

Positive assortative pairing by plumage colour in Spanish imperial eagles

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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*.

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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-

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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

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