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Inheritance patterns of plumage coloration in common buzzards *Buteo buteo* do not support a one-locus two-allele model

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Balancing selection is a major mechanism to maintain colour polymorphisms over evolutionary time. In common buzzards, variation in plumage colour was reportedly maintained by a heterozygote advantage: heterozygote intermediates had higher fitness than homozygote light and dark morphs. Here, we challenge one of the basic premises of the heterozygote advantage hypothesis, by testing whether plumage colour variation in common buzzards follows a one-locus two-allele inheritance model. Using a long-term population study with 202 families, we show that colour variation in buzzards is highly heritable. However, we find no support for a simple Mendelian one-locus two-allele model of inheritance. Our results rather suggest that buzzard plumage colour should be considered a quantitative polygenic trait. As a consequence, it is unlikely that the proposed heterozygote advantage is the mechanism that maintains this genetic variation. We hypothesize that plumage colour effects on fitness might depend on the environment, but this remains to be tested.

1. Introduction

One of the big questions in biology is how genetic variation is maintained in populations over evolutionary time. Some proposed mechanisms involve balancing selection with a form of frequency-dependent feedback, resulting in fitness benefits to the rare allele [1]. Another form of balancing selection is overdominance, where heterozygotes have higher fitness than both homozygotes, but relatively few examples exist in natural populations [2,3].

A prime example of suggested overdominance in nature concerns the colour polymorphism observed in common buzzards *Buteo buteo* [4]. Colour polymorphisms are relatively common in raptors [5–8] and typically involve variation in the amount of melanization. Some evidence suggests that this trait variation is determined by simple Mendelian inheritance [9].

Common buzzard plumage varies along a light–dark continuum, but has been categorized into three morphs [10]: light, intermediate and dark. Parent–offspring resemblance was consistent with a one-locus two-allele model, whereby intermediates (supposedly the heterozygotes) had higher fitness than light and dark morphs (supposedly the homozygotes; [4]). However, this conclusion of
simple Mendelian inheritance with a one-locus two-allele model was based on sparse data: overall 162 offspring with \( n < 5 \) offspring for half of the parental combinations [4]. In two other bute...
additive genetic (1).

3. Results and discussion

In contrast to conclusions from a previous study on common buzzard morphs [4], we found no support for the one-locus two-allele model of inheritance (table 1). Across all scoring scenarios, the observed segregation deviated substantially from the expected one (table 1; electronic supplementary material, figure S1 and table S1). Most importantly, intermediate offspring were greatly overrepresented in intermediate × intermediate pairs and underrepresented in dark × light pairs. Intermediate × intermediate pairs should produce fewer intermediates (expected: 50%) than dark × light pairs (expected: 100%), but observed frequencies are significantly in the opposite direction (p < 0.001).

To assess why our conclusions deviate from those presented earlier [4], we compared sample sizes and observed offspring morph frequencies between the two studies (electronic supplementary material, table S2). The observed frequencies are remarkably similar and do not differ significantly even when using anti-conservative tests on count data that ignore the non-independence of offspring from the same nest or pair (all p ≥ 0.14 in electronic supplementary material, table S2).

Using our seven-morph classification, the animal model (model 1 in table 2) gives a heritability estimate for plumage colour of $h^2 = 0.82$ (95% CrI: 0.75–0.88). Shared nest environment and birth-year effects did not explain additional variation and neither did they alter the estimates of heritability, nor the maternal or paternal effects (model 2 in table 2). The effect of mother identity was not larger than the effect of father identity (table 2; 95% CrI of $(V_M-V_F)/V_F$: −0.1–0.1), suggesting no or minimal additional maternal effects (e.g. via egg composition) on offspring plumage colour. These results, combined with the observation that colour variation in our population is rather continuous and unimodal [10], suggest that plumage colour in buzzards should be considered a quantitive polygenic trait. This is contrary to conclusions based on inheritance patterns of melanic coloration in most other bird species [9], where the melanic forms can either be dominant [5,7,19] or recessive [8,20] (but note that this includes species with two distinct morphs [8,19,20] as well as species with a more continuous colour variation [5,7]).

In our buzzard population, plumage colour was highly heritable, independent of sex and not influenced by environmental factors (table 2). Quantitative genetic studies of plumage coloration in birds such as tawny owls Strix aluco [7], barn owls Tyto alba [21] and common kestrels Falco tinunculus [22] showed similar high heritability values ($h^2 = 0.80$, 0.81 and 0.67–0.83 respectively). This implies that selection can act on the trait and that the variance is either selectively neutral or a mechanism exists that keeps the polymorphism stable.

The maintenance of the colour polymorphism in common buzzards has previously been explained by heterozygote advantage (higher fitness of the intermediate morph), but the present results question this explanation. Under a one-locus two-allele model, heterozygote advantage is sufficient to maintain a stable polymorphism where both alleles should be equally common in the population. However, in a polygenic inheritance system as supported by our data, overdominance would not be an effective mechanism for maintaining many alleles at individual loci [23], and it is more likely that variation is maintained through genotype–environment interactions [24]. We suggest the testable hypothesis that the fitness effects of plumage colour are environment-dependent, which may explain geographical variation in morph frequencies [24].

**Ethics.** Birds were handled by personnel with ringing license (VT 930).

**Data accessibility.** Data are available from the Open Science Framework (https://osf.io/3947z) [25].

**Authors’ contributions.** E.F.K., C.B. and B.K. designed the study. C.d.V and A.A. collected the data. E.F.K. and W.F. analysed the data with input from B.K. E.F.K., C.B. and B.K. wrote the manuscript. All authors revised and approved the manuscript and are accountable for the work herein.

**Competing interests.** We have no competing interests.

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**Table 2.** Proportion of variances and their corresponding 95% CrI from animal models used to partition phenotypic variance ($V_P = 2.24$) into autosomal additive genetic ($V_A$) and environmental components of variance ($V_E = V_N + V_{res}$). The maintenance of the colour polymorphism in common buzzards has previously been explained by heterozygote advantage (higher fitness of the intermediate morph), but the present results question this explanation. Under a one-locus two-allele model, heterozygote advantage is sufficient to maintain a stable polymorphism where both alleles should be equally common in the population. However, in a polygenic inheritance system as supported by our data, overdominance would not be an effective mechanism for maintaining many alleles at individual loci [23], and it is more likely that variation is maintained through genotype–environment interactions [24]. We suggest the testable hypothesis that the fitness effects of plumage colour are environment-dependent, which may explain geographical variation in morph frequencies [24].

**References**


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