.75	1.25	4.00	2.85	4.00	2.40	-4.00	0.00	7.04
<i>Buteo</i>	4	2.95	1.60	1.98	1.48	1.22	0.89	0.00	1.13	0.48	4.90	0.00	2.88	1.53	2.63	1.95	1.46	1.54	2.40	6.63	1.63	1.44	5.38	2.67	4.00	2.86	20.25	2.00	6.29
<i>Buteogallus</i>	4	2.95	1.68	2.04	1.56	1.30	0.91	0.00	1.13	0.97	4.40	0.00	3.00	1.80	1.47	1.97	1.60	1.67	1.15	5.88	1.75	1.56	1.75	2.83	4.25	2.33	3.50	0.50	6.14
<i>Chelictinia</i>	1	2.04	1.54	1.86	1.38	1.29	0.94	0.00	1.00	0.18	4.40	-0.50	2.00	1.17	4.00	1.77	1.48	1.49	1.94	2.75	1.75	1.50	10.00	1.70	2.00	2.70	9.00	3.00	5.95
<i>Circus</i>	6	3.18	1.81	2.19	1.68	1.42	0.91	0.00	1.08	-0.22	3.92	0.00	2.67	2.07	1.00	2.07	1.68	1.89	0.63	6.17	2.04	2.17	3.42	2.71	3.00	2.77	1.67	1.00	6.51
<i>Circus</i>	13	2.67	1.70	2.07	1.57	1.37	0.81	2.92	1.42	0.95	4.43	-0.35	3.46	1.51	3.86	2.11	1.51	1.58	1.81	7.23	1.21	1.94	7.00	2.51	3.15	2.96	10.46	2.08	6.66
<i>Dryotriorchis</i>	1	2.84	1.70	2.00	1.58	1.41	0.91	1.00	2.00	0.70	4.10	0.00	3.00	1.70	1.00	1.70	1.55	1.68	0.50	4.75	2.00	1.50	1.00	2.88	1.00	2.40	0.00	0.00	6.24
<i>Elanoides</i>	1	2.57	1.79	2.11	1.64	1.51	0.93	0.00	1.00	0.70	5.40	-0.13	3.00	1.53	1.83	1.79	1.47	1.72	0.48	2.75	1.00	1.25	1.00	2.78	3.00	2.90	0.50	1.00	7.10
<i>Elanus</i>	4	2.45	1.55	1.95	1.47	1.17	0.92	0.50	1.00	1.37	4.97	-0.19	3.50	1.34	3.88	1.93	1.51	1.54	1.47	7.25	1.75	2.00	8.13	2.55	2.50	2.76	-10.00	0.50	6.63
<i>Erythrorchis</i>	2	2.90	1.71	2.04	1.54	1.37	0.76	1.00	1.50	0.11	2.82	0.00	3.00	1.78	1.60	1.98	1.61	1.72	0.90	8.73	1.75	2.38	1.50	2.82	2.00	2.88	-14.50	0.00	5.82
<i>Eutriorchis</i>	1	2.93	1.80	2.02	1.52	1.44	0.90	0.00	1.00	0.48	2.30	0.00	3.00	1.93	1.00	1.93	1.60	1.79	0.60	7.75	1.50	2.25	1.00	2.63	1.00	2.70	-16.50	0.00	4.22
<i>Gampsonyx</i>	1	1.97	1.38	1.73	1.20	1.00	0.91	0.00	1.50	1.18	4.40	0.00	2.00	1.08	2.50	1.48	1.41	1.54	2.80	5.30	1.50	1.25	7.00	2.86	3.00	2.70	-8.00	0.00	6.88
<i>Geranoaetus</i>	1	3.30	1.85	2.26	1.73	1.36	0.67	0.00	1.00	0.70	4.40	0.00	2.50	1.92	2.00	2.26	1.48	1.86	1.10	7.75	2.00	2.25	9.00	2.48	2.00	3.40	-23.00	0.00	6.90
<i>Geranoospiza</i>	1	2.48	1.67	1.97	1.44	1.35	0.77	0.00	2.00	0.45	5.40	0.00	3.00	1.56	2.00	1.82	1.54	1.65	0.98	4.75	1.25	1.50	2.00	2.85	2.00	2.54	-5.00	0.00	7.11
<i>Gypaetus</i>	1	3.76	2.03	2.42	1.91	1.68	0.97	0.00	1.00	-0.22	4.00	0.68	4.00	2.27	1.50	2.45	1.74	2.07	0.70	12.00	2.75	0.00	9.00	2.18	1.00	3.38	12.00	0.00	6.65
<i>Gypohierax</i>	1	3.17	1.78	2.18	1.63	1.30	0.92	0.00	1.00	1.30	5.40	0.00	3.00	2.02	1.00	2.02	1.64	1.95	0.75	2.25	2.50	0.75	2.00	2.83	5.00	2.70	-7.00	1.00	6.90
<i>Gyps</i>	7	3.87	2.01	2.38	1.82	1.47	0.97	0.00	1.00	0.01	4.08	-0.45	2.00	2.32	1.07	2.36	1.72	2.11	0.53	12.00	2.14	0.00	7.86	2.57	4.14	3.08	12.00	0.43	6.52
<i>Haliaeetus</i>	8	3.57	1.90	2.30	1.76	1.44	0.81	0.00	1.13	0.61	3.76	0.03	3.25	2.07	2.06	2.38	1.60	1.88	0.80	7.94	1.72	2.13	4.44	2.58	3.63	2.90	17.63	1.25	6.27
<i>Haliaeetus</i>	2	2.78	1.71	2.10	1.60	1.36	0.83	0.00	1.00	0.94	5.40	0.00	3.00	1.67	2.10	2.00	1.55	1.71	1.10	8.75	0.00	1.25	4.25	2.67	5.00	2.90	-11.00	0.50	6.80
<i>Hamirostra</i>	1	3.11	1.75	2.18	1.66	1.32	0.94	0.00	1.00	1.18	3.40	1.00	3.00	1.84	1.80	2.10	1.58	1.78	1.10	8.25	0.00	2.00	8.00	2.40	4.00	2.40	-24.00	1.00	6.70
<i>Harpagus</i>	2	2.30	1.54	1.82	1.33	1.18	0.88	0.50	1.00	0.93	4.40	0.00	1.00	1.43	2.00	1.74	1.64	1.47	0.65	2.75	1.50	1.38	1.00	2.85	1.00	2.65	-6.50	0.00	6.83
<i>Harpia</i>	1	3.80	1.99	2.30	1.77	1.60	0.83	0.00	1.00	-0.10	4.40	0.00	1.50	2.12	2.00	2.43	1.75	2.15	0.25	10.75	1.75	3.00	1.00	2.86	1.00	2.60	-4.00	0.00	7.08
<i>Harpohaliaeetus</i>	2	3.47	1.87	2.24	1.72	1.43	0.83	1.00	1.00	-0.30	3.05	0.00	2.00	2.10	1.00	2.10	1.63	1.89	0.40	7.55	1.75	2.13	2.00	2.80	2.00	3.01	-8.50	0.00	6.25
<i>Harpypopsis</i>	1	3.30	1.92	2.20	1.64	1.60	0.64	0.00	1.00	-0.15	3.40	0.00	1.50	2.14	1.25	2.23	1.65	1.94	0.62	10.75	1.50	3.00	1.00	2.86	3.00	3.18	-6.00	0.00	5.87
<i>Hemicopernis</i>	2	2.77	1.72	2.07	1.56	1.47	0.90	0.00	1.00	0.00	3.55	0.00	2.00	1.74	2.15	2.07	1.56	1.70	0.88	4.00	1.50	1.38	1.00	2.85	1.00	3.00	-5.00	0.00	5.23
<i>Heterospizias</i>	1	2.98	1.72	2.12	1.61	1.32	0.86	0.00	1.00	1.30	5.40	0.00	2.00	1.84	1.00	1.84	1.59	1.68	0.70	7.00	0.00	1.75	7.00	2.81	5.00	2.70	-13.00	1.00	7.10
<i>Hieraaetus</i>	7	3.05	1.75	2.12	1.62	1.35	0.80	0.67	1.50	0.47	4.19	0.00	3.50	1.87	1.61	2.08	1.61	1.80	0.72	8.89	1.71	2.79	3.50	2.67	3.17	2.90	6.67	0.75	6.74
<i>Ichthyophaga</i>	2	3.17	1.80	2.15	1.63	1.37	0.75	0.00	1.00	0.48	3.75	0.00	2.00	1.94	2.13	2.27	1.46	1.85	1.04	7.00	2.25	2.00	3.50	2.81	2.50	2.63	15.00	0.00	6.50
<i>Kaupifalco</i>	1	2.52	1.54	1.90	1.35	1.16	0.76	0.00	1.50	1.10	5.70	0.00	1.00	1.46	2.00	1.76	1.53	1.60	0.91	4.10	1.75	1.25	3.00	2.80	2.00	2.70	-7.00	0.00	7.15
<i>Leptodon</i>	2	2.73	1.70	2.00	1.51	1.37	0.94	0.00	2.00	0.18	3.70	0.00	2.00	1.72	2.50	2.12	1.55	1.68	1.17	4.00	1.00	1.50	1.00	2.87	1.00	2.44	-7.00	0.00	5.54
<i>Leucopernis</i>	10	2.75	1.64	1.97	1.46	1.25	0.83	0.00	1.30	1.04	3.71	0.00	2.00	1.71	1.00	1.71	1.54	1.94	0.70	5.48	1.65	1.55	1.00	2.85	1.50	2.79	-3.35	0.00	5.65
<i>Lophaeetus</i>	1	3.11	1.75	2.08	1.58	1.34	0.81	0.00	1.00	0.40	4.54	0.00	3.00	1.84	1.50	2.01	1.62	1.74	0.85	6.50	1.00	2.00	3.00	2.80	3.00	2.70	-8.00	0.00	7.11
<i>Lophoctinia</i>	1	2.77	1.72	2.14	1.67	1.42	0.89	0.00	1.00	0.18	3.40	0.00	3.00	1.63	2.50	2.03	1.60	1.79	1.30	6.90	1.50	2.00	3.00	2.48	4.00	2.70	-25.00	1.00	6.40
<i>Macheiramphus</i>	1	2.80	1.65	2.03	1.59	1.23	0.83	0.00	1.00	-0.10	4.40	0.00	4.00	1.82	1.20	1.90	1.68	1.83	0.80	7.50	2.50	2.50	1.50	2.83	3.00	2.70	-8.00	0.00	7.00
<i>Megatriorchis</i>	1	2.93	1.78	1.99	1.50	1.45	0.65	0.00	1.00	0.30	3.40	0.00	2.00	1.85	1.50	2.02	1.64	1.74	1.00	7.25	1.50	2.00	1.00	2.88	2.00	2.92	-5.00	0.00	5.60
<i>Mellierax</i>	3	2.87	1.68	2.02	1.52	1.36	0.85	0.33	1.00	1.40	5.60	0.23	3.00	1.71	1.58	1.91	1.53	1.67	0.77	6.27	1.50	1.75	4.83	2.64	2.00	2.88	-7.00	0.00	6.51

Appendix 1. (Continued)

Genus	SR	BW	BS	WS	WL	TL	SD	SPD	PP	PD	PS	B/S	DB	EV	CS	CV	IT	FT	RR	P/S	P/Sp	HM	HP	HPr	NB	BA	BL	M	RS
<i>Micronisus</i>	1	2.23	1.51	1.78	1.29	1.23	0.84	0.00	2.00	0.78	5.70	0.00	2.50	1.29	2.25	1.64	1.53	1.51	1.20	7.25	1.75	2.00	7.00	2.70	3.00	2.70	-8.00	0.00	7.11
<i>Milvus</i>	3	2.94	1.79	2.20	1.68	1.49	0.90	0.00	1.00	0.57	5.03	-0.13	2.50	1.73	2.38	2.11	1.50	1.70	0.98	8.88	0.00	1.38	5.00	2.49	6.00	2.70	30.50	2.00	7.00
<i>Morphnus</i>	1	3.24	1.89	2.16	1.65	1.59	0.88	0.00	3.00	0.40	3.30	0.00	1.50	2.03	1.75	2.27	1.65	1.95	0.86	7.40	1.00	2.50	1.00	2.86	1.00	2.48	-5.00	0.00	7.08
<i>Necrosyrtes</i>	1	3.31	1.84	2.25	1.68	1.35	0.95	0.00	1.00	0.30	5.40	0.00	2.50	2.08	1.00	2.08	1.71	2.04	0.38	9.50	1.25	0.50	7.00	2.60	4.00	2.70	-4.00	0.00	7.10
<i>Neophron</i>	1	3.28	1.81	2.21	1.70	1.39	0.98	0.00	1.00	-0.10	4.54	0.68	3.00	1.93	1.75	2.17	1.62	1.89	0.95	11.00	0.00	0.25	10.00	2.40	4.00	3.30	22.00	2.00	6.90
<i>Oraoetus</i>	1	3.29	1.85	2.24	1.70	1.48	0.79	0.00	1.00	0.40	2.54	0.00	3.50	1.98	1.00	1.98	1.65	1.88	0.50	9.75	1.75	3.00	1.00	2.83	2.00	3.34	-7.00	0.00	5.78
<i>Parabuteo</i>	1	2.92	1.72	2.03	1.51	1.36	0.87	0.00	1.00	1.30	4.54	0.90	3.00	1.68	3.00	2.16	1.54	1.60	1.20	10.50	0.75	2.00	8.00	2.78	4.00	3.00	-4.00	0.00	7.02
<i>Pernis</i>	3	2.97	1.75	2.12	1.61	1.41	0.89	0.67	2.33	0.00	5.11	0.00	3.33	1.67	2.00	1.97	1.51	1.61	0.60	3.25	2.25	1.25	1.33	2.63	3.33	2.80	28.33	2.00	6.56
<i>Pitheophaga</i>	1	3.80	1.98	2.30	1.77	1.64	0.90	0.00	1.00	-0.10	2.30	0.00	2.00	2.19	1.00	2.19	1.78	2.22	0.38	10.75	1.50	3.00	1.00	2.88	1.00	3.00	12.00	0.00	5.16
<i>Polemaetus</i>	1	3.66	1.91	2.33	1.79	1.47	0.76	0.00	1.00	0.00	4.40	0.00	2.50	2.21	1.10	2.26	1.69	1.99	0.40	10.00	1.75	3.00	7.00	2.65	5.00	2.70	-8.00	0.00	7.18
<i>Polyboroides</i>	2	2.88	1.82	2.11	1.63	1.48	0.88	0.00	1.00	0.78	4.47	0.00	3.00	1.69	2.00	1.99	1.57	1.70	0.90	5.18	1.63	1.50	2.00	2.71	6.00	2.88	-13.50	0.50	6.52
<i>Sarcogyps</i>	1	3.65	1.90	2.35	1.78	1.39	0.98	1.00	1.00	0.00	3.40	0.00	4.00	2.28	1.00	2.28	1.65	1.92	0.50	12.00	2.00	0.00	7.00	2.76	5.00	3.00	21.00	0.00	6.40
<i>Spilornis</i>	13	2.95	1.74	2.09	1.60	1.40	0.87	0.00	1.13	0.54	3.84	0.00	3.00	1.96	1.00	1.96	1.54	1.78	0.75	7.31	1.75	2.19	1.63	2.81	3.25	2.79	10.50	0.00	5.04
<i>Spizaetus</i>	10	3.10	1.79	2.08	1.57	1.43	0.81	0.20	1.15	0.57	3.70	0.00	3.40	2.00	1.17	1.75	1.65	1.83	0.63	9.36	1.68	2.58	1.00	2.84	1.60	2.92	3.10	0.10	6.00
<i>Spizastur</i>	1	2.93	1.75	2.09	1.59	1.38	0.70	0.00	1.00	0.54	4.30	0.00	3.00	1.86	1.50	2.03	1.57	1.74	0.74	8.10	1.25	2.75	2.00	2.85	4.00	2.70	-3.00	0.00	6.85
<i>Stephanoaetus</i>	1	3.54	1.95	2.26	1.69	1.54	0.76	2.00	1.00	0.30	3.70	0.00	4.00	2.03	1.75	2.27	1.70	2.01	0.40	9.75	2.00	3.00	1.50	2.83	3.00	2.70	-8.00	0.00	6.78
<i>Terathopius</i>	1	3.38	1.78	2.27	1.73	1.04	0.83	2.00	1.50	0.20	4.70	0.00	3.50	2.20	1.00	2.20	1.74	2.00	0.80	6.75	1.00	1.75	7.00	2.70	2.00	2.88	-4.00	0.00	7.08
<i>Torgos</i>	1	3.83	2.06	2.45	1.89	1.55	0.92	0.00	1.00	0.36	3.54	0.00	1.00	2.35	1.25	2.45	1.74	2.11	0.46	11.25	2.00	0.50	8.00	2.40	4.00	3.15	0.00	0.00	6.94
<i>Trigonoceps</i>	1	3.63	1.93	2.36	1.80	1.45	0.93	2.00	1.00	0.08	4.10	0.00	2.00	2.29	1.00	2.29	1.74	2.07	0.30	11.25	2.00	0.50	7.00	2.44	2.00	2.88	-6.00	0.00	6.78
<i>Urotriorchis</i>	1	2.78	1.83	1.94	1.47	1.53	0.84	0.00	1.00	0.70	4.40	0.00	2.00	1.96	2.50	2.36	1.61	1.84	1.22	10.50	1.75	2.50	1.00	2.88	1.00	2.40	1.00	0.00	6.30

Appendix 2. Phylogenetic hypothesis used in the study.

