

Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors

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Genetically based variation in coloration occurs in populations of many organisms belonging to various taxa, including birds, mammals, frogs, molluscs, insects and plants. Colour polymorphism has evolved in raptors more often than in any other group of birds, suggesting that predator–prey relationships was a driving evolutionary force. Individuals displaying a new invading colour morph may enjoy an initial foraging advantage because prey have difficulties in learning the colour of a rare morph (apostatic selection), or because morphs provide alternative foraging benefits allowing differently coloured individuals to exploit distinct food niches (disruptive selection). Plumage polymorphism should therefore have evolved in species that prey upon animals having the physiological ability to distinguish between differently coloured predators but also to flee once a predator has been detected. From this assumption, we can predict that closely related polymorphic and monomorphic species prey upon different animals. They may also differ in morphology, because foraging upon different prey may require different foraging modes, and in turn different morphological structures. We tested these two predictions in a comparative study of raptors. As expected, polymorphic and monomorphic species had a different diet, and there was a difference in wing length between polymorphic and monomorphic species within two genera (*Buteo* and *Accipiter*). Across all raptors for which phylogenetic relationships are known, polymorphic species preyed more often upon mammals than did monomorphic ones. These two types of raptor did not differ in the frequency of birds, insects and reptiles in their diets. We discuss these results in the light of the hypothesis that predator–prey relationships played a role in the evolution of colour polymorphism. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 81, 565–578.

ADDITIONAL KEYWORDS: alternative strategies – apostatic selection – colour morph – disruptive selection – genetic polymorphism.

INTRODUCTION

Individuals of the same animal or plant population can adopt different sets of strategies that are under genetic control and maintained by frequency-dependent selection (Gross, 1996; Sinervo & Lively, 1996). For example, alternative mating strategies have evolved in the ruff (*Philomachus pugnax*) with some males being territorial and others satellites (Lank *et al.*, 1995). Interestingly, alternative mating (Lank *et al.*, 1995; Forsman, 1999), behavioural (Caldow &

Furness, 1991; Ficken, Ficken & Hailman, 1978), reproductive (Furness, 1987; Johnston & Janiga, 1995; Roulin *et al.*, 2001a) and physiological strategies (Mosher & Henny, 1976; Hoffman & Blouin, 2000; Roulin *et al.*, 2000, 2001a, b) are often signalled with a colour trait. Such a trait is denoted ‘genetic colour polymorphism’ when within a population individuals of the same age and sex display one of several colour variants that are genetically inherited but neither sensitive to the environment nor condition-dependent in their expression. Although colour polymorphism is found in many animals and plants, comparative analyses to explain why some species evolved towards polymorphism whereas others retained a monomorphic colour state are virtually lacking.

To our knowledge, the first attempt to compare life-history characteristics of closely related monomorphic

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and polymorphic species was made in diurnal raptors (Paulson, 1973; Rohwer & Paulson, 1987). The authors proposed that raptors preying upon mammals and birds are more likely to evolve towards a polymorphic plumage state. Such a role for predator–prey relationships in the evolution of genetic colour polymorphism can be explained by two mutually non-exclusive hypotheses. Under the apostatic selection hypothesis, a new colour morph can invade a population because individuals have a foraging benefit of being rare (Allen, 1988; Bond & Kamil, 1998). In predators that frequently fail to catch their prey, experienced prey will rapidly learn to avoid predators displaying the same common morph. In contrast, they should have more difficulty in learning the colour morph of unsuccessful attackers displaying a rare morph, since the number of previous contacts is lower. A low number of morphs may therefore invade a population because predators will derive a foraging benefit only if they differ strongly in appearance from the common morph (Rohwer & Paulson, 1987). Under the alternative foraging strategy hypothesis, it is argued that differently coloured individuals exploit distinct food niches, and hence that colour morphs are under disruptive selection (Furness, 1987; Skúlason & Smith, 1995; Bolnick *et al.*, 2003). Colour morphs may confer distinct foraging advantages if prey species vary in their ability to detect and escape differently coloured predators. The display of a given morph may confer an advantage in preying upon a given species, whereas another morph may be beneficial in preying upon another species (Skúlason & Smith, 1995). The reason may be that alternative prey do not have the same genetic background to detect and escape differently coloured predators or, alternatively, do not live in the same environment with one morph being more cryptic in one habitat and the other one in another (Greco & Kevan, 1999). For example, in a Swiss population of barn owls (*Tyto alba*) reddish-brown individuals were found to prey more often upon common voles (*Microtus arvalis*) and light coloured owls upon wood mice (*Apodemus* spp.) (Roulin, 2004).

Using a comparative approach, we tested the hypothesis that predator–prey relationships play a role in the evolution of plumage polymorphism in raptors, as has been shown in two species of predatory spider (Greco & Kevan, 1999; Tso *et al.*, 2002). This mechanism is similar to the apostatic selection hypothesis (Allen, 1988) invoked to explain the evolution of colour polymorphism in snakes (Andrén & Nilsson, 1981), frogs (Hoffman & Blouin, 2000), molluscs (Jones, Leith & Rawlings, 1977; Reid, 1987) and insects (Losey *et al.*, 1997; Bond & Kamil, 1998) in order to avoid being preyed upon. Here, our aim was to investigate whether polymorphic and monomorphic diurnal raptors prey upon different food categories.

More specifically, our goal was to test the following two predictions:

(A) As prey species displaying good visual acuity and escape ability may favour the evolution of genetic colour polymorphism in predators, we predicted that polymorphic raptors would prey more often upon mammals and birds than would monomorphic raptors. These animals that, in contrast to reptiles, are consumed by the majority of raptors, may have favoured the evolution of genetic colour polymorphism in their avian predators because they have keen vision and good locomotion, and because raptors frequently miss their prey.

(B) As a diet based on different animal species may require different foraging modes, and in turn different morphological structures, closely related monomorphic and polymorphic species could vary in morphological traits that are important for foraging activities. For example, if polymorphic raptors preyed more often upon small mammals, they might have longer wings compared with monomorphic ones preying more often upon insects. Longer wings give their bearer higher speed in the open and allow them to glide more, two properties that are important to catch mammals. Polymorphic and monomorphic raptors may also have a different wing shape because they live in different environments, thereby adopting different foraging strategies.

MATERIAL AND METHODS

DATA ON POLYMORPHISM

We gathered information on polymorphism from the book '*Raptors of the world*' (Ferguson-Lees & Christie, 2001). This book indicated whether in the same population one or several colour morphs occur, species that are defined as monomorphic and polymorphic, respectively. We considered as polymorphic species those in which adults displayed two or more colour morphs. In species for which phylogenetic relationships were known ($N = 117$), polymorphism was present in the two sexes. In *Accipiter collaris*, adults are monomorphic, and hence this species is considered as monomorphic even though juveniles can display one of two morphs.

Our study relied on the assumption that polymorphism has a genetic basis and the expression of different morphs is not the outcome of consuming alternative prey or living in different habitats (e.g. Roulin, Richner & Ducrest, 1998; Roulin & Dijkstra, 2003). Observational support for genetic inheritance of colour morphs exists in the Eleonora's falcon (*Falco eleonora*; Wink, Wink & Ristow, 1978), the ferruginous hawk (*Buteo regalis*; Schmutz & Schmutz, 1981) and the common buzzard (*B. buteo*; Krüger, Lindström & Amos, 2001). Because raptors display melanin-

based coloration (black, brown, reddish-brown and yellow), the expression of which is under genetic control and not sensitive to the environment (Hearing & Tsukamoto, 1991; Majerus, 1998), we could assume that the expression of different colour morphs has a strong genetic basis. We did not consider as a polymorphic species the bearded vulture (*Gypaetus barbatus*), which dyes its feathers.

DATA ON DIET

The relative importance of eight food categories of animals (live birds, mammals, reptiles, fishes, amphibians, crustaceans, insects and worms) and carrion in the diet of most raptors was reported in Ferguson-Lees & Christie (2001). We ranked each category from the most important (rank 1) to the least important (rank 9). When a food category was not reported, it was assigned rank 9. We restricted our analyses to the four most frequent food categories 'bird', 'mammal', 'reptile' and 'insect'; the five other categories occurred in a minority of raptors, and hence are unlikely to have played a crucial role in the evolution of plumage polymorphism. We were unable to analyse the relationship between diet and plumage state at a lower taxonomic level than the class of the prey because the data were not available to us. Raw data are given in Appendix 1.

DATA ON BODY SIZE, HABITAT, CLUTCH SIZE, POPULATION SIZE AND SPECIES RANGE

For the majority of species, Ferguson-Lees & Christie (2001) reported range in wing length, and we calculated the midpoint of these two values. When wing length was available in each sex, we calculated the mean value of male and female wing lengths. This mean value was used in the statistical analyses.

Because a comparative analysis results in a correlation and not a causal relationship, we tested whether other variables may have inflated the relationship between diet and plumage polymorphism. Variables included were clutch size, habitat (species living in forests or open country), world population size, and range of breeding land area (log transformed to obtain a normal distribution). These data were extracted from the book of Ferguson-Lees & Christie (2001), and are presented in Appendix 1.

DATA ON PHYLOGENY

We used a molecular-based raptor phylogeny published in Wink (2000) and Wink & Sauer-Gürth (2000). In the meantime, M. Wink analysed 14 other species and we added them to his previous phyloge-

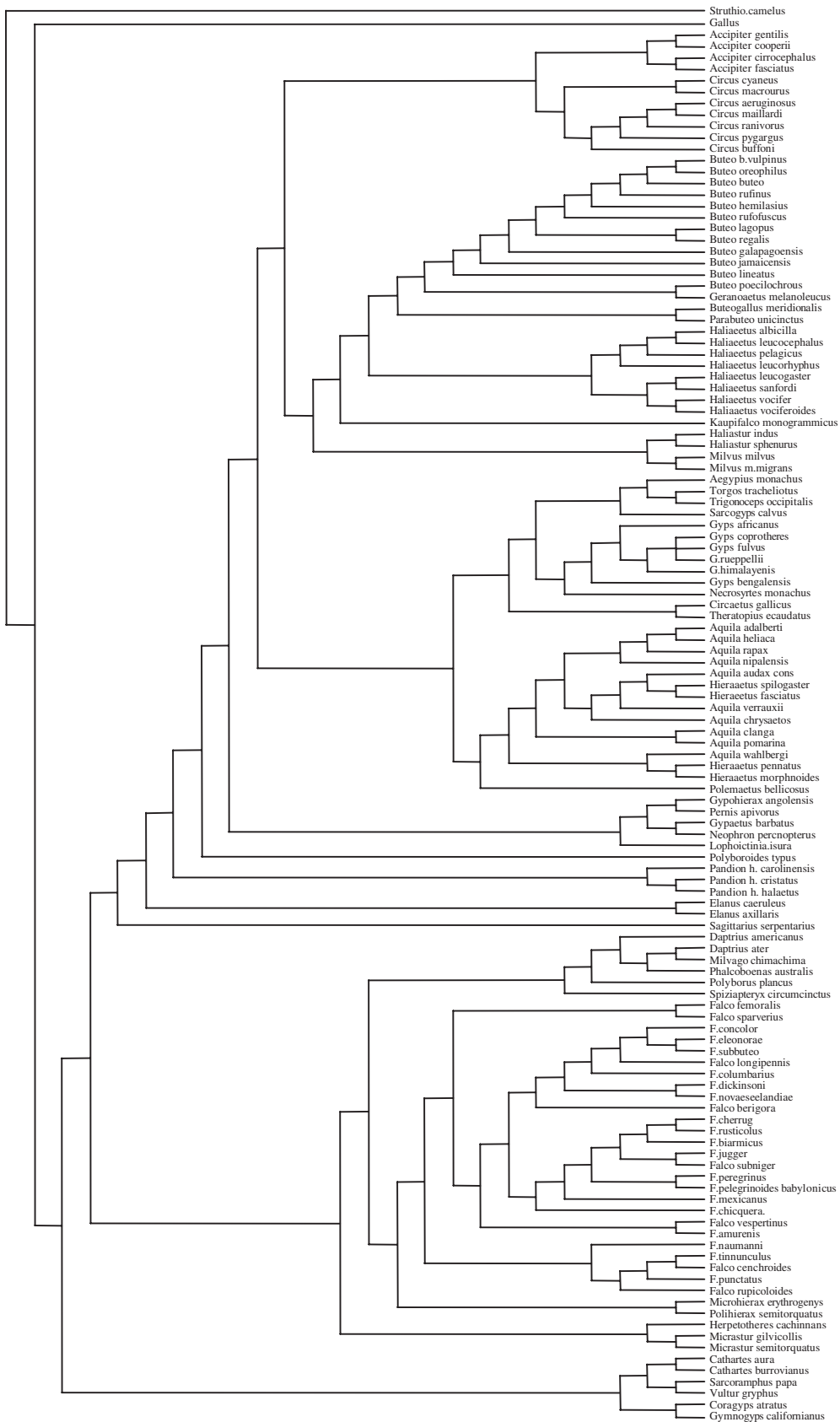
netic tree: *Accipiter cooperi*, *A. cirrhocephalus*, *A. fasciatus*, *Buteo rufofuscus*, *Haliaeetus spheurnus*, *Aquila audax*, *Hieraeetus morphnoides*, *Lophoictinia isura*, *Polyboroides typus*, *Elanus axillaris*, *Falco longipennis*, *F. subniger*, *F. berigora*, *F. cenchroides* (Fig. 1). Phylogenetic relationships among these species were determined using the same molecular methods as for previously analysed species (Wink, 2000; Wink & Sauer-Gürth, 2000).

COMPARATIVE ANALYSES

We performed two types of comparative analysis. First, we investigated whether diet and wing length differed between monomorphic and polymorphic species within the genera *Buteo* (buzzards) and *Accipiter* (hawks). We considered only these two genera because they were the only ones containing enough polymorphic species for reliable statistical analyses. Because phylogenetic relationships were known for a minority of species, we carried out Student's *t*-tests to compare diet categories and wing length.

Without controlling for phylogeny, any comparative studies are doubtful, because two polymorphic species may have the same diet and wing length not because polymorphism coevolved with these two characteristics but because these species share a common ancestry. Therefore, we had to show the transition from a monomorphic to a polymorphic plumage state to be concomitant with a change in diet or wing length. To control for phylogeny at all taxonomic levels, we performed a comparative analysis using the comparative analysis by independent contrasts (CAIC) technique, with the CAIC 2.0 program (Purvis & Rambaut, 1994). At each node in the phylogeny where the test variable varied (e.g. of two related species the polymorphic one eats mammals more often than the monomorphic one), the CAIC program calculated standardized linear contrasts indicating the extent to which closely related taxa differed with respect to diet or wing length. Each contrast can be considered as an independent evolutionary event.

As recommended by Purvis & Rambaut (1994), we transformed the variable 'wing length', but not the categorical diet variables, with the logarithmic function. The variables 'monomorphic' and 'polymorphic' were used as dichotomous variables. Across all standardized linear contrasts a mean (for normally distributed data sets using a paired *t*-test) or median value (for data not normally distributed using the Wilcoxon matched-pair signed-rank test) that was significantly greater than zero indicated that polymorphism coevolved with diet or wing length. Throughout this paper statistical analyses are two-tailed and *P*-values <0.05 considered as significant.



RESULTS

COEVOLUTION BETWEEN COLOUR POLYMORPHISM AND DIET

The food category ‘mammal’ had a significantly lower median rank in polymorphic than in monomorphic *Buteo* species indicating that polymorphic species consumed mammals more often than did monomorphic species (Table 1; raw data in Appendix 2). This relationship remained highly significant (ANOVA with rank as dependent variable and polymorphism as a factor: $F_{1,17} = 31.00$, $P < 0.001$) after controlling for several variables including clutch size (first covariate: $F_{1,17} = 0.14$, $P = 0.71$), wing length (second covariate: $F_{1,17} = 0.55$, $P = 0.47$), habitat (third covariate: $F_{1,17} = 0.17$, $P = 0.69$), population size (fourth covariate: $F_{1,17} = 0.004$, $P = 0.95$) and land area of breeding range (fifth covariate: $F_{1,17} = 1.29$, $P = 0.27$). Diet categories had similar median ranks in polymorphic and monomorphic *Accipiter* species suggesting that these two types of *Accipiter* do not differ in their diet, at least at the taxonomic level of class of prey (Table 1; raw data in Appendix 2).

The CAIC showed that polymorphic raptors consumed mammals more often than did monomorphic species (comparison of standardized linear contrasts of mammal rank in diet, with zero: Wilcoxon matched-pair signed-rank test: $z = 2.44$, $N = 19$, $P = 0.015$). We did not detect a difference in the frequency of consumption of birds (paired t -test: $t = 0.90$, d.f. = 18, $P = 0.38$), reptiles ($t = 0.45$, d.f. = 18, $P = 0.66$) and insects ($t = 1.35$, d.f. = 18, $P = 0.19$) between polymorphic and monomorphic predator species. Without controlling for phylogeny, the relationship between mammal consumption and plumage polymorphism remained highly significant (ANOVA with rank as dependent variable and polymorphism as a factor:

$F_{1,103} = 14.00$, $P = 0.0003$) after controlling for clutch size (first covariate: $F_{1,103} = 7.18$, $P = 0.009$), wing length (second covariate: $F_{1,103} = 0.37$, $P = 0.54$), habitat (third covariate: $F_{1,103} = 0.62$, $P = 0.43$), population size (fourth covariate: $F_{1,103} = 0.51$, $P = 0.48$) and land area of breeding range (fifth covariate: $F_{1,103} = 4.66$, $P = 0.03$).

COEVOLUTION BETWEEN COLOUR POLYMORPHISM AND WING LENGTH

In the genera *Buteo* and *Accipiter*, polymorphic species had significantly longer wings than did monomorphic species (Table 2). This might be explained by a greater propensity of longer-winged *Buteo* species to prey upon mammals (Pearson’s correlation between mammal rank in diet and wing length, *Buteo*: $r = -0.50$, $N = 27$, $P = 0.009$; *Accipiter*: $r = -0.13$, $N = 38$, $P = 0.43$). However, across all raptors for which phylogenetic relationships were known, wing length was not significantly different between monomorphic and polymorphic species (CAIC: $t = 0.79$, d.f. = 18, $P = 0.87$). This indicates that in genera other than *Buteo* and *Accipiter*, polymorphic species may not systematically have longer wings compared with monomorphic species.

DISCUSSION

Our study found that polymorphic raptors ate mammals more often than did monomorphic raptors, suggesting that the consumption of this food category favours the evolution or the maintenance of plumage polymorphism. This relationship remained significant after controlling for several variables including clutch size and habitat (forest vs. open country) potentially indicating that in raptors predator–prey relation-

Table 1. Relative importance (mean rank) of four prey categories in the diet of polymorphic and monomorphic *Buteo* and *Accipiter* species

Genus	Plumage state	Sample size (N)	Mammal		Bird		Reptile		Insect	
			Mean rank	P	Mean rank	P	Mean rank	P	Mean rank	P
<i>Buteo</i>	Polymorphic	16	1.13	<0.001	3.00	0.65	4.25	0.26	4.19	0.26
	Monomorphic	11	2.64		3.27		2.91		5.27	
<i>Accipiter</i>	Polymorphic	10	5.10	0.33	2.30	0.70	4.10	0.93	4.40	0.47
	Monomorphic	28	4.07		2.00		4.21		3.75	

P -values are from Student’s t -test.

Figure 1. The phylogeny of raptors used in the comparative analysis by independent contrasts. Reconstruction via maximum likelihood.

Table 2. Wing length of polymorphic and monomorphic *Buteo* and *Accipiter* species

Genus	Plumage state	Sample size	Wing length (mm)	
			(mean \pm SD)	<i>P</i>
Buteo	Polymorphic	16	396 \pm 62	0.003
	Monomorphic	12	314 \pm 69	
Accipiter	Polymorphic	11	244 \pm 43	0.03
	Monomorphic	36	209 \pm 46	

P-values are from Student's *t*-test.

ships was an important factor in the evolution and maintenance of genetic colour polymorphism (e.g. Skúlason & Smith, 1995). Paulson (1973) first proposed this relationship. However, he did not control for phylogeny in his analyses because the necessary data and statistical tools were not available at that time. For this reason, his results may have been pseudo-replicated, because Paulson's analyses implicitly assumed that the evolution of polymorphism in two closely related species is an independent evolutionary event. This methodological drawback may explain why Paulson's proposition that the consumption of birds also promoted the evolution of plumage polymorphism was not corroborated by our comparative analyses.

Following apostatic selection (Allen, 1988) and alternative foraging strategies (or disruptive selection; Furness, 1987; Skúlason & Smith, 1995; Bolnick *et al.*, 2003), plumage polymorphism can evolve in species that prey upon animals having the ability to learn the colour morph of unsuccessful attackers or to distinguish between differently coloured predators but also to flee once a predator has been detected. Mammals have keen vision and certainly better locomotion than do insects (humans are able to capture insects but not mammals by hand), so that the finding that polymorphic raptors consume mammals more often than do monomorphic raptors is consistent with the proposition that predator-prey relationships are important in the evolution and maintenance of colour polymorphism in predators. Even in the genus *Accipiter*, in which we did not detect any difference in diet between polymorphic and monomorphic species, this mechanism may nevertheless have played a role in the evolution of polymorphism. Indeed, polymorphic species had longer wings, suggesting that they adopt different foraging modes or live in different habitats compared with monomorphic species. Because most *Accipiter* species prey primarily upon birds, the difference in diet between polymorphic and monomorphic species should probably be analysed at a taxonomic level lower than class of the prey.

If it is not surprising that the consumption of insects does not covary with the presence or absence of polymorphism, it is less evident why the consumption of birds also did not covary. Birds have very good vision (Jacobs, 1992), memory capacity (Clayton & Lee, 1998) and ability to rapidly flee once disturbed. A possible explanation accounting for the suggestion that the food category 'mammal' rather than 'bird' played a role in the evolution or maintenance of polymorphism is that birds are attacked mainly by surprise. Therefore, they may not have enough time to recognize the colour morph of the attacker. In contrast, raptors often capture mammals by flying in the open above the ground or by sitting on a perch and waiting for passing prey. In such situations, mammals may have more time to discriminate between differently coloured individuals and escape once the predator has been recognized.

If predator-prey relationships played a role in the evolution and maintenance of colour polymorphism in raptors, the challenge in the future is to assess the relative importance of the apostatic and alternative foraging strategies. Because experiments may be extremely difficult to undertake in raptors, detailed within-species observations are required. In particular, data are needed on whether within-species diet and foraging success on alternative prey species differs between morphs. For example, in spiders and barn owls different morphs show alternative foraging strategies (Greco & Kevan, 1999; Roulin, 2004).

Predator-prey relationships may have driven or reinforced the evolution and maintenance of a number of, but certainly not all, plumage colour polymorphisms in raptorial birds. Our phylogenetic analyses showed that diet was significantly different between polymorphic and monomorphic closely related species, but there is still variation that needs to be explained. For example, in the barn owl the number and size of black spots displayed on the plumage of females, a trait that is heritable and not sensitive to the environment (Roulin *et al.*, 1998; Roulin & Dijkstra, 2003), signals offspring quality (Roulin *et al.*, 2000, 2001b, 2003). Covariation between female plumage spottiness and quality is independent of diet, and hence the functional value of genetic colour polymorphism can be diverse. More phylogenetic analyses need to be performed to understand the full range of selective pressures that promote the evolution of genetically inherited variation in colour patterns.

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APPENDIX 1

Polymorphism, habitat (species are living mainly in forest or open country), wing length, diet, clutch size, world population size, and range of breeding land area (km²) among raptors. Data from Fergusson & Christie (2001).

Species	Polymorphism*	Habitat	Wing length (mm)	Diet (rank)					Clutch size	Population size	Range (km ²)
				Mammal	Bird	Reptile	Insect				
<i>Accipiter gentilis</i>	No	Forest	341	2	1	3	4		3.5	6.5	30 000 000
<i>Accipiter cooperii</i>	No	Forest	244	2	1	3	5		4.5	6	8 000 000
<i>Accipiter cirrocephalus</i>	No	Forest	225	4	1	3	2		3.5	5.25	6 000 000
<i>Accipiter fasciatus</i>	No	Forest	278	1	2	3	5		3	6	6 500 000
<i>Circus cyaneus</i>	No	Open	359	2	1	4	6		5	6	15 000 000
<i>Circus aeruginosus</i>	Yes	Open	405	1	2	3	7		4.5	6	-
<i>Circus maillardi</i>	No	Open	365	3	4	2	5		4.5	4	594 000
<i>Circus ranivorus</i>	No	Open	367	1	2	6	4		3.5	4.25	2 500 000
<i>Circus pygargus</i>	Yes	Open	370	1	2	4	3		4.5	5.75	9 000 000
<i>Circus buffoni</i>	Yes	Open	422	2	3	4	9		3.5	5	7 500 000
<i>Circus macrourus</i>	No	Open	351	1	2	4	3		4.5	5	4 250 000
<i>Buteo buteo</i>	Yes	Forest	394	1	2	3	5		3	7	22 000 000
<i>Buteo oreophilus</i>	No	Forest	342	1	4	2	3		2	4.25	800 000
<i>Buteo rufofuscus</i>	Yes	Open	428	1	3	2	4		2	5.25	1 600 000
<i>Buteo hemilasius</i>	Yes	Open	476	1	2	9	4		3.5	5.25	5 000 000
<i>Buteo lagopus</i>	Yes	Open	435	1	2	9	5		4	6	2 000 000
<i>Buteo regalis</i>	Yes	Open	435	1	2	3	5		3.5	4.5	2 400 000
<i>Buteo rufinus</i>	Yes	Open	452	1	3	2	4		3.5	6	3 000 000
<i>Buteo galapagoensis</i>	No	Open	401	4	3	2	1		2.5	3	7 845
<i>Buteo jamaicensis</i>	Yes	Forest	383	1	2	3	7		2.5	6.25	12 000 000
<i>Buteo lineatus</i>	No	Forest	331	3	5	1	4		3.5	5.25	4 000 000
<i>Buteo poecilochrous</i>	Yes	Open	456	1	3	9	2		2	4.5	750 000
<i>Gerandactes melanoleucus</i>	No	Open	542	1	2	3	5		2	5	2 000 000
<i>Parabuteo unicinctus</i>	No	Open	327	1	2	3	4		2	5.25	10 500 000
<i>Buteogallus meridionalis</i>	No	Open	409	1	7	2	4		1	6	12 000 000
<i>Haliaeetus albicilla</i>	No	Open	648	4	3	9	9		2	5	15 000 000
<i>Haliaeetus leucocephalus</i>	No	Open	618	4	3	5	6		2.5	6	10 000 000
<i>Haliaeetus pelagicus</i>	No	Open	598	4	3	9	9		2	4	1 300 000
<i>Haliaeetus leucorhynchus</i>	No	Open	578	3	2	5	9		2.5	4	1 000 000

APPENDIX 1 Continued

Species	Polymorphism*	Habitat	Wing length (mm)	Diet (rank)					Clutch size	Population size	Range (km ²)
				Mammal	Bird	Reptile	Insect				
<i>Haliaeetus leucogaster</i>	No	Open	582	4	3	1	9	2	4.75	10 000 000	
<i>Haliaeetus sanfordi</i>	No	Forest	544	3	4	9	9	—	3	40 000	
<i>Haliaeetus vocifer</i>	No	Open	532	3	2	4	6	2	6	10 000 000	
<i>Haliaeetus vociferoides</i>	No	Open	505	9	9	9	9	2	2.75	120 000	
<i>Haliastur indus</i>	No	Open	384	5	6	4	8	2	6	11 000 000	
<i>Haliastur sphenurus</i>	No	Open	416	1	2	3	6	2.5	6	8 000 000	
<i>Milvus milvus</i>	No	Open	498	2	3	4	6	2	5.25	6 500 000	
<i>Milvus migrans</i>	No	Open	451	2	3	4	7	2.5	7.25	67 500 000	
<i>Kaupifalco monogrammicus</i>	No	Forest	223	3	5	2	1	2	6.25	10 000 000	
<i>Aquila heliaca</i>	No	Open	597	1	2	3	5	2.5	4	6 500 000	
<i>Aquila rapax</i>	Yes	Open	525	1	2	3	4	2	6	15 000 000	
<i>Aquila nipalensis</i>	No	Open	593	1	2	3	4	2	6	8 000 000	
<i>Aquila audax</i>	No	Open	631	1	4	3	9	1.5	6	7 000 000	
<i>Aquila verreauxii</i>	No	Open	598	1	2	4	9	2	5	4 000 000	
<i>Aquila chrysaetos</i>	No	Open	640	1	2	3	6	2	6	27 000 000	
<i>Aquila clanga</i>	Yes	Forest	511	1	2	4	6	2	4.25	8 000 000	
<i>Aquila pomarina</i>	No	Forest	475	1	4	3	5	2	5.5	4 000 000	
<i>Hieraetus fasciatus</i>	No	Open	510	2	1	3	4	2	5	7 000 000	
<i>Hieraetus wahlbergi</i>	Yes	Forest	429	2	3	1	5	1	6	10 000 000	
<i>Hieraetus pennatus</i>	Yes	Forest	387	3	1	2	4	2	5	5 000 000	
<i>Hieraetus morphnoides</i>	Yes	Forest	377	1	2	3	5	1.5	5	7 000 000	
<i>Polemaetus bellicosus</i>	No	Open	613	1	2	3	9	1	5	15 000 000	
<i>Aegyptius monachus</i>	No	Open	797	—	—	—	—	1	4.75	7 000 000	
<i>Torgos tracheliotus</i>	No	Open	773	2	3	4	9	1	4.25	8 000 000	
<i>Sarcogyps calvus</i>	No	Open	598	9	9	9	9	1	4	5 000 000	
<i>Trigonoceps occipitalis</i>	No	Open	635	4	2	7	3	1	4.5	8 000 000	
<i>Gyps africanus</i>	No	Open	595	9	9	9	9	1	6	10 000 000	
<i>Gyps coprotheres</i>	No	Open	676	9	9	9	9	1	4.25	1 400 000	
<i>Gyps fulvus</i>	No	Open	734	9	9	9	9	1	6	—	
<i>Gyps rueppellii</i>	No	Open	690	9	9	9	9	1	5	1 000 000	
<i>Gyps himalayensis</i>	No	Open	783	9	9	9	9	1	6	2 750 000	

<i>Gyps bengalensis</i>	No	Open	572	9	9	9	9	9	9	1	4	6 000 000
<i>Coragyps atratus</i>	No	Open	430	7	3	4	6	6	7	2	7	22 000 000
<i>Gymnogyps californianus</i>	No	Open	838	9	9	9	9	9	2	1	2	130 000
<i>Neocorys monachus</i>	No	Open	480	9	9	9	2	2	1	1	6	10 000 000
<i>Circaetus gallicus</i>	No	Open	552	2	4	1	5	5	1	1	5	—
<i>Terathopus ecaudatus</i>	Yes	Open	531	1	2	3	5	5	1	1	5.25	12 000 000
<i>Gypohierax angolensis</i>	No	Forest	427	5	6	7	4	4	1	1	6	8 000 000
<i>Pernis apivorus</i>	Yes	Forest	408	5	6	3	1	1	2	2	6.75	10 000 000
<i>Gypaetus barbatus</i>	No	Open	809	3	4	9	9	9	2	2	5	5 000 000
<i>Neophron percnopterus</i>	No	Open	503	9	9	9	2	2	2	2	5.25	—
<i>Lophocitina isura</i>	No	Forest	471	5	2	4	1	1	2.5	4	4	2 500 000
<i>Polyboroides typus</i>	Yes	Forest	462	2	3	1	4	4	1.5	6	6	10 000 000
<i>Elanus caeruleus</i>	No	Open	274	1	2	4	3	3	3.5	7	7	22 500 000
<i>Elanus axillaris</i>	No	Open	295	1	4	3	2	2	3.5	6	6	150 000
<i>Pandion haliaetus</i>	No	Open	483	3	4	5	9	9	2.5	5	5	25 000 000
<i>Sagittarius serpentarius</i>	No	Open	644	2	4	3	1	1	2	5	5	15 000 000
<i>Daptrius americanus</i>	No	Forest	372	9	9	9	1	1	2.5	6	6	8 500 000
<i>Daptrius ater</i>	No	Forest	310	9	2	3	5	5	2.5	5	5	6 500 000
<i>Milvago chimachima</i>	No	Open	290	6	5	9	2	2	2	2	6.25	12 000 000
<i>Phalcoboenus australis</i>	No	Open	408	3	2	9	9	9	2.5	2.5	4.25	18 000
<i>Polyborus plancus</i>	No	Open	406	3	2	4	4	7	2.5	6	6	8 500 000
<i>Spizapteryx circumcinctus</i>	No	Open	165	3	4	2	1	1	3	3	4.25	900 000
<i>Falco femoralis</i>	No	Open	252	3	1	4	2	2	2.5	2.5	5.5	12 000 000
<i>Falco sparverius</i>	Yes	Open	191	2	4	3	1	1	5	7	7	33 000 000
<i>Falco peregrinus</i>	No	Open	334	2	1	4	9	9	3.5	5	5	54 000 000
<i>Falco pelegrinoides</i>	No	Open	290	2	1	9	9	9	3	4	4	3 000 000
<i>Falco cherrug</i>	No	Open	377	1	2	3	4	4	4	5	5	9 000 000
<i>Falco rusticolus</i>	Yes	Open	386	2	1	9	9	9	3.5	4.75	4.75	16 500 000
<i>Falco biarmicus</i>	No	Open	335	2	1	4	3	3	3.5	6.25	6.25	13 000 000
<i>Falco jugger</i>	No	Open	333	3	1	2	4	4	3.5	4.75	4.75	4 200 000
<i>Falco subniger</i>	Yes	Open	383	2	1	3	4	4	3.5	4.25	4.25	2 000 000
<i>Falco mexicanus</i>	No	Open	326	1	2	3	4	4	4	4.75	4.75	3 600 000
<i>Falco chicquera</i>	No	Open	212	2	1	3	4	4	3.5	5	5	11 500 000
<i>Falco berigora</i>	Yes	Open	345	1	4	3	2	2	2.5	6.25	6.25	8 000 000
<i>Falco concolor</i>	No	Open	279	3	2	4	1	1	2.5	5.25	5.25	5 000 000
<i>Falco eleonorae</i>	Yes	Open	328	3	2	4	4	4	2.5	5	5	700 000
<i>Falco subbuteo</i>	No	Forest	263	3	2	4	1	1	3	6	6	27 500 000

APPENDIX 1 Continued

Species	Polymorphism*	Habitat	Wing length (mm)	Diet (rank)					Clutch size	Population size	Range (km ²)
				Mammal	Bird	Reptile	Insect				
<i>Falco longipennis</i>	No	Forest	251	3	1	9	2		3	4.75	6 000 000
<i>Falco columbarius</i>	No	Open	198	3	1	4	2		4.5	6.25	20 000 000
<i>Falco novaeseelandiae</i>	No	Forest	262	2	1	3	4		3	4.75	111 500
<i>Falco dickinsoni</i>	No	Open	225	4	5	2	1		3	5	3 400 000
<i>Falco naumanni</i>	No	Open	239	3	4	2	1		4	5	5 000 000
<i>Falco tinnunculus</i>	No	Open	249	1	2	3	4		4.5	7	16 000 000
<i>Falco cenchroides</i>	No	Open	254	2	1	4	3		4	6.25	7 500 000
<i>Falco punctatus</i>	No	Forest	178	4	3	1	2		3	3	1 640
<i>Falco rupicoloides</i>	No	Open	277	4	3	2	1		3.5	5.75	3 500 000
<i>Falco verpertinus</i>	No	Open	244	2	3	5	1		3.5	6.25	8 000 000
<i>Falco amurensis</i>	No	Forest	230	9	2	9	1		3.5	6	3 800 000
<i>Microhierax erythrogenys</i>	No	Forest	113	9	9	2	1		3.5	4	200 000
<i>Polihierax semitorquatus</i>	No	Open	115	3	4	2	1		3	5.25	2 500 000
<i>Herpethotes cachinnans</i>	No	Forest	280	2	4	1	9		1	5.25	10 000 000
<i>Micrastur gilvicollis</i>	No	Forest	186	9	3	1	2		-	6.5	4 000 000
<i>Micrastur semitorquatus</i>	Yes	Forest	257	1	2	3	5		2.5	6	12 000 000
<i>Cathartes aura</i>	No	Open	498	9	4	9	2		2	7	33 000 000
<i>Sarcoramphus burrovianus</i>	No	Open	448	9	9	9	2		2	6	12 000 000
<i>Sarcoramphus papa</i>	No	Forest	499	9	9	2	9		1	5	12 000 000
<i>Vultur gryphus</i>	No	Open	803	9	9	9	9		1	4.5	5 950 000

*'Yes' is for polymorphic species and 'No' for monomorphic species. Food categories are ranked in order of importance in the diet (most important category = rank 1; least important = rank 9). If a food category was not reported as belonging to the diet of a given species, it was assigned rank 9. World population size is given in the range 1-7 (1 is 1-10 birds, 2 is 11-100 birds, 3 is 101-1000 birds, 4 is 1001-10 000 birds, 5 is 10 001-100 000 birds, 6 is 100 001-1 000 000 birds, 7 is over 1 million birds).

APPENDIX 2

Polymorphism, wing length (mm) and diet among *Buteo* and *Accipiter* species. Data are from Fergusson & Christie (2001)

Species	Polymorphism*	Wing length (mm)	Diet (rank)			
			Mammal	Bird	Reptile	Insect
<i>Buteo albigula</i>	No	295	1	2	9	9
<i>B. albonotatus</i>	No	400	2	1	3	9
<i>B. auguralis</i>	No	355	3	4	1	6
<i>B. brachypterus</i>	No	316	3	4	2	7
<i>B. exsul</i>	No	400	1	2	9	9
<i>B. galapagoensis</i>	No	401	4	3	2	1
<i>B. leucorrhous</i>	No	228	–	–	–	–
<i>B. lineatus</i>	No	331	3	5	1	4
<i>B. magnirostris</i>	No	222	4	6	1	2
<i>B. nitidus</i>	No	248	5	2	1	3
<i>B. oreophilus</i>	No	342	1	4	2	3
<i>B. ridgwayi</i>	No	234	2	3	1	5
<i>B. albicaudatus</i>	Yes	434	2	7	3	1
<i>B. augur</i>	Yes	420	1	3	2	4
<i>B. brachyurus</i>	Yes	295	2	1	3	5
<i>B. buteo</i>	Yes	394	1	2	3	5
<i>B. hemilasius</i>	Yes	476	1	2	9	4
<i>B. jamaicensis</i>	Yes	383	1	2	3	7
<i>B. lagopus</i>	Yes	435	1	2	9	5
<i>B. platypterus</i>	Yes	271	1	5	2	4
<i>B. poecilochrous</i>	Yes	456	1	3	9	2
<i>B. polyosoma</i>	Yes	400	1	5	4	2
<i>B. regalis</i>	Yes	435	1	2	3	5
<i>B. rufinus</i>	Yes	452	1	3	2	4
<i>B. rufofuscus</i>	Yes	428	1	3	2	4
<i>B. solitarius</i>	Yes	285	1	2	9	3
<i>B. swainsoni</i>	Yes	393	1	4	2	3
<i>B. ventralis</i>	Yes	379	1	2	3	9
<i>Accipiter badius</i>	No	203	4	3	1	2
<i>A. brachyurus</i>	No	188	–	–	–	–
<i>A. brevipes</i>	No	227	3	4	1	2
<i>A. butleri</i>	No	177	9	9	1	2
<i>A. castanilius</i>	No	166	2	1	3	4
<i>A. cirrhocephalus</i>	No	225	4	1	3	2
<i>A. collaris</i>	No	165	–	–	–	–
<i>A. cooperii</i>	No	244	2	1	3	5
<i>A. erythrauchen</i>	No	184	–	–	–	–
<i>A. erythropus</i>	No	159	9	1	9	2
<i>A. fasciatus</i>	No	278	1	2	3	5
<i>A. francesii</i>	No	167	5	4	1	2
<i>A. gentilis</i>	No	341	2	1	3	4
<i>A. griseiceps</i>	No	186	4	2	1	3
<i>A. griseogularis</i>	No	247	–	–	–	–
<i>A. gularis</i>	No	177	3	1	9	2
<i>A. gundlachi</i>	No	260	9	1	9	9
<i>A. henicogrammus</i>	No	237	3	2	1	4
<i>A. henstii</i>	No	302	2	1	9	9
<i>A. luteoschistaceus</i>	No	201	–	–	–	–
<i>A. madagascariensis</i>	No	205	9	1	3	4
<i>A. melanochlamys</i>	No	237	4	1	9	3
<i>A. minullus</i>	No	150	3	1	4	2

APPENDIX 2 *Continued*

Species	Polymorphism*	Wing length (mm)	Diet (rank)			
			Mammal	Bird	Reptile	Insect
<i>A. nanus</i>	No	165	9	2	9	1
<i>A. nisus</i>	No	219	2	1	3	6
<i>A. poliogaster</i>	No	260	–	–	–	–
<i>A. princeps</i>	No	270	–	–	–	–
<i>A. rhodogaster</i>	No	185	–	–	–	–
<i>A. ruftorques</i>	No	219	4	1	3	2
<i>A. rufiventris</i>	No	218	2	1	9	3
<i>A. soloensis</i>	No	192	5	4	3	2
<i>A. striatus</i>	No	163	2	1	3	5
<i>A. superciliosus</i>	No	152	2	1	9	9
<i>A. trinotatus</i>	No	158	5	6	1	2
<i>A. trivirgatus</i>	No	237	3	1	2	5
<i>A. virgatus</i>	No	165	2	1	3	4
<i>A. albogularis</i>	Yes	229	9	1	2	3
<i>A. bicolor</i>	Yes	224	2	1	3	4
<i>A. haplochrous</i>	Yes	219	3	4	1	2
<i>A. hiogaster</i>	Yes	243	4	3	1	2
<i>A. imitator</i>	Yes	193	–	–	–	–
<i>A. melanoleucus</i>	Yes	317	2	1	9	9
<i>A. meyerianus</i>	Yes	317	9	1	9	9
<i>A. novaehollandiae</i>	Yes	282	2	1	3	5
<i>A. ovampensis</i>	Yes	237	9	1	9	2
<i>A. poliocephalus</i>	Yes	203	9	9	1	2
<i>A. tachiro</i>	Yes	221	2	1	3	6

*‘Yes’ is for polymorphic species and ‘No’ for monomorphic species. Food categories are ranked in order of importance in the diet (most important category = rank 1; least important = rank 9). If a food category was not reported as belonging to the diet of a given species, it was assigned rank 9.