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RESEARCH ARTICLE

Shared pattern in morph inheritance system and recessive gene conservation mechanisms in two polymorphic *Hieraaetus* species

Patrón compartido en el sistema de herencia de los morfos y mecanismos de conservación de genes recesivos en dos especies polimórficas de *Hieraaetus*

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ABSTRACT

Disruptive selection, non-random transmission of alleles and sexual selection are considered one of the main mechanisms for the maintenance of genetic colour polymorphism in some bird species. We analyse the influence of these mechanisms and Mendelian inheritance on the maintenance and evolution of the colour polymorphism in two polymorphic raptor species: the booted eagle *Hieraaetus pennatus* and the little eagle *Hieraaetus morphnoides*. Using observational data from successful breeding events, we examine three populations in Spain (booted eagle) and New South Wales, Australia (little eagle). Our results showed that the dark offspring produced in breeding events involving mixed-morph pairs formed by a light male and a dark female far exceeds the expected value under the Hardy-Weinberg equilibrium. In addition, the low number of dark eaglets born from pairs formed by light individuals indicates that the number of breeding events of heterozygous light morph pairs was much less than expected. As the plausible existence of a transmission ratio distortion phenomenon in heterozygous light morph males does not, alone, explain the disproportionate number of dark eaglets observed, our results suggest that one or two selective mating phenomena may be occurring in this polymorphic system. Finally, we discuss our results suggesting that the two species share a similar mechanism for the maintenance of colour polymorphism since these would come from a common ancestor during the Pleistocene period.

Keywords: booted eagle, disassortative mating, disruptive selection, little eagle, morph inheritance.

RESUMEN

La selección disruptiva, la transmisión no aleatoria de alelos y la selección sexual se consideran uno de los principales mecanismos para el mantenimiento del polimorfismo genético en algunas especies de aves. Analizamos la influencia de estos mecanismos y de la herencia mendeliana en el mantenimiento y evolución del polimorfismo en dos especies de rapaces polimórficas: el águila calzada *Hieraaetus pennatus* y el águila

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australiana *Hieraaetus morphnoides*. Utilizando datos observacionales de eventos reproductivos exitosos, nosotros examinamos tres poblaciones en España (águila calzada) y Nueva Gales del Sur, Australia (águila australiana). Nuestros resultados mostraron que la descendencia oscura producida en los eventos de cría que implican parejas mixtas formadas por un macho claro y una hembra oscura excede con mucho el valor esperado bajo el equilibrio Hardy-Weinberg. Además, el bajo número de aguiluchos oscuros nacidos de parejas formadas por individuos claros indica que el número de eventos de cría de parejas heterocigóticas de morfos claros fue mucho menor de lo esperado. Dado que la plausible existencia de un fenómeno de distorsión de la relación de transmisión en los machos heterocigotos de morfo claro no explica por sí sola el desproporcionado número de aguiluchos oscuros observado, nuestros resultados sugieren que en este sistema polimórfico pueden estar produciéndose uno o dos fenómenos de apareamiento selectivo. Finalmente, discutimos nuestros resultados sugiriendo que las dos especies comparten los mismos mecanismos para el mantenimiento del polimorfismo de color procedentes de un ancestro común durante el Pleistoceno.

Palabras clave: águila australiana, águila calzada, apareamiento disasortativo, herencia morfológica, selección disruptiva.

INTRODUCTION

Colour polymorphism is a common phenomenon in different animal taxa and consists of the existence of two or more colour morphs, not linked with age or/and sex and genetically dependent, in an animal population (Huxley 1955). In birds of prey, this phenomenon occurs in approximately 20% of the species, depending on taxonomic treatment and the recent increase in the number of recognised species across the hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes) (Galeotti *et al.* 2003; Chakarov *et al.* 2011; Robinson *et al.* 2024). The maintenance of genetic colour polymorphism in animal species and the mechanisms involved have been the subject of intense study for decades (Galeotti *et al.* 2003; Roulin 2004; Roulin & Bize 2007; Robinson *et al.* 2024). For birds, up to seven mechanisms have been described to explain the maintenance of colour polymorphism (Roulin 2004; Robinson *et al.* 2024). Among these, the main with respect to raptors are disruptive selection (or balanced polymorphism), transmission ratio distortion of alleles (hereafter TRD), sexual selection (assortative or disassortative mating), and possible heterozygote advantage (Galeotti *et al.* 2003; Robinson *et al.* 2024). Pleiotropy/linkage of melanogenesis (colour morphs genetically covarying with behavioural or physiological differences) may also play a role (Ducrest *et al.* 2008; Robinson *et al.* 2024).

Disruptive selection influences the frequency of alleles in which extreme values for a trait are favoured against intermediate values. In this case, selection acts on the variance of a trait to produce two or more distinct groups. Thus, more individuals acquire peripheral character value at both ends of the distribution. Disruptive selection can establish differential foraging efficiencies in different habitats and/or light conditions and preying upon different species (Roulin & Wink 2004; Tate & Amar 2017).

The TRD (Huang *et al.* 2013; Ducret *et al.* 2016) occurs when some alleles are transmitted to the offspring in a ratio lower or higher than expected following the Mendelian 1:1 ratio. This phenomenon could originate during meiosis, by a non-random segregation of alleles, or due to gamete competition during the post-meiotic phase, which could cause different viability of haploid gametes (Pardo-Manuel de Villena & Sapienza 2001). Thus, TRD can favour the maintenance of polymorphism by transmitting the recessive character in proportions greater than the 1:1 relationship of Mendel's first law.

The sexual selection hypothesis based on colour morph establishes that the maintenance of different colour morphs may depend on the preferences at the time of mating (Galeotti *et al.* 2003). When assortative, individuals with similar colour characteristics mate and when disassortative, the preference is for opposite morphs (Roulin & Bize 2007). Although sexual selection and therefore mate choice are two important processes in colour polymorphic systems, maintaining colour polymorphisms also requires some form of correlational (with other traits) or balancing selection (i.e. heterozygote advantage or negative frequency-dependent selection)

which points to the complexity of the mechanisms involved (Wellenreuther *et al.* 2014).

Disassortative mating favours the production of heterozygous offspring (Galeotti *et al.* 2003; Roulin 2004; Roulin & Bize 2007) and can maintain genetic diversity by negative frequency-dependent morph mating (Wellenreuther *et al.* 2014).

The phenomenon of speciation occurs when a population is isolated from the rest of the populations of the same species, due to a geographical barrier or for other reasons, such as mating preference (Newton 2003; Abbott *et al.* 2008). Only under these conditions is an independent evolutionary path produced, free of gene flow from other populations. New species of birds are produced, over time, by the transformation of one species into another, in a process called anagenesis, or by the transformation of one species into two or more species by cladogenesis after an allopatric isolation (Newton 2003). Allopatric speciation may also act as a process in the evolution of genetic colour polymorphism (Roulin 2004).

Isolation of populations may also be a precursor to the development of different colour morphs, which on secondary contact may form a polymorphic population (Robinson *et al.* 2024).

According to previous studies carried out in the Iberian Peninsula and in Australia, the booted eagle *Hieraaetus pennatus* (Gmelin, 1788) and the little eagle *Hieraaetus morphnoides* (Gould, 1841) present a discrete polymorphism, with two colour morphs, light and dark, with the light morph being the dominant for both species, with a similar morph inheritance pattern, although two genes and two alleles with epistasis are suggested for the booted eagle (Bosch 2019; Bosch *et al.* 2019; Larkin & Debus 2020). In a study on the phylogeny and taxonomy of booted eagles, Lerner *et al.* (2017) established that the two species were closely related and belonged to the genus *Hieraaetus*, that currently comprises five species, including the Ayres eagle *H. ayresii* and the Wahlberg's eagle *H. wahlbergi* of Africa, and the pygmy eagle *H. weiskei* of New Guinea, formerly considered a subspecies of the little eagle, all also exhibiting two discrete colour morphs. The extinct Haast's eagle *H. moorei* also belonged to the same genus (Bunce *et al.* 2005).

In this study we specifically compare the observed vs. expected polymorphisms based on the Hardy-Weinberg equilibrium using observational data on successful breeding events from the Spanish (booted eagle) and Australian (little eagle) populations to evaluate how different factors (*e.g.* the disruptive selection, non-random transmission of alleles, and sexual selection), considered primary drivers of genetic colour polymorphism, in conjunction with Mendelian inheritance, influence identically on the maintenance and evolution of colour polymorphism on both species, the booted eagle and the little eagle. Both species are currently geographically and genetically separated, having shared a common ancestor ~0.8 million years ago (Mindell *et al.* 2018; Catanach *et al.* 2024). We here consider the mechanisms of disruptive selection, non-random transmission of the dark allele and sexual selection. We also discuss the genesis of the speciation phenomena that occurred related to both species in relation to the general question of this study.

MATERIALS AND METHODS

Study areas

The three studied booted eagle populations in Spain are located in central Catalonia (41°51' N, 1°34' E), Els Ports Natural Park (South Catalonia; 40°48' N, 0°19' E) and the Special Protection Area " Sierras de Burete, Lavia y Cambrón" (38°01' N, 1°47' W), in the centre of Murcia province, characterized mainly by both Eurosiberian and Mediterranean forests of Black Pine *Pinus nigra* and Aleppo Pine *Pinus halepensis*, respectively, interspersed with scrubland and cultivated areas (more details in Bosch *et al.* 2019).

The study area in Australia was centred on Armidale (30°30' S, 151°40' E) on the Northern Tablelands of New South Wales, extending 60–80 km north-west to south, but mostly within a 20-km radius of the city. Little Eagles inhabit remnant eucalypt open forest and woodland in undulating country at ~1000 m above sea level, and their foraging extends into more open habitats (scattered woodland and adjoining pasture). The climate is temperate subhumid (more details in Larkin *et al.* 2020).

Data collection

The data used in the present study are those obtained in the previous studies by Bosch *et al.* (2020) (Table 1) and Larkin & Debus (2020) (Table 2), respectively, which collected pair types, number of expected and observed breeding events, colour morph and morph ratio of the fledged eaglets in the three booted eagle populations studied in Spain (1995-2018)(see Bosch *et al.* 2019 for more details) and in the little eagle near Armidale, New South Wales (Australia) from the 1980s, 2006-2009 and 2017-2019 (see Larkin *et al.* 2020 for more details; Fig. 1).

TABLE 1. Pair types, number of expected and observed breeding events, colour morph and morph ratio of the fledged eaglets in the three booted eagle populations studied in Spain (1995-2018; Bosch *et al.* 2020). / Tipos de pareja, número de eventos reproductivos esperados y observados, morfo de color y proporción de morfos de los aguiluchos volantones en las tres poblaciones de águila calzada estudiadas en España (1995-2018; Bosch *et al.* 2020).

	Breeding events		Eaglets fledged		Light/dark eaglets ratio	
Male-female morphs	**Expected**	**Observed**	**Light**	**Dark**	**Expected**	**Observed**
Light-Light	395	393	610	5	17.75:1	122:1
Light-Dark	56	58	38	53	3.89:1	0.72:1
Dark-Light	28	30	29	15	2.84:1	1.93:1
Dark-Dark	4	2	0	3		
Total	483	483	677	76		

FIGURE 1. Left panels: adult light-morph and dark-morph booted eagles in flight. Photos: Carlos González Revelles. Right panels: adult light-morph and dark-morph little eagles in flight. Photos: David Whelan, adapted from Larkin & Debus (2020). / Paneles izquierdos: adultos en vuelo claro y oscuro de águila calzada. Fotos: Carlos González Revelles. Paneles derechos: adultos en vuelo claro y oscuro de águila australiana. Fotos: Davil Whelan, adaptado de Larkin & Debus (2020).

TABLE 2. Pair types, number of expected and observed breeding events, colour morph and morph ratio of the fledged eaglets in the little eagle near Armidale, New South Wales (Australia). Data pooled from the 1980s, 2006-2009 and 2017-2019 (Larkin & Debus 2020). / Tipos de parejas, número de eventos reproductivos esperados y observados, morfo de color y proporción de morfos de los aguiluchos volantones en el águila australiana cerca de Armidale, Nueva Gales del Sur (Australia). Datos agrupados de las décadas de 1980, 2006-2009 y 2017-2019 (Larkin & Debus 2020).

	Breeding events		Eaglets fledged		Light/dark eaglets ratio	
Male-female morphs	**Expected**	**Observed**	**Light**	**Dark**	**Expected**	**Observed**
Light-Light	32	32	32	0	9.67:1	32:0
Light-Dark	3	5	1	4	2:1	0.25:1
Dark-Light	12	12	7	5	2.83:1	1.4:1
Dark-Dark	2	1	0	1		
Total	49	50	40	10		

Colour morphs of parents and all offspring were checked in all reproductive event record data. In the cases in which the colour morph of an adult or a single chick was not verified, its incorporation into the analysis was rejected.

Although it is possible (Hirschauer & Wolter, 2017; Le Gouar *et al.* 2011; Rosenfield *et al.* 2015), we never observed extra-pair copulations in our study areas (Mougeot 2004), and anyway, extra-pair young are scarce in raptors (Roulin *et al.* 2004). In the same way, we only observed one case of a trio (a pair with a helper in the Murcia population) (Martínez *et al.* 2005), which was not included in the study, although this phenomenon is frequent in the high-density population of Sierra de Guadarrama, Madrid (Díaz 2006) but very rare in other Spanish populations.

Statistical methods

The data obtained have been compared with the expected theoretical data from the nine possible combinations of genotypes, following the Hardy-Weinberg equilibrium, according to the equation $p^2+ 2pq+ q^2 = 1$ to estimate the frequency of the carrier state (2pq) for an autosomal recessive trait, from the proportion of recessive dark morph individuals.

However, the accuracy of the Hardy-Weinberg equation relies on several assumptions, such as no gene flow, no selection and no non-random allelic transmission, the last two of which are not met in the populations studied. The results for the two species and the deviations from the Hardy-Weinberg equilibrium have been compared with each other with chi-square tests to look for parallels and similarities between the two species and their possible explanations.

RESULTS

The studies of colour morph inheritance in the booted eagle *H. pennatus* and in the little eagle *H. morphnoides* showed that mixed pairs with the light morph male and the dark morph female had a significant deviation between the proportion of expected light/dark offspring and those obtained. For booted eagle the expected ratio was 3.89:1 light/dark and the obtained was 0.72:1 light/dark ($\chi^2 = 25.024$, df = 1, $p < 0.001$) and for little eagle the expected ratio was 2:1 light/dark and the obtained 0.25:1 light/dark ($\chi^2 = 39.91$, df = 1, $p < 0.001$) (Fig. 2).

On the other hand, in the reproductive events of mixed pairs with the male of the dark morph and the female of the light morph, the morph ratio of the nestlings obtained hardly differs from that expected according to the Hardy-Weinberg equilibrium. For booted eagle the expected ratio was 2.84:1 light/dark and the ratio obtained was 1.93:1 light/dark and for little eagle the expected ratio was 2.83:1 light/dark and the obtained 1.4:1 light/dark. Although for the two species the proportions of the obtained dark morph offspring were higher than the expected, the differences were not statistically significant: $\chi^2 = 0.491$, df = 1, $p = 0.483$ for booted eagle and $\chi^2 = 0.422$, df = 1, $p > 0.05$ for little eagle (Fig. 3).

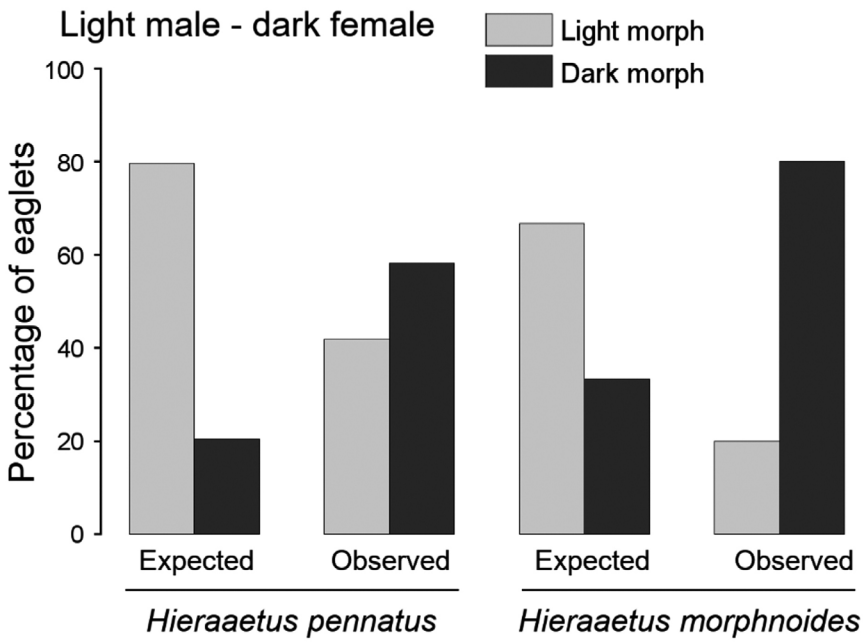

FIGURE 2. Expected and observed proportions of light/dark offspring of booted and little eagles from ♂light/♀dark morph reproductive events (χ^2 = 0.930, df = 1, *p* =0.335). / Proporciones esperadas y observadas de crías claras/oscuras de águilas calzadas y australianas procedentes de eventos reproductivos de morfos ♂claros/♀oscuros (χ^2 = 0,930, df = 1, *p* =0,335).

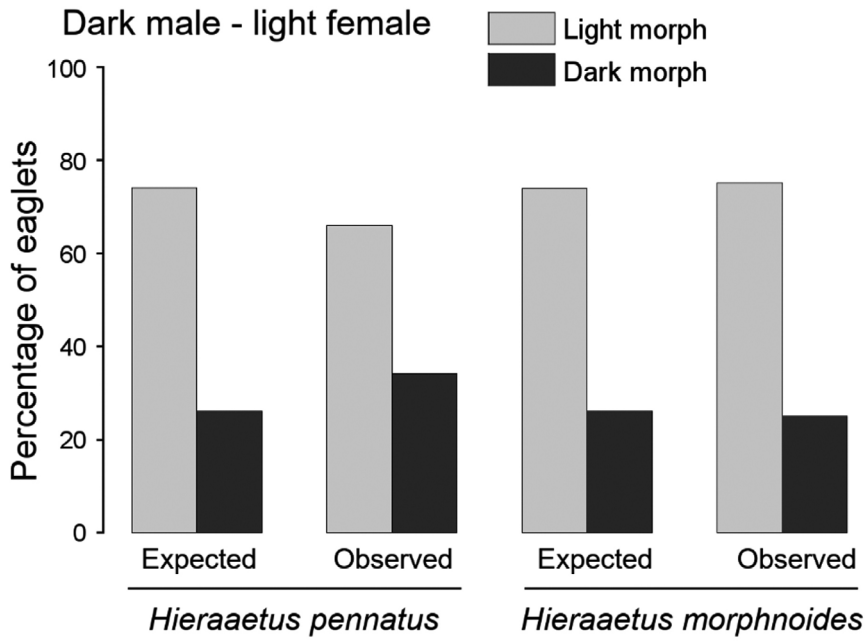

FIGURE 3. Expected and observed proportions of light/dark offspring of booted and little eagles from ♂dark/♀light morph reproductive events (χ^2 = 0.236, df = 1, *p* =0.627). / Proporciones esperadas y observadas de crías claras/oscuras de águilas calzadas y australianas de eventos reproductivos de morfos ♂oscuros/♀claros (χ^2 = 0,236, df = 1, *p* =0,627).

In the reproductive events of the pairs formed by the two individuals of the light morph, an offspring morph ratio of 17.75:1 light/dark was expected in the booted eagle and 9.67:1 light/dark in the little eagle, but a ratio of 122:1 light/dark was obtained in the booted eagle and in the little eagle all offspring were of the light morph, fact which can be attributed to the low sample size for this species and combination of morphs (n = 32) (Fig. 4). The proportion of pairs with the two heterozygous light morph individuals must also be much lower than expected from Hardy-Weinberg equilibrium results.

Comparing the results of the reproductive events of the mixed pairs with a male of the light morph and a female of the dark morph between booted and little eagles, no significant differences were found (χ^2 = 0.930, df = 1, p = 0.335) (Fig. 2). In the reverse case, of mixed pairs with the male of the dark morph and the female of the light morph, there were no significant differences between the offspring obtained in both species (χ^2 = 0.236, df = 1, p = 0.627) (Fig. 3).

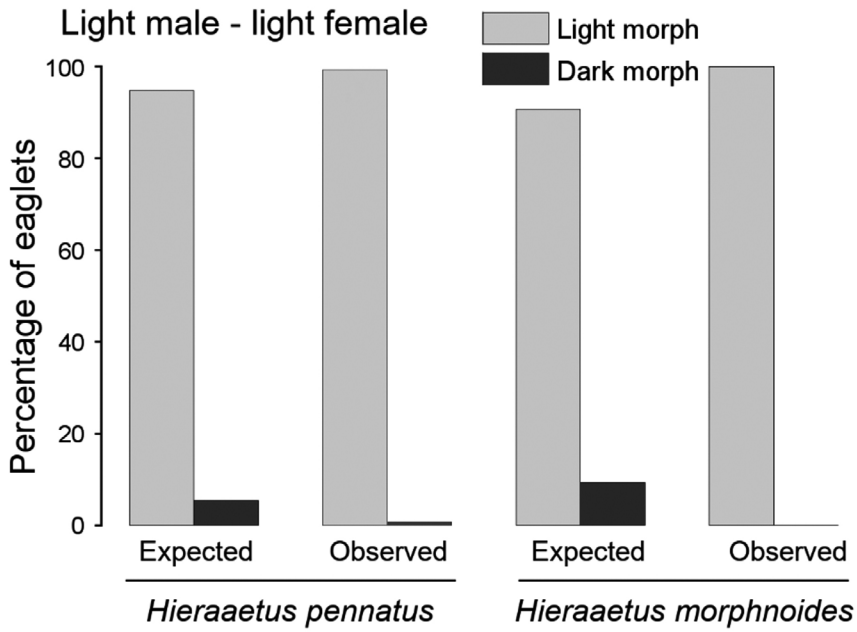

FIGURE 4. Expected and observed proportions of light/dark offspring of booted and little eagles from ♂light/♀light morph reproductive events. **/** Proporciones esperadas y observadas de crías claras/oscuras de águilas calzadas y australianas de eventos reproductivos de morfos ♂claros/♀claros.

DISCUSSION

Our results show a parallelism between the proportions of the offspring of the four possible combinations of the two discrete colour morphs which, surprisingly, gives almost identical results in all cases, although the sample size for the little eagle (n = 50) is notably much lower than in the booted eagle (n = 483). These results suggest the same phenomena in the transmission of the dark recessive trait by heterozygous males of the light morph in the two studied species, TRD (Bosch *et al.* 2019) and selective mating, based on the imprinting of heterozygous males of the light morph, born from homozygous dark mothers (Bosch *et al.* 2020).

Even assuming a non-random transmission of the dark character (TRD) by the heterozygous males of the light morph, in the event that all of them transmitted only the dark allele, the proportion of the expected morphs would be 1.44:1 for the booted eagle and 0.5:1 for the little eagle, quite far from the 0.72:1 and 0.25:1 obtained. On the other hand, assuming selective mating by imprinting in the reproductive events involving a dark morph female with a light morph male and in the absence of non-random transmission of the dark allele by the

heterozygous light morph males, the expected morph ratio of the offspring obtained would be 1:1, a result also quite far from the 0.72:1 obtained in the booted eagle and 0.25:1 in the little eagle. Therefore, TRD and selective mating must concur simultaneously, since each of them, by itself, does not explain the results obtained.

These phenomena have already been described previously in the booted eagle (Bosch *et al.* 2019, 2020) and in other species, for example, in the house mouse *Mus musculus* and fruit fly *Drosophila melanogaster* for the transmission ratio distortion (TRD) (Lewontin & Dunn 1960; Lyon 1984; Hartl *et al.* 1967) and in the common buzzard *Buteo buteo* and the Eleonora's falcon *Falco eleonorae* for non-random mating (Krüger *et al.* 2001; Walter 1979).

The fact that in the reverse case, of mixed pairs with the male of the dark morph and the female of the light morph, there are no significant differences between the proportions, expected and obtained, of offspring morphs is evidence that these differences are caused by the heterozygous males of the light morph. However, since the offspring were controlled as fledglings, the competition of selective phenomena in the nest cannot be ruled out, such as the death of embryos and due to differences in feeding and in the survival of chicks, favouring the dark morph. In this sense, in a study carried out in the province of Murcia, the fledgling productivity in reproductive events with mixed pairs was higher than in light morph pairs, although no significant differences were found (Martínez *et al.* 2016).

Moreover, we must rule out that the transmission of the dark allele is linked to sex, since dark morph chicks are produced both in mixed pairs with the dark morph male and also with the dark morph female.

Finally, the proportion of pairs with the two heterozygous light morph individuals of both species must also be much lower than expected from Hardy-Weinberg equilibrium results, suggesting selective mating of heterozygous light morph individuals with homozygous individuals of the same colour morph (Bosch *et al.* 2020).

This parallelism may support the earlier theory that these two species, together with the pygmy eagle of New Guinea, would constitute a superspecies due to similarities in size, proportions, plumage, and behavioural aspects (Ferguson-Lees & Christie 2001; Debus 2017). This similarity suggests that the three species likely share a common ancestor, or that the little eagle has derived into a different species by separating, at some point in history, from the population of the booted eagle or its ancestor, from which it thought to have originated. Therefore, raptor species show different degrees of differentiation with respect to their origins, leading to different genera, while others are conspecific with their Eurasian ancestors, such as the black kite *Milvus migrans* or Australasian pipit *Anthus novaeseelandiae* (Newton 2003).

The case of the little eagle could belong to the first assumption, a product of a radiation of migrating ancestor of booted eagles, which would have colonized the Australian continent for a long period of time in one or several radiations related to the Pleistocene glaciations, which would be contributed to the genetic variation by geographically isolating populations from each other (Taberlet *et al.* 1998; Negro *et al.* 2022), through the conglomerate of existing volcanic islands between the Eurasian continent and Australia. This period would extend from the Pliocene (from five to two million years ago) to the early to mid-Pleistocene (from 1.8 to 0.7 million years ago), when the extinct Haast's eagle, which inhabited the South Island of New Zealand, differed genetically from its predecessors, the booted eagle and the little eagle (Bunce *et al.* 2005).

It is known nowadays that most of Asian booted eagles winters on the Indian subcontinent. However, even today, a few of them reach Indonesia Sumatra (Zulkifli *et al.* 2012; Purwanto *et al.* 2015), Java, Bali (van Balen & Noske 2006; Nijman 2003), and the other islands of the Wallacea area, Bintan island (Seng 1997), Batam island (Rajathurai 2011), Lombok (Germi 2005), Timor, Flores, Sumba, Komodo, Sulawesi and the Moluccas (Eaton *et al.* 2016). All this conglomerate of islands is very close to New Guinea, where the pygmy eagle lives (Gjershaug *et al.* 2009), and also to the northern coast of Australia, so even in the absence of records, it would not be unreasonable to think that few booted eagles could reach New Guinea and/or Australia.

This study addresses mainly observable questions about the polymorphic patterns of the booted eagle and the little eagle, so future research lines may address the genomic aspects that give rise to these observed patterns (Bourgeois *et al.* 2017; Gangoso *et al.* 2015), as well as valuable insights on the evolutionary origin of these species and its divergence.

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