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Relationship between Red-tailed Hawk Polymorphism and Ectoparasite Load

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ABSTRACT.—Plumage polymorphisms are relatively common in raptors and often show relationships with climate and geography; however little is understood about what drives those relationships. Because melanin improves feather resilience and may reduce ectoparasites, we investigated whether this could be related to observed plumage clines in Red-tailed Hawks (*Buteo jamaicensis*). Specifically, we examined the relationships between amount of plumage melanization, age (i.e., adult versus juvenile), and ectoparasite loads in migrating Red-tailed Hawks in Marin County, California, USA. We found that adults with more melanin had lower ectoparasite loads, while juveniles did not show a relationship between plumage and ectoparasite loads. Greater feather melanization may contribute to raptors' resistance to ectoparasites.

KEY WORDS: *feather lice*; *migrant*.

RELACIÓN ENTRE EL POLIMORFISMO DE *BUTEO JAMAICENSIS* Y LA CARGA DE ECTOPARÁSITOS

RESUMEN.—Los polimorfismos de plumaje son relativamente comunes en las rapaces y a menudo denotan relaciones con el clima y la geografía; sin embargo, los motivos qué impulsan esas relaciones no son bien comprendidos. Dado que la melanina mejora la rigidez de las plumas y puede reducir la carga de ectoparásitos, investigamos si esto pudiera estar relacionado con las variaciones graduales en las características del plumaje observadas en *Buteo jamaicensis*. Específicamente, examinamos las relaciones entre la cantidad de melanina del plumaje, la edad (i.e., adultos versus juveniles) y la carga de ectoparásitos en individuos migratorios de *B. jamaicensis* en el Condado de Marin, California, EEUU. Encontramos que los adultos con más melanina tenían menores cargas de ectoparásitos, mientras que los juveniles no mostraron una relación entre el plumaje y la carga de ectoparásitos. Una mayor cantidad de melanina en las plumas puede contribuir a la resistencia de las rapaces frente a los ectoparásitos.

[Traducción del equipo editorial]

INTRODUCTION

Plumage polymorphisms (i.e., differing plumages within the same age and sex class within a population) occur in approximately 3.5% of bird species; however, the factors that maintain those polymorphisms are generally poorly understood in most species (Galeotti et al. 2003, but see review in Robinson et al. 2024). Relative proportions of morphs may also change across a species' range; this is often true for melanin-based plumages in

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large populations (Galeotti et al. 2003). For example, greater precipitation and humidity are often correlated with higher proportions of individuals that have darker plumage (i.e., more melanin; reviewed in Delhey 2017), and species with large distributions are likely to encounter large variations in climatic condition (Galeotti et al. 2003). This relationship can lead to clines in melanism in species with large distributions (Roulin and Randin 2015, Amar et al. 2019). Some melanin-environment relationships are well described, such as Tawny Owls' (*Strix aluco*) relationship with temperature, in which gray morphs are more tolerant of colder climates than rufous morphs (e.g., Roulin et al. 2003). Despite more detailed information of a few species, the mechanism of the observed clines in relative melanism and their relationships with spatial differences in environmental conditions are still often unknown.

Increasing melanization improves the strength of feathers by increasing abrasion resistance (e.g., Barrowclough and Sibley 1980, Burtt 1986, Schreiber et al. 2006), which may also provide resistance to feather ectoparasites (Burtt and Ichida 2004), such as feather degrading bacteria (Goldstein et al. 2004) or chewing lice (reviewed in Clayton et al. 2010). For example, Barn Swallows (*Hirundo rustica*) with larger white spots were preferred by chewing lice and the spots had greater incidence of breakage (Kose and Møller 1999) and more holes (Kose et al. 1999) relative to the melanized portion of the feather. Individuals with more chewing lice can have lower condition or survival, so lower ectoparasite loads may contribute to individual fitness. However, it is not clear whether invertebrate ectoparasite abundance is related to melanin concentration. For example, feather lice were equally fit when fed melanized and unmelanized feathers, and lice showed no preferences for Rock Pigeon (*Columba livia*) feathers based on their melanin characteristics (Bush et al. 2006). Because melanin may reduce food availability for ectoparasites, individuals with more melanin may have an advantage reducing feather wear and associated flight or thermoregulatory costs. Therefore, the clines in melanin may be related to feather ectoparasites' sensitivity to environmental gradients, such as temperature (e.g., Meléndez et al. 2014, Castaño-Vázquez and Merino 2022). In other words, ectoparasites could drive polymorphism clines through their inability to survive certain climates, reducing the need for melanin in areas with low ectoparasite loads.

Polymorphic species may provide good opportunities to test the relationship between plumage and ectoparasites generally, and even feather-chewing ectoparasites more specifically. Red-tailed Hawks (*Buteo jamaicensis*), like many species of buteos, can vary in amount of plumage melanin, including in the western subspecies (*B. j. calurus*; Wheeler 2003). Overall plumage melanization likely does not change over an individual's lifetime (Amar et al. 2013, Briggs et al. 2010, Kappers et al. 2017). Annual survival of Red-tailed Hawks is also correlated with endoparasite abundance (Briggs et al. 2022) and therefore demonstrates that parasites may be drivers of evolutionary change.

We investigated whether feather melanization was related to ectoparasite intensity of Red-tailed Hawks migrating through the Marin Headlands, California, USA. We predicted that if melanin can deter invertebrate ectoparasites or limit their populations then we would see fewer ectoparasites on individuals with more overall melanin. Because age is also often associated with ectoparasite load (Dowling et al. 2001, Hamstra and Badyaev 2009), we also examined how ectoparasites differed between age groups (i.e., whether adults or juveniles had higher ectoparasite loads), as older individuals may have more opportunity to pick up ectoparasites (e.g., Potti and Merino 1995). Migrating Red-tailed Hawks at this site tend to come from central California in the early migration season, and from the Great Basin later in the migration (Hull et al. 2009, Briggs et al. 2020), and therefore are primarily the western subspecies (*B. j. calurus*), which tends to be more polymorphic relative to most other Red-tailed Hawk subspecies.

METHODS

From 2015–2022, excluding 2020, we trapped migrating Red-tailed Hawks from August through December at banding stations in the Marin Headlands (see Hull et al. 2009 for details on trapping methodology). We banded hawks with US Geological Survey (USGS) bands and took morphometric measures (e.g., weight, wing chord, tail length, etc.). We classified birds as hatch-year (hatched in the current calendar year) or adult (all other birds). After capture, individuals were placed in a well-fitted tube as described in Hull and Bloom (2001). Tubes are only used once per day and sterilized by soaking in a 10% bleach solution at the end of the day to prevent transmission of parasites between individuals. While processing, the bander noted if birds had ectoparasites present. When ectoparasites were present, the bander subsequently classified ectoparasite presence: "Some" (i.e., 1–10 ectoparasites were observed in the process of handling that individual) or "Many" (i.e., >10 ectoparasites were observed while handling that individual). The bander classified the bird as having "None" if no ectoparasites were observed. The ectoparasite category included all invertebrate ectoparasites observed and did not differentiate between ectoparasite groupings (e.g., Mallophaga, Hippoboscidae, etc.; i.e., we did not differentiate hematophagus species that may not be affected by feather melanin, but see Dubey and Roulin 2014).

After processing, we photographed individuals to document plumage. One observer (EJZ) used the photographs to classify each individual on an ordinal 10-point scale from light morph with little melanization of the belly and breast (i.e., 1), to dark morph with full melanization of belly and breast feathers (i.e., 10; sensu Briggs et al. 2023).

Because processing time varied across individuals (e.g., due to number of birds captured), we used a one-way ANOVA to examine whether parasite intensity was related to handling time to ensure birds held longer were not more likely to have parasites observed (i.e., if longer handling time was associated with higher detection probability of ectoparasites). There was no difference in how long an individual was handled across our ectoparasite categories ($F_{2,941} = 0.381$; $P = 0.683$). We therefore excluded handling time from our overall analysis.

We used the *ordinal* package (Christensen 2023) in R 4.4.1 (R Core Team 2021) to create cumulative linked mixed-models regressions to examine whether our ordinal measure of ectoparasite load was related to plumage melanization or individual age (i.e., juvenile versus adult). Specifically, we used ectoparasite intensity as our response variable and age (i.e., adult versus juvenile), morph, and the interaction between age and morph as our predictor variables. Bander was used as a random effect to account for potential differences in banders' ability to detect parasites. We evaluated model performance using AIC$_c$ (Burnham and Anderson 2002). To visualize the model results we created estimates of the 95% confidence intervals for predicted probabilities of ectoparasite load across morphological scores by fitting a cumulative probit regression and we simulated 1000 draws from the posterior distribution of model coefficients. Predicted category probabilities were calculated over a range of values in a structured prediction grid.

RESULTS

During the study period we trapped, photographed, and documented the plumage of 944 Red-tailed Hawks. Of those, 53 were adults and 891 were juveniles. Of all individuals trapped, 420 were observed with ectoparasites, and 185 of those had many (i.e., >10 parasites) detected.

Juveniles appeared more likely to have ectoparasites than adults, though our regression estimate highly overlapped 0 (Fig. 1; $\beta_{\text{Adult}} = -0.18 \pm 0.87$). For adults, there was an inverse relationship between parasite load and percent of melanization ($\beta_{\text{Morph}} = -0.33 \pm 0.22$). Morph was not related to relative ectoparasite abundance for juveniles. However, there was support for a relationship between morph and adult relative ectoparasite abundance as the interaction of morph and age ($\beta_{\text{Age x Morph}} = 0.35 \pm 0.23$) was the best model by 7.1 AIC$_c$ units (Table 1; Fig. 2).

DISCUSSION

We found evidence for lower ectoparasite loads for adult Red-tailed Hawks with more feather melanin. This may be due to reduced prevalence of feather-chewing ectoparasites in darker plumage, or even from limited colonization of individuals with more melanin in their plumage. Similarly, Common Barn-Owl (*Tyto alba*) individuals with more dark spots experienced reduced ectoparasite egg laying (Roulin et al. 2001). More melanization may therefore inhibit some ectoparasite populations through decreased digestibility or even through increases of melanin in organ and muscle tissues, which may aid in endoparasite defense (Roulin et al. 2024).

For adults, melanin may help limit ectoparasite populations, which can confer large fitness benefits. For example, feather ectoparasites can reduce host reproduction (Fitze et al. 2004, Alves et al. 2021) and survival (Brown et al. 1995; but see Brown et al. 2006). Therefore, a reduction in ectoparasite burden would be highly selected for in long-lived species (Fitze et al. 2004) and may help explain slightly higher survival of dark morph Swainson's Hawks (*Buteo swainsoni*) compared to light morphs (Briggs et al. 2011). Because Red-tailed Hawks do not molt all feathers each year (Clark et al. 2004), reducing feather ectoparasite damage may be especially beneficial as some feathers may be retained for multiple breeding seasons. Alternatively, dark plumage may change the feather microbiome (Al Rubaiee et al. 2021), which may influence feather mites (Matthews 2024), and potentially the entire feather community structure. In contrast, gene(s) responsible for melanin in plumage may be pleiotropic with

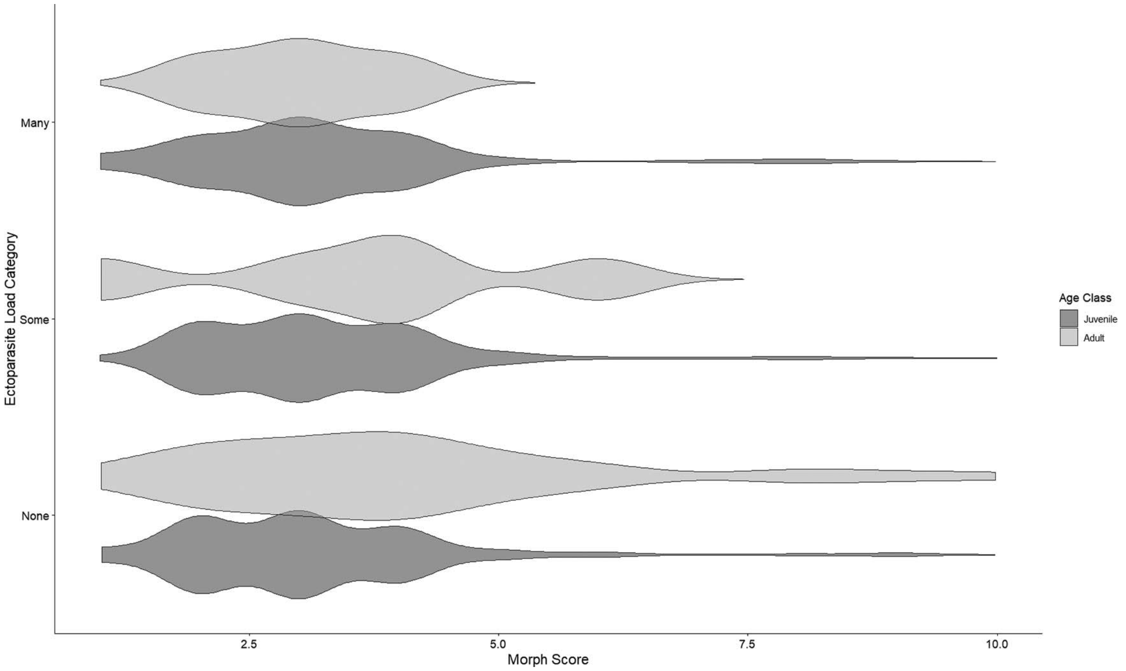

Figure 1. Violin plot of morph classifications of adult (light gray) and juvenile (dark gray) fall migrant Red-tailed Hawks trapped in Marin County, California, USA, between 2015 and 2022. Morph score was assigned on an ordinal 10-point scale, ranging from 1 (light morph, minimal melanization of belly and breast) to 10 (dark morph, full melanization of all belly and breast feathers).

other traits, such as behavior, or may influence immunity (e.g., Gangoso et al. 2015). Therefore, ectoparasite load may be a response to those other factors (e.g., Roulin et al. 2000, Ducrest et al. 2008).

In contrast to adults, juvenile Red-tailed Hawks did not differ in ectoparasite loads across melanization levels, despite similar overall levels of ectoparasites between the two age groups. It is unclear why darker adult plumage was associated with lower ectoparasite presence or abundance. Although ectoparasite communities and populations change seasonally and over the lifetime of an individual, there are often no differences in host ages (Hamstra and Badyaev 2009). However, when there are age differences, adults often had the greater ectoparasite burdens (Potti and Merino 1995, Takagi 2022). For example, adult Yellow-shouldered Blackbirds (*Agelaius xanthomus*) had higher parasite load, perhaps due to the increased energetic cost of

Table 1. Model results of factors related to ectoparasite load on migrant Red-tailed Hawks in Marin County, California, USA, from 2015–2022. Age is a binomial of adult versus juvenile, morph is an ordinal 10-point scale from light morph with little melanization of the belly and breast (i.e., 1), to dark morph with full melanization of all belly and breast feathers (i.e., 10).

Model	K	ΔAIC_c	AIC_c Weight	Log Likelihood	Cum. Weight
Age * Morph	7	0.00	0.96	−908.96	0.96
Day of Year	4	7.13	0.03	−915.56	0.99
Age	4	10.39	0.01	−917.20	1.00
Age + Morph	5	12.29	0.00	−917.13	1.00
Year	3	14.92	0.00	−914.38	1.00
Null	4	16.32	0.00	−921.17	1.00
Morph	4	18.34	0.00	−921.17	1.00

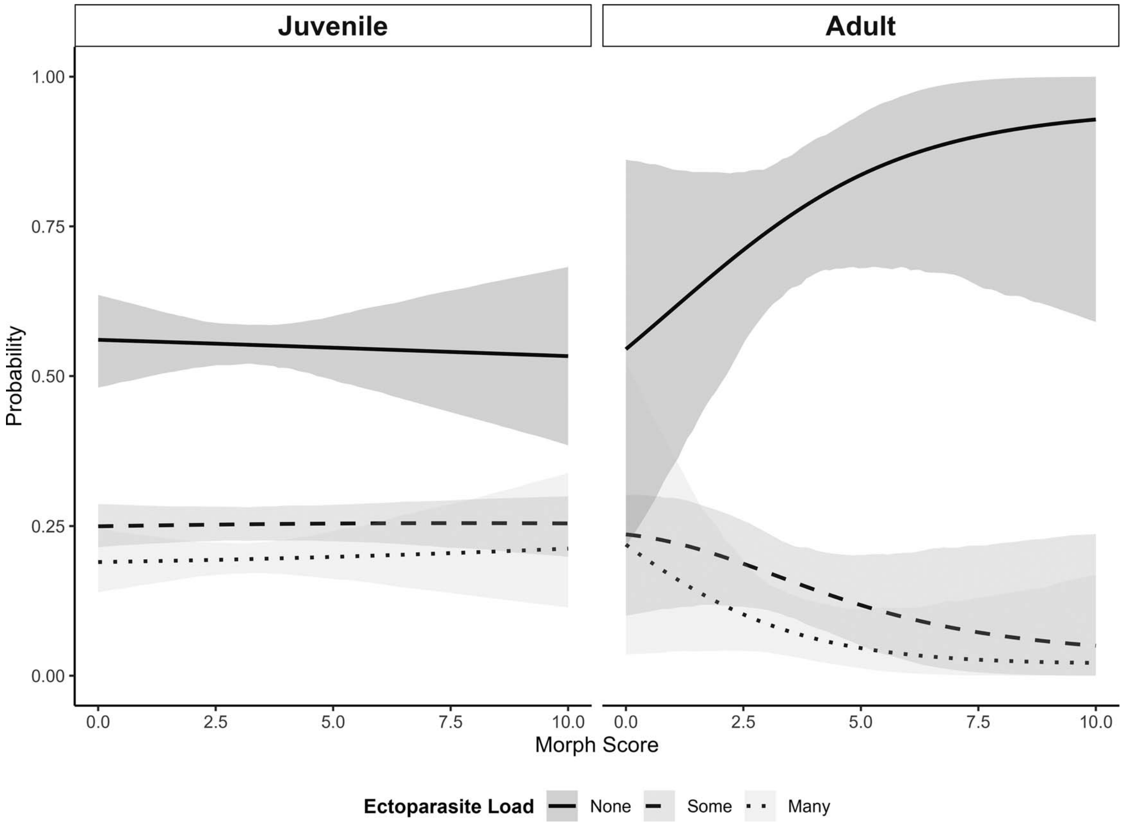

Figure 2. Mean predicted probability (±95% confidence interval) of Red-tailed Hawks exhibiting no (solid line), some (dashed line), or many (dotted line) ectoparasites, as a function of morph classification, for juvenile and adult fall migrants trapped in Marin County, California, from 2015–2022. Morph score was assigned on an ordinal 10-point scale, ranging from 1 (light morph, minimal melanization of belly and breast) to 10 (dark morph, full melanization of all belly and breast feathers).

breeding (Post 1981). As adult Red-tailed Hawks migrating through the Marin Headlands may have completed breeding months earlier, it is unclear whether breeding costs could carry over to ectoparasite burden when they are trapped during the fall. In addition, adult Red-tailed Hawks may have more recently molted, which may function to reduce ectoparasite burden relative to juveniles (Ash 1960, Post 1981, Moyer et al. 2002). It is also likely some of the adults trapped in our study may not have bred in the summer prior to capture as some individuals may forego breeding; and age of first reproduction is variable but often occurs after the second year (Preston and Beane 2024).

Behavioral differences between ages may also play a role in ectoparasite differences. For example, if young individuals are less efficient at hunting (e.g., Kitowski 2003, Penteriani et al. 2013), it may mean that juveniles have less time to devote to preening, which can lead to higher ectoparasite burdens (Clayton et al. 2010, Bush and Clayton 2023). In fact, Common Barn-Owls with more melanin preened less frequently than their lighter counterparts (Roulin 2007) and Rough-legged Hawks (*Buteo lagopus*) with higher ectoparasite loads were in lower body condition (Maron et al. 2024). However, adults captured in the Marin Headlands are, on average, in lower body condition (i.e., lighter relative to their size) than the juveniles (Briggs et al. 2022). Because most ectoparasite transmission is through physical contact from parents to offspring or through contact with other individuals (Proctor and Owens 2000), young birds from nests with siblings or interacting with other juveniles as they begin migration might have more opportunities to have horizontal transmission and proliferation of ectoparasites relative to adults.

Though we detected a relationship between ectoparasite load and plumage of adult individuals, we note that we did not quantify numbers of individual ectoparasites but instead took a coarse ordinal measure of ectoparasite load. The use of a more rigorous ectoparasite sampling (e.g., dust ruffling; Clayton and Walther 1997) would be beneficial for answering questions about overall parasite load (Moyer et al. 2002). Similarly, we did not assess ectoparasite diversity or different functional groups. Biting ectoparasites (e.g., ticks, hippoboscid flies, etc.) may not be affected by feather melanin unless those feathers create a better or worse microenvironment for them (Dube et al. 2018). In addition, feather melanin may not drive the relationship between ectoparasites and plumage, but instead those relationships could be mediated through skin melanin levels, which may also affect hematophagous ectoparasites (Dubey and Roulin 2014).

The drivers of this plumage polymorphism are likely a complex mix of selective pressures that maintain a balancing selection, which results in a stable polymorphism (e.g., Robinson et al. 2025). It may be that variable plumage within and between individuals is helpful as greater plumage variability may allow for easier detection of ectoparasite lice (Bush et al. 2019). Alternatively, other selective pressures, such as endoparasites, may create a balancing selection with plumage morphs (e.g., Chakarov et al. 2008). Similarly, other factors (e.g., climatic, solar radiation, etc.) could interact with parasites or create multiple selection pressures that create the complex mosaic of plumages sometimes present in species with large geographic distributions (e.g., Galeotti et al. 2003). In addition, ectoparasite loads may reflect an individual's underlying quality or condition that may be, in part, a function of the individuals' morph and their interaction with the environment. Future work would benefit from a more standardized and rigorous sampling approach to ectoparasite collection that more accurately counts both numbers of individuals and different taxonomic groupings, as well as documenting relative amounts of eu- and pheomelanin in those feathers.

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