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INHERITANCE PATTERNS OF PLUMAGE MORPH IN SWAINSON'S HAWKS

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Persistent plumage polymorphisms (i.e., different plumage morphs within the same age class and sex of a breeding population) occur in a wide array of taxa. Polymorphisms are relatively common among raptors compared to other taxa, with 30% of raptors having some polymorphism (Fowlie and Krüger 2003) versus 3.5% of all avian species (Galeotti et al. 2003). Mechanisms and inheritance of morphological characteristics have been poorly examined in wild raptor populations, in spite of the regularity of multiple plumage morphs occurring within the same population in raptors.

Although morph inheritance has been rarely examined among wild raptors, Schmutz and Schmutz (1981) demonstrated that Ferruginous Hawks (*Buteo regalis*) generally followed the basic Mendelian inheritance pattern. The dark allele was dominant to the light, conforming to an autosomal one-locus, two-allele inheritance pattern. The Swainson's Hawk (*Buteo swainsoni*), unlike the Ferruginous Hawk, which exhibited dimorphic plumages (Schmutz and

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Table 1. Observed pairings of Swainson's Hawks in Butte Valley, California. Observed morphs are adult offspring of the observed parental pairings of the given morph classes (L = light, I = intermediate, D = dark). Total offspring indicates the total number of young observed from given parental morph pairings. Expected morph is the frequency of morphs expected from a one-locus, two-alleles controlling plumage morph with the dark allele incompletely dominant to the light allele. P reports the significance of the Chi-square test with a Monte Carlo of 100 000 replicates.

		OBSERVED MORPH			EXPECTED MORPH				
OBSERVED PAIRINGS	TOTAL OFFSPRING	L	I	D	L	I	D	X^2	P
L $\times$ I	7	3	4	0	3.5	3.5	0	0.14	1.00
I $\times$ I	4	0	3	1	1	2	1	1.50	0.90
I $\times$ D	19	0	12	7	0	9.5	9.5	1.32	0.36
D $\times$ D	1	0	0	1	0	0	1	N/A	N/A
Totals	31	3	19	9	4.5	15	11.5	1.69	0.21

Schmutz 1981), exhibits an ostensibly continuous variation of plumage polymorphism in the belly and underwing coverts. Such variation is not possible in a one-locus, two-allele inheritance pattern, and variations in the intermediacy of the individual may be controlled by other genes.

Swainson's Hawks have almost continuous variation in the belly, flanks, and underwing coverts, ranging from light to very dark. Generally, individuals are lumped into three basic morph types: light, intermediate, and dark (Clark and Wheeler 2001). Morph coloration of an individual does not appear to change over the course of an individual's lifetime, further indicating genetic, rather than environmental correlation (Briggs et al. 2010). In our study population, intermediate morph (66%) Swainson's Hawks have been more common than light (4%) or dark (30%) morphs among documented individuals (B. Woodbridge unpubl. data). Our objective was to examine the hypothesis that most morph variation in Swainson's Hawks is associated with a one-locus, two-allele system. Under this hypothesis, dark morphs are the result of being homozygous for a dark allele, light morphs were homozygous for the recessive light allele, and intermediate morphs heterozygous for the dark and light allele. This would be a one-locus, two-allele autosomal inheritance pattern, one that closely matches several other avian species, including the pattern observed in Ferruginous Hawks (Schmutz and Schmutz 1981) and Snow Geese (*Chen caerulescens*; Cooke and Cooch 1968). Using the above assumption, we can predict the proportions of offspring associated with each pairing type (e.g., light $\times$ intermediate), using simple Mendelian genetics. The link between juvenile morph and adult morph has not yet been established in any *Buteo* species, to our knowledge. Thus, we limited our analysis to individuals in Basic plumage (Pyle 2008) of known morph that had parents whose morph had also been documented.

METHODS

We conducted our study in the Butte Valley, California, (49°41′N, 122°00′W) from 1979 to 2007. We captured 247

adult hawks using bal-chatri traps baited with mice or a dho-gaza-style net with a live Great Horned Owl (*Bubo virginianus*) lure near nest sites (Bloom et al. 1992). We banded captured hawks with a 2-digit numeric color band for individual identification, in addition to a U.S. Geological Survey aluminum band. Adults were photographed opportunistically in hand over the course of the study to document morph. Nest sites were located by observation of nest-building, territorial behavior, and copulations early in the season (Apr–May), and prey deliveries late in the season (May–Aug). Nestlings were banded with U.S. Geological Survey aluminum bands 1–2 wk prior to fledging. This protocol was approved by the University of Nevada, Reno IACUC #00115.

Adults observed building nests, delivering prey, or actively defending the area immediately around the nest site were considered the parents of any nestlings. Extra-pair copulations (EPCs) have been observed in the population (B. Woodbridge unpubl. data), but we were unable to document the frequency in this population.

We categorized birds as light, intermediate, or dark morphs. Individuals were light if they had no visible melanistic plumage on their belly underneath the bib, flanks, or underwing coverts. Intermediate morphs had some melanistic plumage on their belly and flanks, although not always in their underwing coverts. Dark plumage of intermediate morphs never entirely covered the area under the bib, allowing the observer to distinguish the bib. The bib in dark-morph individuals was indistinguishable from the belly or flanks due to extensive pigmentation across those areas. Additionally, there was always some pigmentation in the underwing coverts (Briggs et al. 2010).

We used a chi-square test to examine differences between the expected and observed distributions of the results of observed morph pairings as well as the overall observed distribution of observed offspring. We used a randomization test of goodness-of-fit, due to low expected numbers in our sample, using a Monte Carlo simulation in SAS 9.1 to generate 100 000 replicates. A nonsignificant *P*-

value would indicate support for our hypothesis of a one-locus, two-allele system. We did not remove observations of multiple offspring from the same parents, which may present a potential pseudoreplication problem. However, pseudoreplication artificially inflates the Chi-square statistic; thus, the data seem significantly correlated when they are not (Hurlbert 1984). Thus, this test is a conservative estimate of power in this study. Each individual offspring would represent an independent sample if random and independent assortment of genes for each gamete were occurring.

RESULTS AND DISCUSSION

We photographically documented the morph of 31 adult Swainson's Hawks where morphs of both parents were also documented, representing four of the six possible breeding morph combinations; no recruits from light/light and light/dark pairings were observed. We did not observe any ''impossible'' individuals (i.e., individuals that could not be conceived with the one-locus, two-allele system; Table 1). Our observed data closely matched that expected from our hypothesis of a one-locus, two-allele system. No significant difference was detected in the overall frequencies of observed offspring and that predicted by Mendelian genetics ($\chi^2 = 2.04$; $P = 0.36$). Therefore, we accepted the null hypothesis, and have confidence that this polymorphism is likely controlled by a one-locus, two-allele gene. Although we were not able to statistically quantify the single offspring from the dark/dark pairing, we note that the individual produced was dark, following our predictions and providing further support for our hypothesis.

Our results were similar to, and not statistically different from, what would be predicted from a one-locus, two-allele system where the dark allele is incompletely dominant over the light. However, the possibility of EPCs is present, and future studies should address the parentage of nestlings to determine how reliable observational studies are in paternal assignment. Although EPCs are always a concern with observational studies, we had no way to correct for this possibility, and to our knowledge there are no published studies examining EPCs or extra-pair paternity in any predominantly monogamous *Buteo* species. An additional caveat of these results is the observation of polyandry in this population of Swainson's Hawks. Although no individuals included in this analysis were from known polyandrous nests, polyandry would provide additional uncertainty about the paternity of the offspring, and is difficult to confirm in our study area.

Offspring from the pairings of two homozogous individuals (i.e., light/light, light/dark, or dark/dark) are particularly useful for this analysis because there is only one possible morph outcome for each of those potential matings. However, we only observed one recruited offspring between two presumably homozygous individuals (i.e., a light/light, light/dark, or dark/dark pairing) to support our hypothesis. Although the one recruit that was observed

conformed to the hypothesized one-locus, two-allele system, we recognize that more offspring from pairing of homozygous individuals would help clarify the genetic underpinnings of this trait.

Similarly, Common Buzzards (*Buteo buteo*) may represent another system where a *Buteo* species has multiple morphs that may be associated with a one-locus, two-allele gene (Krüger et al. 2001). However, this study correlated offspring in juvenile plumage (Pyle 2008) with their parents in Definite Basic plumage. While it may be reasonable to assume that juvenile plumage type is correlated to future Definite Basic plumage (Howell et al. 2003), no study has correlated these plumages in any *Buteo* species. Other raptor species also seem to follow a one-locus, two-allele system. For example, the Eleonora's Falcon (*Falco eleonorae*) also demonstrates considerable heterogeneity in morph type (Ristow et al. 1998), and similarly follows the described one-locus, two-allele pattern we observed in Swainson's Hawks (Wink et al. 1978).

Future work should focus on determining the gene(s) associated with morph variation in Swainson's Hawks. One potential candidate is one or more point mutations in the gene controlling melanin production, the melanocortin-1 receptor gene (MC1R; Mundy 2005). This gene was found to be responsible for dark morphs in Snow Geese (Mundy et al. 2004), Parasitic Jaeger (*Stercorarius parasiticus*; Mundy et al. 2004), Red-footed Boobies (*Sula sula*; Baião et al. 2007) and Bananaquits (Theron et al. 2001). Although a point mutation of this gene could not explain all the variability observed in Swainson's Hawk plumages, it may be able to explain why individuals are light, intermediate, and dark. Future work will also need to focus on the genetic underpinnings of different levels of melanization between intermediate individuals. Understanding the mechanism of inheritance may help us determine the causes of the plumage polymorphism observed in this and other Swainson's Hawk populations, and have implications in the genetic underpinnings of this trait in other *Buteo* species.

PATRONES DE HERENCIA DEL MORFOTIPO DE PLUMAJE EN *BUTEO SWAINSONI*

RESUMEN.—La herencia de los polimorfismos basados en melanina es poco conocida a pesar de ser relativamente común entre las rapaces. Examinamos la hipótesis de que el plumaje oscuro se hereda mediante un sistema de un locus con dos alelos en *Buteo swainsoni*. Presumimos que los individuos de plumaje oscuro y de plumaje claro eran homocigotos, mientras que los heterocigotos presentaban alguna forma intermedia de plumaje. Examinamos el morfotipo de 31 adultos de *B. swainsoni* y los comparamos con los fenotipos parentales. Todos los individuos se ajustaron a nuestra hipótesis de herencia mediante un locus con dos alelos. No existió una diferencia significativa entre lo que se esperaría de acuerdo a ese sistema y lo que nosotros observamos, lo que representa evidencia adicional de

que el morfotipo en *B. swainsoni* está asociado con un patrón de herencia de un locus con dos alelos.

[Traducción del equipo editorial]

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