

Positive assortative pairing by plumage colour in Spanish imperial eagles

Gary R. Bortolotti^{a,*}, Luis Mariano González^b, Antoni Margalida^c,
Roberto Sánchez^d, Javier Oria^e

^a Department of Biology, University of Saskatchewan, 112 Science Pl., Saskatoon, SK, Canada S7N 5E2

^b Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, Madrid, Spain

^c Bearded Vulture Study and Protection Group, Pont de Suert (Lleida), Spain

^d TRAGSA - División Servicios Medioambientales, Madrid, Spain

^e Boscaje, Segovia, Spain

Received 9 October 2007; received in revised form 10 January 2008; accepted 14 January 2008

Abstract

Intraspecific variation in plumage may have a functional significance in mate choice. As a result, breeding birds are often paired assortatively with respect to colour. However, whether this within-pair correlation is a result of homotypic preference whereby individuals pick a mate that looks like themselves, or directional preference whereby all individuals have the same phenotypic preference, is often unknown. Using data collected between 1989 and 2006, we describe intraspecific variation in the striking white feathers on the leading edge of the wing, lesser coverts and mantle of 144 Spanish imperial eagles (*Aquila adalberti*), one of the most endangered birds of prey in the world. Females had, on average, more white than males, and pairs mated in a positive assortative fashion. Coloration was not related to age of the bird, food supply (i.e., territory quality) or breeding productivity. Our results are most consistent with the process of homotypic-preference assortative mating, and this may be a result of sexual imprinting, and function as a mechanism to optimize the degree of outbreeding. This pattern of mate selection may explain the rapid evolutionary divergence of *A. adalberti* from the continental population of imperial eagle *A. heliaca*.

© 2008 Elsevier B.V. All rights reserved.

Keywords: Coloration; Mate choice; Outbreeding; Plumage

1. Introduction

Animals may use phenotypic variation, be it in colour, size or behaviour, to optimize the selection of sexual partners. At the most basic and important level, the appearance of an individual identifies its species. Intraspecific variation may allow the evaluation of a potential mate's quality if the expression of the phenotype is condition dependent, as it often is in carotenoid-dependent coloration and other sexually selected traits (Hill, 2006). Alternatively, physical or behavioural traits may function as markers allowing mate choice for an optimal ratio of inbreeding to outbreeding (Bateson, 1978). While mate choice can be inferred by non-random associations of phenotypes, i.e., assortative mating, the process that forms such a pattern, and hence function, is not easily inferred (Burley, 1983; Gimelfarb, 1988; Ferrer and Penteriani, 2003). The role of mate choice within

the framework of sexual selection has been exhaustively studied (Hill, 2006), but there is also abundant evidence for coloration to be important in mate choice in other contexts (Roulin, 2004). Many researchers have failed to realize the ambiguity of the term assortative mating, and to recognize that there are alternative processes and functions with regard to selecting a mate.

When animals prefer to mate with phenotypes similar to themselves, the process is "homotypic preference" (Cézilly, 2004) (also known as like preference, Burley, 1983). This contrasts with the more common understanding of mate choice whereby all individuals, regardless of their own phenotype, have a "directional preference" for a particular type of individual (Cézilly, 2004) (also known as type preference, Burley, 1983). The type being preferred is typically related to an attribute, or correlate, of quality as is so often reported in studies of sexual selection. In many species of birds both sexes contribute to parental investment and so both should be selective when it comes to partners (Trivers, 1972). Individuals of high quality should be more selective than those of low quality. As a result high-quality birds will mate with others of high-quality, and low-

* Corresponding author. Tel.: +1 306 966 4439; fax: +1 306 966 4439.

E-mail address: gary.bortolotti@usask.ca (G.R. Bortolotti).

Table 1
Summary of hypotheses, predictions and results regarding plumage variation in wild Spanish imperial eagles

Attribute	Result	Hypotheses					
		Homotypic preference mate choice	Directional preference mate choice	Badge	Individual identification	Territory occupancy	Adaptive by natural selection
Assortative mating	Strong positive	Yes ^a	Yes	Possibly	No	No	No
Quality of bird (reproduction and habitat)	None	Yes	No	No	Yes	Yes	No
Develops in sexually mature birds	Yes	Yes	Yes	Yes		Yes	No
Variation among individuals	Considerable	Yes	Yes	Yes	Yes	No	No
Costly to develop	Unlikely	Yes	No	No	Yes	Yes	
Consistent throughout life	Yes	Yes	No		Yes		yes
Mismatched pairs and habitat	None	Yes	No				
Mismatched pairs and reproduction	None	No	Possibly				

^a Yes and no refer to whether or not the hypothesis is supported by the result. Blanks are not relevant to that hypothesis.

quality individuals with low-quality mates (Burley, 1983). The two processes are indistinguishable from the sole observation of positive assortative mating (Cézilly, 2004). Directional preference should not result in this pattern if only one sex chooses (Burley, 1983).

In recent years, there has been a considerable amount of research into the meaning of phenotypic variation in avian coloration (see Hill and McGraw, 2006a,b). In particular, the role of mate choice, as directional preference, in sexual selection has been featured prominently (Hill, 2006). In contrast, homotypic preference has received relatively little study. Perhaps the question of why “like prefers like” has been considered too obvious given its presumed role as an isolating mechanism maintaining species. In other words, birds seek breeding partners of the same species, as they are phenotypically similar to themselves to avoid the costs of hybridization. However, recently there has been renewed interest in understanding avian colour variation, especially plumage polymorphisms, from the perspective of mechanisms of speciation (Newton, 2003; Roulin, 2004).

In this paper we investigate the nature of phenotypic variation in plumage colour in the Spanish imperial eagle (*Aquila adalberti*), one of the most endangered birds of prey in the world (BirdLife International, 2004) with the entire population numbering about 200 breeding pairs (González and Oria, 2003). This small, peripheral population is of interest as a model of speciation processes (see below), and also from the question of the unusual nature of its plumage pattern. The adult or definitive feathering of most large eagles of the genus *Aquila* (*chrysaetos*, *rapax*, *audax*, *gurneyi*, *pomarina*, *clanga*) is dark brownish-grey, with small light areas which are only visible at close proximity (Brown and Amadon, 1968; Ferguson-Lees and Christie, 2001). These birds are primarily asocial and prey on animals with highly developed visual capabilities that allow effective predator detection, i.e., mammals and birds (Brown and Amadon, 1968). In contrast, highly social piscivorous eagles in the genus *Haliaeetus* are coloured by large areas of bright white feathers (Orians, 1980). Thus a relaxation of natural selection for crypsis, or the use of conspicuous colours for communication, could

explain the differences in plumage between these two groups of birds (Orians, 1980; Savalli, 1995; Bortolotti, 2006). However, *A. adalberti* has striking white feathers on the leading edge of the wing and lesser coverts and on the mantle (Hiraldo et al., 1976; Ferguson-Lees and Christie, 2001; Ferrer, 2001). Whether this atypical conspicuousness in *A. adalberti* is functional is part of our interest in coloration of this species. In addition, as we show, there is considerable inter-individual variation in extent of white feathering that has not been explained.

The evolution of avian plumage coloration and mechanisms maintaining colour variation have been subjects particularly rich in theory (Hill and McGraw, 2006a,b). We limit our analyses to six hypotheses from the many possible explanations for coloration (Table 1). We believe these to be the most plausible given the biology of our study species (see also Section 4). The conspicuous white feathers of this eagle may be non-functional, have arisen from natural selection (e.g., crypsis, thermoregulation, see Bortolotti, 2006) or may be a social signal (Dale, 2006). Potential messages conveyed by plumage signals include individual quality (typically in sexual selection, Dale, 2006), a badge of social dominance (Senar, 2006), or be used as a marker of territory occupancy or individual identity (Whitfield, 1986; Roulin, 2004; Dale, 2006). The predictions of each of these hypotheses, relative to our data, are presented in Table 1. Although using somewhat different terminology, the rationales for directions of the predictions are presented in Dale (2006).

2. Methods

2.1. Study species

The Spanish imperial eagle, originally named the white-shouldered eagle (Dresser, 1873), was considered a separate species until the middle of the last century (Swan and Wetmore, 1945). It was later placed as a subspecies (*Aquila heliaca adalberti*) of the eastern imperial eagle (*A. h. heliaca*) by Hartert (1914), until more recent genetic analyses confirmed species status (Seibold et al., 1996). Its range has been restricted to the Iberian Peninsula (González and Oria, 2003) where it arrived

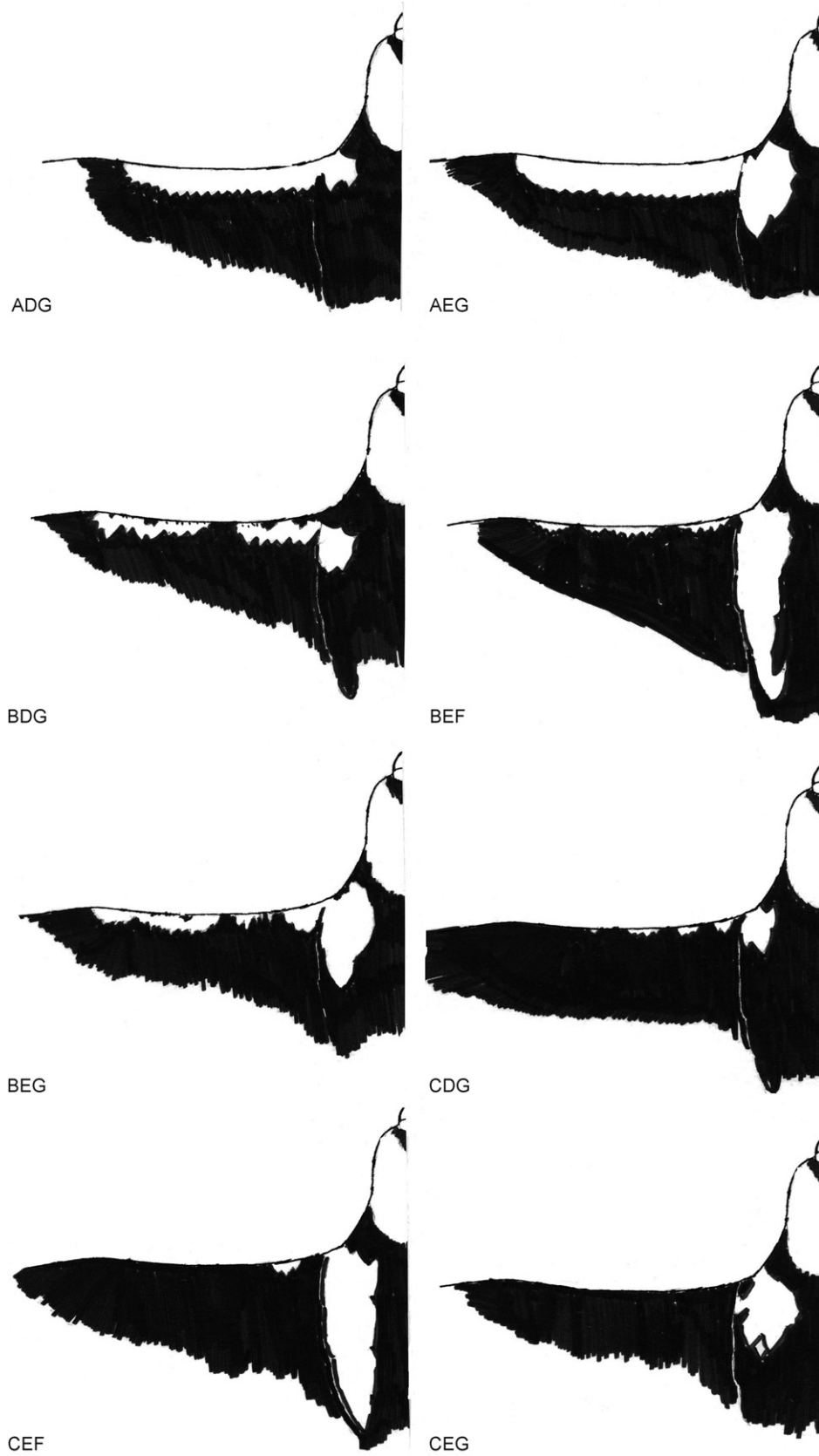


Fig. 1. Categories of the extent of the white feathering on the wing and mantle of Spanish imperial eagles: (1) code ADG; (2) code AEG; (3) code BDG (4) code BEF; (5) code BEG; (6) code CDG; (7) code CEF; (8) code CEG.

at the end of the Pleistocene or beginning of the Holocene, and originated by reproductive isolation (González, 2008). It has only recently diverged genetically from *A. heliaca* (see Section 4) (Martínez-Cruz, 2004; Martínez-Cruz and Godoy, 2007).

The Spanish imperial eagle differs behaviourally from *A. heliaca*. The former is said to be highly sedentary and asocial, while the latter forms large flocks during migration (Ferguson-Lees and Christie, 2001; Ferrer, 2001; BirdLife International, 2005). In its current distribution, the Spanish imperial eagle reaches its highest densities on plains and mountain ranges with scattered Mediterranean forest and open savannah where European rabbits (*Oryctolagus cuniculus*), their main prey, are abundant (González et al., 1990).

2.2. Classification of phenotype

Data were collected between 1989 and 2006 in 86 territories of the four subpopulations of the five defined (González and Oria, 2003). Our study constitutes 85% of the total breeding pairs of this species. During the regular monitoring of the breeding population (Margalida et al., 2007, 2007b), the extent and pattern of the white feathers on the mantle and wings of adults that occupied breeding territories were recorded. These individuals were observed within their breeding territory and identified from prominent viewing spots using binoculars and 20–60× spotting scopes approximately 600–800 m from the nest. The sex of the individuals was identified by observing copulation behaviour and participation in incubation (Margalida et al., 2007).

The extent of the white feathers on the wing and mantle was a continuously varying trait, but as is typically the case for analysis (Roulin, 2004) discrete categories were identified: (A) continuous white in the marginals and lesser supra coverts, (B) discontinuous white in the marginals and lesser supra coverts, (C) very few or no white in the lesser supra coverts and marginals, (D) white in the mantle feathers and lesser scapulars, (E) white in the lesser and median scapular feathers and black in the greater scapulars, (F) white in the lesser, median and greater scapular feathers, (G) black in the greater scapulars and all other areas. A priori we did not know that the frequencies in some categories were small enough to be problematic statistically; therefore, we subsequently grouped these codes into three categories—“Abundant”: continuous extension of white feathers on the wing and scapulars (codes AEG, ADG, BEF, CEF, Fig. 1(1)–(4)); “Intermediate”: discontinuous extension of white feathers (codes BEG, BDG, Fig. 1(5) and (6)); “Scarce” absence or minimal presence of white on the wing (codes CDG, CEG, Fig. 1(7) and (8)).

One potentially confounding factor in studies of plumage variation in studies such as this one is that coloration may vary with age. By monitoring the plumage of individuals over time, we found that patterns remained constant during successive annual moults. Of 11 individuals observed in captivity over a period of 2–8 years (mean = 6.4, S.D. = 1.63), none changed in the extent of whiteness of the plumage. Similarly, the colour of 39 birds in the wild (17 of which were banded) monitored for 2–16 years (mean = 8.5, S.D. = 3.91) remained constant.

2.3. Quality of territory

In accordance with the classification established in the studies of rabbit abundance carried out in our area (Blanco and Villafuerte, 1993; Villafuerte et al., 1995) territories considered to be of “high quality” were those in which the 10 × 10 UTM grid where the nest is situated, the density of rabbits was higher than 1 rabbit/ha and those of “low quality” were those that were less than 1 rabbit/ha. To see whether there was a relationship between productivity and plumage, data were analyzed from 53 territories and 404 breeding attempts. To avoid problems of pseudoreplication the average value of productivity for each territory was used.

3. Results

3.1. Frequency of plumage types

Of 144 individuals identified (Table 2), the most frequently observed plumage pattern (33%) was the AEG (continuous white coverts and white lesser and median scapulars and black greater scapulars), followed by BDG (24%) (discontinuous white coverts, white lesser scapulars and black greater scapulars) and ADG (17%) (continuous white coverts and white lesser scapulars).

Females mainly showed pattern AEG (41%), followed by ADG (23%), BDG (15%) and CDG (8%). In contrast, type BDG (34%) dominated the males, followed by AEG (25%), BEG (15%) and CDG (13%), with the difference between the sexes being statistically significant ($\chi^2 = 22.48$, d.f. = 7, $p = 0.0021$). Similarly, considering the three categories that define the amount of white in the plumage (Abundant, Intermediate and Scarce), females had a higher frequency of the plumages with more white than males ($\chi^2 = 18.03$, d.f. = 2, $p = 0.00012$).

3.2. Non-random pairing

It was possible to determine the typology of plumage of both members of a pair in 44 territories. There was a high degree of positive assortative mating ($\chi^2 = 21.49$, d.f. = 4, $p < 0.001$) (Table 3).

Table 2

Design and extension of white feathers in the wings and back of male and female wild Spanish imperial eagles with definitive plumage

Plumage code	Females	Males
ADG	18	7
AEG	30	18
BDG	11	24
BEF	3	1
BEG	2	11
CDG	6	9
CEF	1	1
CEG	2	0
Total	73	71

Table 3
Plumage categories of mated pairs of wild Spanish imperial eagles

	Female plumage		
	Abundant	Intermediate	Scarce
Male plumage			
Abundant	11	4	1
Intermediate	10	13	1
Scarce	1	0	3

3.3. Quality of habitat and productivity

In low-quality territories, the distribution of plumage categories for females was 50% Abundant, 42% Intermediate and 8% Scarce category. In the high-quality territories, these proportions were almost the same: 48% Abundant, 42% Intermediate and 10% Scarce. There was no difference between habitats ($\chi^2 = 0.04$, d.f. = 2, $p = 0.98$). For males in low-quality territories, the distribution of plumage categories was 34% Abundant, 53% Intermediate and 13% Scarce. In the high-quality territories the proportions were 27, 60 and 13%, respectively, and there was no difference between habitats ($\chi^2 = 0.08$, d.f. = 2, $p = 0.80$).

The females of the different plumage categories did not differ statistically in productivity (mean \pm S.D. number of offspring per year, Abundant: 1.48 ± 0.14 , $n = 26$; Intermediate: 1.20 ± 0.17 , $n = 19$; Scarce: 1.27 ± 0.26 , $n = 8$, ANOVA: $F_{2,52} = 0.78$, $p = 0.46$). Similarly, males of the different plumage categories did not differ statistically in productivity (Abundant: 1.38 ± 0.76 , $n = 19$; Intermediate: 1.53 ± 0.69 , $n = 35$; Scarce: 1.3 , $n = 2$, ANOVA: $F_{2,50} = 0.27$, $p = 0.76$).

Given assortative mating, there may be differences in habitat quality or reproduction if males and females belong to the same plumage category, or are mismatched. According to directional-preference, habitat should be associated with the number of mismatches, i.e., few in good areas where choosy high-quality birds reside. Homotypic-preference on the other hand does not predict any association with habitat (Table 1). A test of independence showed no association between coloration matching within pairs and quality of habitat ($\chi^2 = 0.327$, d.f. = 1, $p = 0.57$). For mean number of young produced, an ANOVA with habitat (low- or high-quality) and within-pair matching (yes or no) as factors, and number of years monitored as a potential confounding covariate, revealed that only habitat explained productivity ($F_{1,38} = 5.120$, $p = 0.029$) after removal of non-significant terms. High-quality territories ($n = 19$) reared on average (\pm S.E.) 1.7 ± 0.20 young, while low-quality territories ($n = 21$) reared 1.1 ± 0.15 .

4. Discussion

4.1. Explanations for coloration

While clearly no one hypothesis can easily explain plumage variability in *A. adalberti*, some ideas are more plausible than others (Table 1). We see no obvious function for the conspicuous white feathers of the Spanish imperial eagle from the perspective of making the bird better adapted to the Iberian Peninsula

(Table 1). Being white, the feathers are devoid of melanin pigments. Consequently they would not have abrasion resistance compared to dark feathers. Unpigmented feathers should be nominally less costly to produce, but potentially more costly from the perspective of making the predator more conspicuous to prey (Bortolotti, 2006). It is more plausible, that white plumage has some signalling function.

Many of the possible signal functions could have arisen secondarily, i.e., they were unlikely to have been the target of selection. For example, the white feathers contrast against the dark brown body and the dark colours of the forested environment. As such they may mark occupancy of the territory or, as suggested for Ospreys (*Pandion haliaetus*) (Bretagnolle and Thibault, 1993), enhance visual displays. The fact that plumage variation in eagles allows birds to be identifiable as individuals, even to humans, suggests a potential function. According to Dale (2006), Falconiformes are among the most variably coloured orders of birds, and attributes of their coloration (e.g., melanin-based and genetically determined) plus their territorial behaviour are consistent with the individual identity hypothesis. The advantage of such a mechanism may be to reduce costs of repeated territory intrusions and contests over resource monopolisation, particularly from floaters (Roulin, 2004). Non-breeding Spanish imperial eagles generally spend time in temporary settlement areas and occasionally visit breeding areas (González et al., 1989; Ferrer, 1993; Ferrer and Penteriani, 2003). However, since coloration and habitat quality were unrelated, our finding of assortative mating is likely attributable to a behavioural choice by the birds.

Badges that signal social dominance, or fighting ability, are frequently melanin-based (Jawor and Breitwisch, 2003; Senar, 2006). The constant colour pattern over successive moults in eagles is consistent with the observation that melanin-based colours and plumage polymorphisms are often genetically determined (Roulin, 2004; Mundy, 2006). However, there should be expectations that colour would be related to habitat quality or reproductive output if white feathering was a badge (at least during the breeding season) (Table 1).

4.2. Assortative mating

The genetic control over colour allows for an important condition necessary for adaptive mate choice. An individual may use a heritable phenotype as a marker of life-history, behavioural or physiological strategies to optimize selection of a reproductive partner. Increasingly, studies are considering the need to consider genetic complementarity as an important criterion in mate choice (Tregenza and Wedell, 2000; Dale, 2006). In his recent review, Roulin (2004) found genetic colour polymorphisms to be associated with physiological processes (5 species), reproductive parameters (16 species) and behaviour (14 species). Behaviour has come under increasing attention given the recent interest in avian personalities (e.g., Groothuis and Carere, 2005). 'Like prefers like' is particularly appealing as an explanation given most of our findings (Table 1), and the behaviour of raptorial birds. For birds with long-term pair relationships, such as is the case in our species, the compatibility of mates has

been cited as a major factor determining reproductive success (e.g., Choudhury, 1995; Spoon et al., 2006). In particular, less compatible birds show higher rates of aggression (Spoon et al., 2004). The importance of a compatible mate may be amplified in birds of prey because of the physical danger they possess to their mates. It is not uncommon in captivity for females to injure or kill the smaller males when two raptors are merely placed in a cage together (D. Bird, pers. commun. and personal observation). In fact, a reduction in aggression to enhance pairing has been proposed as an explanation for reversed sexual size dimorphism in birds of prey (Smith, 1982). In virtually all captive breeding facilities, pairs are created by their keepers, often with a limited population from which to draw. It is well known in a variety of animals that higher reproductive success occurs when individuals pair with preferred than non-preferred mates (e.g., Bottoni et al., 1993; Drickamer et al., 2003; Bluhm and Gowaty, 2004). The Spanish imperial eagle, despite many years in breeding facilities, has yet to be bred successfully in captivity. To our knowledge, phenotype of potential mates has never been considered.

The lack of association between colour and a measure of quality of bird (either food supply on the territory or reproduction), suggests directional preference is less plausible than homotypic preference as a process in our study (Table 1). The one finding that casts some doubt on homotypic preference is that mismatched pairs did not have lower reproductive success (Table 1); however, this may not be very strong evidence. Firstly, any sample is biased by the fact that only successful pairings can be observed. Secondly, most “mismatches” in pairing were in fact the result of the lack of white males (given sexual dichromatism) rather than errors per se, and the errors were typically made on the nearest category (Table 3). Lastly, if pairs are choosing an optimal mate on the basis of, e.g., behavioural or physiological complementarity, mismatches of plumage may not be errors as the phenotype/genotype correlation for the trait and for colour are unlikely to be perfect. Variation in both plumage and personality can have a significant environmental component (Groothuis and Carere, 2005; Mundy, 2006). Also some of our mismatched pairs arose when pairs formed before acquisition of full definitive feathering (González et al., 2006, personal observation).

How preference is manifested at the time of pairing may involve any number of behavioural patterns, which could be a product of personality, endocrine status, etc., correlated with colour type (Black and Owen (1995) and Poisbleau et al. (2005)). However, preference per se, may have been determined much earlier in life. Sexual imprinting is a process whereby young animals learn the attributes of sexual partners later in life (Bateson, 1978; Witte and Sawka, 2003). While initially interpreted as a mechanism to learn the correct species, it is now acknowledged that it may be used to optimize the degree of inbreeding by recognizing the physical attributes of kin vs. non-kin (Bateson, 1978).

4.3. Consequences of coloration and non-random mating

The genetic diversity and distinctiveness of this population has been of concern to systematists and conservation biologists

for sometime (Negro and Hiraldo, 1994; Ferrer and Negro, 2004; Martínez-Cruz, 2004; Martínez-Cruz et al., 2004; Martínez-Cruz and Godoy, 2007). It is plausible that regardless of function, coloration and assortative mating may have played a role in speciation of the Spanish imperial eagle. González (2008) proposed that like most birds it is likely that *A. adalberti* arose through isolation, divergence and genetic differentiation (for coloration see also Newton, 2003; Roulin, 2004). Furthermore, he proposed that this species' specialization on the hunting of rabbits (see also Ferrer and Negro, 2004) and the subsequent change from being migratory, as are ancestral *A. heliaca* (Ferguson-Lees and Christie, 2001; BirdLife International, 2005), to sedentary, were critical in the speciation process. These changes in ecology of imperial eagles after colonizing Iberia may have also resulted in their much earlier breeding phenology, and as such may have made them reproductively isolated from *A. heliaca* (see also Connors, 1983; Monteiro and Furness, 1998; Bearhop et al., 2005). The proviso is that the incipient species must mate assortatively.

Pairing ‘like with like’ within the peripheral, sedentary population of Iberia could have genetic advantages, as local adaptations would not be lost through interbreeding with migrants of the ancestral stock. The striking white feathers of the adult plumage of *A. adalberti* may be a perfect candidate as an attribute for mate choice. Although González (2008) proposed that white feathering may be attributable to the founder effect, it is also likely that the plumage of the Spanish imperial eagle arose by sexual imprinting on an evolutionary novel trait (see Witte and Sawka, 2003). The latter may be the most parsimonious explanation for observed colours and patterns in eagle plumages. Any number of alternatives may have been equally effective. Homotypic-preference assortative mating for a novel mutation, and the associated phenotypic divergence, could have been effective isolating mechanisms and may explain, in part, the rapid evolution of the Iberian eagles as a species; currently believed to be only a few thousand years old (Martínez-Cruz and Godoy, 2007).

Acknowledgements

Thanks to Javier Sánchez, Víctor García, Julio Caballero, Maria Fernández, Javier Caldera and Luís Prada for their help with the fieldwork. We thank Maud Ferrari and Frank Cézilly for comments on the MS. Valuable information was provided by the Autonomous Regions of Madrid, Castilla-León, Castilla-La Mancha, Extremadura and Andalucía, all represented in the National Spanish Imperial Eagle Working Group. This study was funded by the Dirección General para la Biodiversidad del Ministerio de Medio Ambiente. GRB was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

References

- Bateson, P., 1978. Sexual imprinting and optimal outbreeding. *Nature* 273, 659–660.

- Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P., Farnsworth, K., 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* 21, 502–504.
- BirdLife International, 2004. Threatened Birds of the World 2004. BirdLife International, Cambridge (CD-ROM).
- BirdLife International, 2005. Imperial Eagle—Birdlife Species Factsheet. BirdLife International, Cambridge.
- Black, J.M., Owen, M., 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *J. Anim. Ecol.* 64, 234–244.
- Blanco, J.C., Villafuerte, R., 1993. Factores ecológicos que influyen sobre las poblaciones de conejos, incidencias en la enfermedad hemorrágica. Informe técnico. Empresa de Transformación Agraria TRAGSA, Madrid.
- Bluhm, C.K., Gowaty, P.A., 2004. Social constraints on female mate preferences in mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Anim. Behav.* 68, 977–983.
- Bortolotti, G.R., 2006. Natural selection and avian coloration: protection, concealment, advertisement or deception? In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration*, vol. 2: Function and Evolution. Harvard University Press, Cambridge, pp. 3–35.
- Bottoni, L., Massa, R., Lea, R.W., Sharp, P.J., 1993. Mate choice and reproductive success in the red-legged partridge (*Alectoris rufa*). *Horm. Behav.* 27, 308–317.
- Bretagnolle, V., Thibault, J.C., 1993. Communicative behavior in breeding ospreys (*Pandion haliaetus*): description and relationship of signals to life history. *Auk* 110, 736–751.
- Brown, L.H., Amadon, D., 1968. Eagles, Hawks and Falcons of the World. Country Life Books, Feltham.
- Burley, N., 1983. The meaning of assortative mating. *Ethol. Sociobiol.* 4, 191–203.
- Cézilly, F., 2004. Assortative mating. In: Bekoff, M. (Ed.), *Encyclopedia of Animal Behavior*, vol. 3. Greenwood Press, Westport, CT, pp. 876–881.
- Choudhury, S., 1995. Divorce in birds: a review of the hypotheses. *Anim. Behav.* 50, 413–429.
- Connors, P.G., 1983. Taxonomy, distribution, and evolution of golden plovers (*Pluvialis dominica* and *Pluvialis fulva*). *Auk* 100, 607–620.
- Dale, J., 2006. Intraspecific variation in coloration. In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration*, vol. 2: Function and Evolution. Harvard University Press, Cambridge, pp. 36–86.
- Dresser, H.E., 1873. A History of the Birds of Europe, vol. 1, London.
- Drickamer, L.C., Gowaty, P.A., Wagner, D.M., 2003. Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Anim. Behav.* 65, 105–114.
- Ferguson-Lees, J., Christie, D.A., 2001. Raptors of the World. Houghton Mifflin Company, Boston.
- Ferrer, M., 1993. Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish imperial eagle (*Aquila adalberti*). *Ibis* 135, 132–138.
- Ferrer, M., 2001. The Spanish Imperial Eagle. Lynx Edicions, Barcelona.
- Ferrer, M., Negro, J.J., 2004. The near extinction of two large European predators: super specialists pay a price. *Conserv. Biol.* 18, 344–349.
- Ferrer, M., Penteriani, V., 2003. A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Anim. Behav.* 66, 137–143.
- Gimelfarb, A., 1988. Processes of pair formation leading to assortative mating in biological populations—encounter-mating model. *Am. Nat.* 131, 865–884.
- González, L.M., 2008. Origin and formation of the Spanish imperial eagle (*Aquila adalberti*). *J. Ornithol.*, 149, 000–000 doi:10.1007/s10336-007-052-z.
- González, L.M., Oria, J., 2003. Águila imperial ibérica, *Aquila adalberti*. In: Martí, R., del Moral, J.C. (Eds.), Atlas de las Aves Reproductoras de España. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid, pp. 186–187.
- González, L.M., Heredia, B., González, J.L., Alonso, J.C., 1989. Juvenile dispersal of the Spanish imperial eagle (*Aquila adalberti*). *J. Field Ornithol.* 60, 269–379.
- González, L.M., Bustamante, J., Hiraldo, F., 1990. Factors influencing the present distribution of the Spanish imperial eagle (*Aquila adalberti*). *Biol. Conserv.* 51, 311–319.
- González, L.M., Oria, J., Margalida, A., Sánchez, R., 2006. Effective natal dispersal and age of maturity in the threatened Spanish imperial eagle (*Aquila adalberti*): conservation implications. *Bird Study* 53, 285–293.
- Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* 29, 137–150.
- Hartert, E., 1914. Die Vögel der Palaarktischen Fauna. Vol. 2: 1014–1212. Verlag von R. Friedländer und Sohn. Berlin.
- Hill, G.E., 2006. Environmental regulation of ornamental coloration. In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration*, vol. 1: Mechanism and Measurements. Harvard University Press, Cambridge, pp. 507–560.
- Hill, G.E., McGraw, K.J. (Eds.), 2006a. *Bird Coloration*, vol. 1: Mechanism and Measurements. Harvard University Press, Cambridge.
- Hill, G.E., McGraw, K.J. (Eds.), 2006b. *Bird Coloration*, vol. 2: Function and Evolution. Harvard University Press, Cambridge.
- Hiraldo, F., Delibes, M., Calderón, J., 1976. Sobre el status taxonómico del Águila imperial Ibérica. *Doñana Acta Vertebr.* 3, 171–182.
- Jawor, J.M., Breitwisch, R., 2003. Melanin ornaments, honesty, and sexual selection. *Auk* 120, 249–265.
- Margalida, A., González, L.M., Sánchez, R., Oria, J., 2007a. Parental behaviour of Spanish imperial eagles (*Aquila adalberti*): sexual differences in a moderately dimorphic raptor. *Bird Study* 54, 112–119.
- Margalida, A., González, L.M., Sánchez, R., Oria, J., Prada, L., Caldera, J., Aranda, A., Molina, J.I., 2007b. A long-term scale study of the breeding biology of Spanish imperial eagles. *J. Ornithol.* 148, 309–322.
- Martínez-Cruz, B., 2004. Genética de la conservación del Águila imperial ibérica (*Aquila adalberti*). Ph.D. Thesis. Universidad de Sevilla, Sevilla.
- Martínez-Cruz, B., Godoy, J.A., 2007. Genetic evidence for a recent divergence and subsequent gene flow between Spanish and eastern imperial eagles. *BMC Evol. Biol.* 7, doi:10.1188/1471-2148-7-170.
- Martínez-Cruz, B., Godoy, J.A., Negro, J.J., 2004. Population genetics after fragmentation: The case of the endangered Spanish imperial eagle (*Aquila adalberti*). *Mol. Ecol.* 13, 2243–2255.
- Monteiro, L.R., Furness, R.W., 1998. Speciation through temporal segregation of Madeiran storm petrel (*Oceanodroma castro*) populations in the Azores? *Philos. Trans. Roy. Soc. Lond. B* 353, 945–953.
- Mundy, N.I., 2006. Genetic basis of color variation in wild birds. In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration*, vol. 2: Function and Evolution. Harvard University Press, Cambridge, pp. 469–506.
- Negro, J.J., Hiraldo, F., 1994. Lack of allozyme variation in the Spanish imperial eagle *Aquila adalberti*. *Ibis* 136, 87–90.
- Newton, I., 2003. The Speciation and Biogeography of Birds. Academic Press, New York.
- Orians, G.H., 1980. Why are bald eagles bald? In: Knight, R.L., Allen, G.T., Stalmaster, M.V., Servheen, C.W. (Eds.), Proceedings of the Washington Bald Eagle Symposium. Seattle, pp. 3–11.
- Poisbleau, M., Fritz, H., Dano, S., Lambrechts, M.M., 2005. Body measurements and hormonal within-pair covariation in wintering and spring staging dark-bellied brent geese *Branta bernicla*. *Ardea* 94, 127–131.
- Roulin, A., 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biol. Rev.* 79, 815–848.
- Savalli, U.M., 1995. The evolution of bird coloration and plumage elaboration. A review of hypotheses. *Curr. Ornithol.* 12, 141–190.
- Seibold, I., Helbig, A.J., Meyburg, B.U., Negro, J.J., Wink, M., 1996. Genetic differentiation and molecular phylogeny of European *Aquila* eagles according to cytochrome *b* nucleotide sequences. In: Meyburg, B.U., Chancellor, R.D. (Eds.), Eagle Studies. World Working Group on Birds of Prey, London, pp. 1–15.
- Senar, J.C., 2006. Color displays as intrasexual signals of aggression. In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration*, vol. 2: Function and Evolution. Harvard University Press, Cambridge, pp. 36–86.
- Smith, S.M., 1982. Raptor “reverse” dimorphism revisited: a new hypothesis. *Oikos* 39, 118–122.
- Spoon, T.R., Millam, J.R., Owings, D.H., 2004. Variation in the stability of cockatiel (*Nymphicus hollandicus*) pair relationships: the roles of males, females, and mate compatibility. *Behaviour* 141, 1211–1234.

- Spoon, T.R., Millam, J.R., Owings, D.H., 2006. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Anim. Behav.* 71, 315–326.
- Swan, H.K., Wetmore, A., 1945. A Monograph of the Birds of Prey (Order Accipitres), vols. 1 and 2. Wheldon and Wesley Ltd., London.
- Tregenza, T., Wedell, N., 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Mol. Ecol.* 9, 1013–1027.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man*. Aldine Publishing Co., Chicago, pp. 139–179.
- Villafuerte, R., Calvete, C., Blanco, J.C., Lucientes, J., 1995. Incidence of viral haemorrhagic disease in wild rabbit populations in Spain. *Mammalia* 59, 651–659.
- Whitfield, D.P., 1986. Plumage variability and territoriality in breeding turnstone *Arenaria interpres*: status signalling or individual recognition? *Anim. Behav.* 34, 1472–1482.
- Witte, K., Sawka, N., 2003. Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ. *Anim. Behav.* 65, 195–203.