


Phylogenetic analyses support flush-pursuit foraging and flocking behaviors as evolutionary drivers of flash plumage signals in North American passerines

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ABSTRACT

Animal coloration patterns are wildly variable. Despite this, there are plumage traits that occur similarly across taxonomic groups, suggesting the possible action of widespread selective regimes. Here, we investigate why so many avian species have “flash” plumage signals—color patches that are not visible when an animal is still but become visible with movement. Flash patches have been hypothesized to warn conspecifics of danger and coordinate prey escape behaviors among flocking species. Other hypotheses suggest that flash signals function in prey capture, species recognition, or social (including sexual) selection. To test these hypotheses, we scored 326 species of North American passerines for the presence of 3 flash and 2 static patches on bird rumps, wings, and tails. We combined those data with social and ecological information from available datasets and used phylogenetically controlled analyses to test the hypotheses that flash color patch evolution is driven by (1) flocking-associated behaviors, (2) social selection, and/or (3) foraging strategy. Our data show that flash signals are common among North American passerines, occurring in 54% of species, and that most wing and tail patches are white in color. We recovered evidence that rump flash patches can be predicted by winter flocking, migration, and diets specialized on plants, consistent with functions in flock cohesion or species recognition, as previously reported in shorebirds. Flash plumage patch evolution was not predicted by breeding system or territoriality and was therefore not consistent with social selection as a broad evolutionary driver. In contrast, we found evidence that the flush-pursuit foraging strategy predicts the presence of avian wing and tail flash patches. These results fit with multiple single-taxon studies that have shown flash plumage signals to function in flush-pursuit foraging. Our results underscore that natural selection, not just social selection, can drive the evolution of conspicuous coloration in animals.

Keywords: flash signals, flock cohesion, flush-pursuit foraging, passerine birds, plumage

How to Cite

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LAY SUMMARY

- Many animals use “flash signals” that only become visible when the animal moves, allowing for dynamic signaling to group-mates, potential predators, or other receivers.
- Among birds, flash plumage signals are often found on the wings, outer tail feathers, and rump; although these taxonomically widespread signals are similar in form, it is unclear whether they consistently serve the same functions across species.
- We tested multiple hypotheses about evolutionary pressures that might promote convergence in flash signals across North American passerines.
- Phylogenetically controlled analyses indicated that wing and tail flash plumage signals consistently coevolved with a flush-pursuit foraging strategy. Rump flashes, by contrast, were associated with migratory movement, winter flocking, and seed and/or fruit-based diets, consistent with a role for flock cohesion in their evolution.
- While social (including sexual) selection is thought to drive much of the evolution of conspicuous coloration in birds, our results suggest that particular foraging niches and movement strategies can underlie natural selection regimes conducive to the evolution of conspicuous coloration.

Los análisis filogenéticos apoyan los comportamientos de forrajeo mediante destello y persecución y de bandada como impulsores evolutivos de señales de destello del plumaje en paseriformes de América del Norte

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RESUMEN

Los patrones de coloración en animales son extremadamente variables. A pesar de esto, existen características del plumaje que aparecen de manera similar en diferentes grupos taxonómicos, lo que sugiere la posible acción de regímenes selectivos extendidos. Aquí, investigamos por qué tantas especies de aves tienen señales de “destello” del plumaje—parches de color que no son visibles cuando el animal está inmóvil, pero se vuelven visibles con el movimiento. Se ha planteado la hipótesis de que los parches de destello advierten a los congéneres sobre el peligro y coordinan los comportamientos de escape de las presas entre especies que se agrupan en bandadas. Otras hipótesis sugieren que las señales de destello funcionan en la captura de presas, en el reconocimiento de especies o en la selección social (incluyendo la selección sexual). Para probar estas hipótesis, evaluamos 326 especies de paseriformes de América del Norte usando la presencia de 3 parches de destello y 2 parches estáticos en la rabadilla, las alas y la cola de las aves. Combinamos estos datos con información social y ecológica de bases de datos disponibles y utilizamos análisis controlados filogenéticamente para probar las hipótesis de que la evolución de los parches de destello de color está impulsada por (1) comportamientos asociados con agrupación en bandada, (2) selección social y/o (3) estrategia de forrajeo. Nuestros datos muestran que las señales de destello son comunes entre los paseriformes de América del Norte, estando presentes en el 54% de las especies, y que la mayoría de los parches en las alas y la cola son de color blanco. Encontramos evidencia de que la presencia de parches de destello en la rabadilla puede ser predicha por la agrupación en invierno, la migración y las dietas especializadas en plantas, lo cual es consistente con funciones en la cohesión en bandada o en el reconocimiento de especies, como se ha reportado anteriormente en aves playeras. La evolución de los parches de destello del plumaje no fue predicha por el sistema de apareamiento o la territorialidad, y, por lo tanto, no fue consistente con que la selección social sea un impulsor evolutivo amplio. En contraste, encontramos evidencia de que la estrategia de forrajeo mediante destello y persecución predice la presencia de parches de destello en las alas y la cola de las aves. Estos resultados concuerdan con estudios en taxones individuales que han mostrado que las señales de destello del plumaje funcionan en el hábito de forrajeo mediante destello y persecución. Nuestros resultados subrayan que la selección natural, y no solo la selección social, puede impulsar la evolución de la coloración conspicua en los animales.

Palabras clave: aves paseriformes, cohesión de la bandada, forrajeo mediante destello y persecución, plumaje, señales de destello

INTRODUCTION

The widely variable color patterns of animals provide fertile ground for studies of evolutionary mechanisms and outcomes (Caro *et al.* 2017, Cuthill *et al.* 2017). Researchers have demonstrated that animal color patterns can be shaped by environmental factors, as well as by signaling functions including signaling availability to prospective mates, agonistic interactions, species recognition, predator avoidance, and more (Delhey *et al.* 2023, Dunn *et al.* 2015, Endler 1980, Hill 2006, Hill and McGraw 2006). While the functions of many animal visual signals are known, there are also recurrent color patterns for which widespread explanations are lacking (Brooke 1998 2010). One class of these is “flash” signaling—dynamic signaling via color patches that are not visible when an animal is still but that become visible with movement. Such signals are common across taxonomic groups, from insects to mammals (Brooke 1998, Loeffler-Henry *et al.* 2021, Murali 2018). In insects, many flash signals serve anti-predator functions (Loeffler-Henry *et al.* 2019). Early interpretations of flash signaling in birds and mammals were that these signals warned conspecifics of danger and coordinated prey escape behavior for animals in groups (Bildstein 1983, Buechner 1970, Estes and Goddard 1967). Grouping can be advantageous for multiple reasons, so flash signals could confer a range of benefits related to group cohesion during movement, foraging, and other activities (Krause and Ruxton 2002, Negro *et al.* 2020). Grouping, however, is not the only explanation for these traits. Among birds and mammals, flash signals may also function in contexts including identity signaling, mate choice, and flush-pursuit foraging (Brooke 1998, Caro *et al.* 2020, Hailman 1960). By examining multiple potential functions simultaneously, we can better elucidate the selective factors shaping flash signal evolution.

Avian flash plumage signals occur on multiple parts of a bird’s body, including the outer tail feathers, secondary wing feathers, and dorsal rump (Beauchamp and Heeb 2001, Brooke 1998). All 3 of these areas are revealed when a bird takes flight but are generally hidden when the bird is perched (Figure 1). Birds may also choose to reveal these patches in contexts other than flight by opening their wings or spreading their tails (Burt 1986, Lovette and Fitzpatrick 2016). Flash patches are, by definition, conspicuous when revealed, and

many avian flash-signal patches are white. White provides contrast against most colors and can signal feather quality, giving flash patches the potential for high signal value (Laczi *et al.* 2021, Mennill *et al.* 2003). In this way, flash color patches offer a dynamic signal that is conspicuous at particular times. Birds have evolved multiple strategies for balancing crypsis with conspicuousness; the flash-signaling strategy offers the advantage of rapid temporal control in some circumstances (Gomez and Théry 2007, Hutton *et al.* 2015, Schön 2009). Several hypotheses have been advanced to explain the widespread existence of flash signals across avian species. Here we examine whether evolutionary trait correlations support 3 sets of these functional hypotheses in a well-studied group of birds, North American passerines.

Hypothesis Group 1: Flash Signals Evolve to Promote Flocking Behaviors:

Across animal groups, flash color patches have been hypothesized to promote effective group movement, composition, and cohesion. In birds, flash plumage patches are revealed when an individual takes flight (Baker and Parker 1979, Brooke 1998). The appearance of that signal, therefore, indicates movement and could allow flock members to coordinate activity (Raveling 1969). Doing so should have advantages for general group cohesion, food finding, other resource access, and predator avoidance or deterrence (Krause and Ruxton 2002). Flocking is known to be an effective anti-predator strategy (Beauchamp 2021, Cresswell 1994, Goodale *et al.* 2020, Jullien and Clobert 2000). Signals that maintain flock cohesion and composition, therefore, could confer fitness benefits and evolve by viability selection. Additionally, conspicuous color patches on birds can promote species recognition (reviewed in Mason and Bowie 2020); early authors discussed whether flash plumage patches could function in this way (Baker and Parker 1979). If species recognition is particularly important for birds in flight or in other situations where the wings and tail are spread, then flash patches can be a highly effective signal of species identity, especially in mixed-species groups (Carney 1992, Justice 1996).

The group cohesion hypothesis for the function of animal flash signals has received mixed support. Some, but not all, group-living mammals have white rumps or tails that

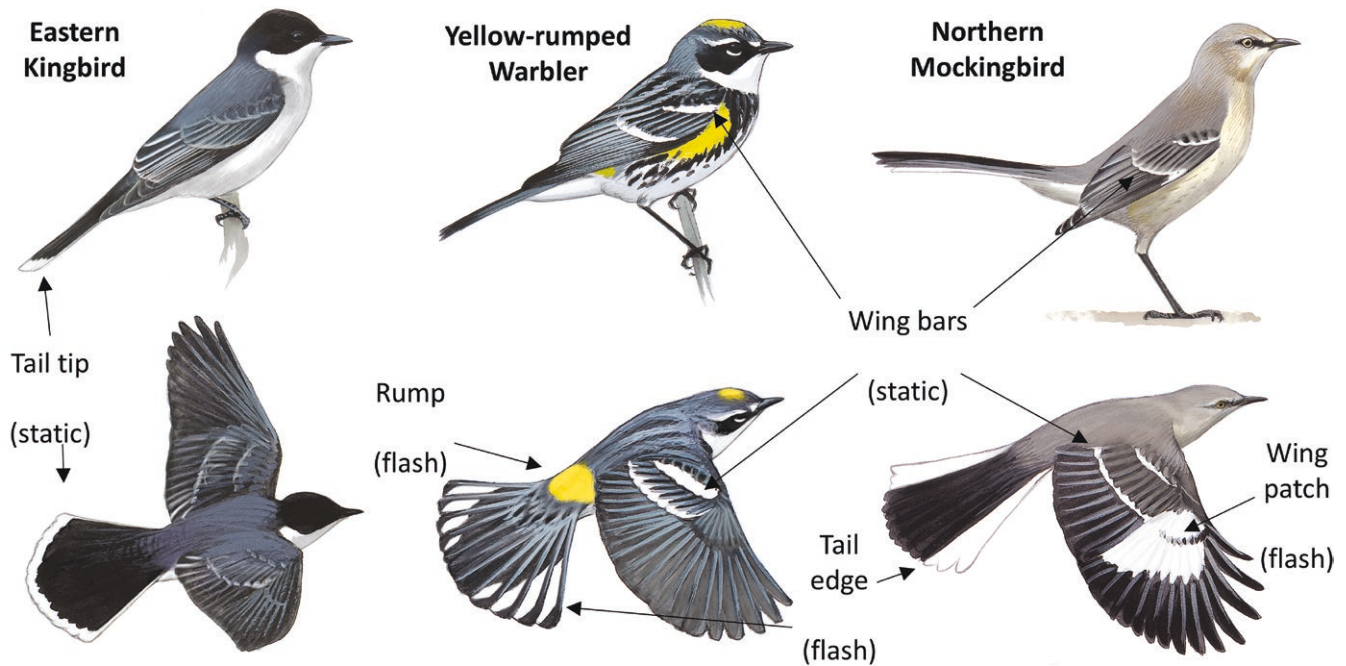


FIGURE 1. Examples of static (tail tip, wing bar) and “flash” (tail edge, rump, wing patch) plumage patches on 3 species of North American passerines. Illustrations © David Sibley (courtesy of *The Sibley Guide to Birds*, 2014, Alfred A. Knopf).

function in communication with conspecifics and could coordinate herd movements, though flash signaling in particular is not clearly associated with group-living (Caro et al. 2020). Among shorebirds in the order Charadriiformes and rails in the family Rallidae, flash plumage patches on the wings, back, and rump correlate with flocking and have been hypothesized to confuse or deter predators (Brooke 1998, Stang and McRae 2009). Across all avian groups, however, an analysis of 80 pairs of species found that flash signals did not correlate with social foraging, although white plumage in general did (Beauchamp and Heeb 2001). At a single-species level, experiments show that the white wing patches of *Myrmotherula axillaris* (White-flanked Antwren) do not serve to maintain flock cohesion (Botero 2002).

Our study extends existing work by testing for an evolutionary association between flocking behavior and the presence of flash plumage patches on the rumps, wings, and tails of 294 North American passerine species. Among this group, researchers have noted a number of species across different families that are (at least seasonally) open-country, flocking, ground foragers with flash signals (e.g., *Sturnella* meadowlarks, *Junco hyemalis* [Dark-eyed Junco], *Eremophila alpestris* [Horned Lark], and longspurs and buntings *Calcariidae*). One study found that winter flocking, ground-foraging birds were more likely to have flash plumage patches (Baker and Parker 1979). Therefore, we tested whether flocking, ground foraging, and habitat openness might promote flash signals among open-habitat species.

Our study also assessed whether flock composition might drive the evolution of flash-plumage patches. Flash signals of species identity could help birds with similar foraging ecology, and habitat requirements to quickly assort by species within mixed traveling groups (Jones and Robinson 2020). Mixed flocks often contain birds of similar sizes and colors, providing a functional opportunity for varied flash signaling of species

identity (Bangal et al. 2021, Sridhar et al. 2012, Zhou et al. 2022). Accordingly, we tested for an association between flash plumage signals and mixed-species flocking as a proxy for species recognition pressure. Alternatively, flash signals could help heterospecifics to form appropriate mixed flocks if they all use similar flash signals (Kimball et al. 2023). In that case, we would also expect to see elevated rates of flash signals among species that join mixed-species flocks, but as an indicator of guild-affiliation, rather than species identity.

Hypothesis Group 2: Flash Signals Evolve via Sexual and/or Social Selection

Avian color patches can signal social status and can indicate quality in mate-choice situations (Hill and McGraw 2006). Classic examples of this phenomenon are the white forehead and white wing patch in *Ficedula hypoleuca* (Pied Flycatcher), which function in both intra- and inter-sexual selection (Järvistö et al. 2013, Morales et al. 2014, Qvarnström et al. 2000, Török et al. 2003). The *F. hypoleuca* color patches are static (visible on a perched bird), but many birds also use flash color patches in mate selection or competition, and others use plumage patches that are minimally visible on perched birds but enlarge when the bird flies, to create a partial flash. Examples include the white wing bars of *Passer domesticus* (House Sparrow), the yellow wing stripes of *Spinus spinus* (Eurasian Siskin), and the white wing spots of *Setophaga caerulea* (Black-throated Blue Warbler), all of which function in intra- and inter-sexual selection (Cline et al. 2016, Moreno-Rueda and Hoi 2012, Senar et al. 2005). Many species with tail markings use those tails in display, often in ways that incorporate flash signals (Fitzpatrick 1998). Species including *Vermivora chrysoptera* (Golden-winged Warbler), *S. cerulea* (Cerulean Warbler), and *Hirundo rustica* (Barn Swallow) have flash marks on their tails that indicate individual quality (Jones et al. 2017, Purves et al. 2016, Saino et al. 2015).

Like any color patch, flash signals might evolve due to social (including sexual) selection. Levels of social selection are hard to quantify across all species, so we sought relevant proxies. Mating systems can drive levels of sexual selection, with polygyny and polyandry expected to select for elaboration of male and female signaling traits respectively (Emlen and Oring 1977, Shuster 2009). Research has supported this link in multiple bird species, and levels of polygyny and polyandry have been used in previous large-scale analyses of trait evolution (Collet *et al.* 2012, Delhey *et al.* 2023, Iglesias-Carrasco *et al.* 2019). Competition over territorial resources can also drive sexual and social selection (Pärt and Qvarnström 1997, Searcy 1979, Tobias *et al.* 2016). Accordingly, we tested the hypothesis that social selection promotes the evolution of flash plumage signals by looking for an association between flash signal presence and 3 measures of mating system and social competition. We used levels of social polygyny as a proxy for sexual selection in males, social polyandry for sexual selection in females, and territoriality as a proxy for selection on territorial signaling, following Delhey *et al.* (2023). In all cases, we tested for patterns among males and females separately because it is possible for the 2 sexes to experience different social selection regimes. For example, plumage dichromatism in some North American passerine groups has been attributed to losses of color among females experiencing reduced social selection pressure relative to males (Shultz and Burns 2017, Simpson *et al.* 2015).

Hypothesis Group 3: Flash Signals Evolve in Conjunction with Diet and Foraging Strategy

Focused studies of individual species have revealed that birds use flash plumage patches during flush-pursuit foraging (Peltier *et al.* 2019, Randler 2016). Evidence for this function has been particularly well documented in American parulid warblers that use their flash patches to flush insects (Mumme 2002, 2014, Mumme *et al.* 2006). Most insectivorous birds glean their prey, rather than using a flush-pursuit strategy (Jabłoński and McInerney 2005). Thus, despite the strong empirical evidence that flash patches can function in this capacity, it is unclear how widespread or important this factor might be in driving flash plumage evolution across larger groups of birds. We gathered data on flush-pursuit foraging and used that information to test whether contrasting wing patches and outer tail feathers coevolved with this foraging technique. Tail and wing flashes are both used to flush prey and were therefore predicted to coevolve, but flush-pursuit foraging should not promote rump flash patches (Hailman 1960, Mumme 2014). For comparative purposes, we also assessed whether tail, wing, and rump flash patches were predicted by an insectivorous or granivorous diet more generally.

In the study reported here, we simultaneously tested the 3 groups of hypotheses detailed above for the function of avian wing, tail, and rump flash plumage patches. We compared the occurrence and covariates of flash patches with the occurrence and covariates of 2 static color patches that serve as a form of control: wing bars and tail tips. We report on the prevalence of these plumage patches among North American passerines, and we explore patterns of phylogenetic conservatism among these plumage traits. We note that none of the hypotheses listed above are mutually exclusive and that there is overlap between our hypothesis groups; we recognize that

species might use flash plumage signals in varied ways, and we looked for evidence that multiple factors might drive the evolution of flash signals in birds.

METHODS

Plumage Scoring

We chose to use North American passerines as our test group because they are well-studied, consistently illustrated, and species descriptions are detailed for this group in the *Birds of the World* (formerly *Birds of North America*) reports (Billerman *et al.* 2023). Plumage scoring for all 326 species was done by 2 observers using *The Sibley Guide to Birds* (Sibley 2009), which illustrates all passerine species in a series of set poses. Observers recorded the presence of 2 static plumage color patches, and 3 flash plumage color patches as defined below. When the first 2 observers did not agree on the presence or absence of a flash patch, a third observer broke the tie. Patches could be any color. Observers noted the color of each patch, as well as the color of the plumage surrounding the patch. Patches were scored for adult breeding plumage, although most adult color patches did not change across seasons or molts.

We scored the presence of 2 static plumage color patches: wing bars and contrasting tail tips (Figure 1). Wing bars are stripes formed by contrasting color at the tips of the primary or secondary coverts, relative to the background wing colors. Tail tip patches occur when the tips of all rectrices contrast with the background tail colors. This must be true of the central rectrices, as well as outer rectrices, for tails to be scored as having distinct tail tip patches instead of tail edge patches. Both wing bars and tail tips are visible on a perched bird. We scored the presence of 3 flash plumage color patches: wing patches, tail patches, and rumps (Figure 2). Wing flash patches are patches of color that contrast with the background colors of the wing, and for which the majority of the patch area is not visible when the wing is closed. Tail flash patches include patches of color on the outer rectrices that contrast with the background colors of the closed tail, and for which the majority of the patch area is not visible when the tail is closed. Tail flash patches took multiple forms, including uniquely colored outer rectrices, spots on outer rectrices, and “tail corners” with contrasting coloration on the tips of the outer rectrices. Rump flash patches occur when a bird’s rump color contrasts with the colors of its back. When perched, the rump is covered by the bird’s folded wings, making the rump patch most visible in flight.

We scored all flash patches on dorsal body surfaces, as these are most consistently illustrated in our sources, and would be most visible to flock-mates. Rump patches, in particular, are only visible from above or behind. The majority of wing flash patches were produced by primaries and secondaries, and therefore dorsal colors would be visible on the ventral side of the wing as well. Tail flash patches would also be visible from below in flight, and sometimes while a bird is perched.

Non-Plumage Trait Scoring

Flocking

We scored winter flocking and mixed-species flocking from data in the *Birds of the World* reports (Billerman *et al.* 2023). We selected winter flocking as our main flocking variable because it is common, widespread, and has previously been

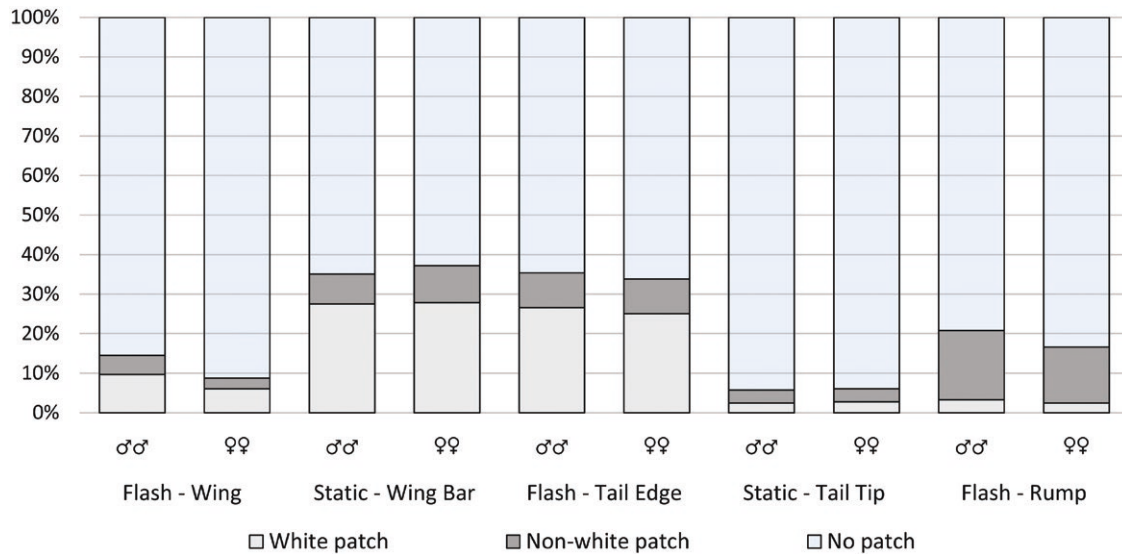


FIGURE 2. Percentages of male and female North American passerines with 5 types of plumage coloration patches. Static patches are visible on perched birds. Flash patches are revealed when birds move.

associated with flash signals (Baker and Parker 1979). Winter flocking captures overall flocking behavior, as species that flock in the breeding season or during migration also flock in the non-breeding season. To test our hypothesis that flash signals are used in species recognition we scored whether each species typically joins nonbreeding mixed-species flocks, here defined as groups of 2 or more species moving and foraging together (Morse 1970); such associations exclude aggregations around static resources such as fruiting or seeding plants, pools of water, or food aggregations. Winter and mixed-species flocking behavior was scored as either present or absent for each species.

Habitat

To account for variation among habitat structure and visual environments that could impact flash signaling, we scored species for the relative openness of their typical environments. To this end, we simplified the habitat openness scores of Delhey *et al.* (2023) to include only 3 levels: 1 = closed (forest), 2 = varied or intermediate (e.g., shrublands), and 3 = open (desert or grassland). We then scaled this variable and treated it as numerical, such that its coefficient estimate magnitudes can be directly compared with the other numerical variable predictors in our analyses. As a prior study (Baker and Parker 1979) found that flash signals were disproportionately common among ground-foraging birds, we also included as a predictor variable the fraction of foraging time spent on the ground (Wilman *et al.* 2014). This variable incidentally also captures some variation in habitat openness, as open-country birds are more likely to be ground-foragers than are forest birds.

Foraging and diet

We scored whether or not each species was a flush-pursuit forager using descriptions of foraging behavior in the *Birds of the World* reports (Billerman *et al.* 2023). Because the specific terminology used in species accounts varied, we defined “flush-pursuit” behavior according to (Remsen and Robinson 1990) as deliberately flushing or dislodging prey from a substrate and then chasing it. Where possible, we used quantitative measures of foraging behavior to deter-

mine if this maneuver is frequently used by the species; we scored species that infrequently or uncommonly flush-pursue prey as not using the behavior. Finally, we obtained data on species’ diets from the EltonTraits database (Wilman *et al.* 2014). This database had 5 categories representing the diet of the passerines in our dataset. To prevent model-fitting issues, we collapsed these 5 categories into 3 categories. Specifically, we combined those species categorized as eating fruit and nectar ($n = 3$) with those categorized as eating plant material and seeds ($n = 43$) into a new category representing plant-based diets. We also combined those species scored as having omnivorous diets ($n = 62$) with those scored as eating vertebrates or fish or scavenging ($n = 2$). Our final 3 diet categories were plant-based diets, omnivorous diets, and insectivorous diets.

Social selection

To investigate the hypothesis that variation in social selection regimes among species explains the evolution of flash signals, we included 3 predictors that may collectively describe such regimes. We represented the intensity of sexual selection on males with a variable representing the extent of social polygyny, and similarly represented the intensity of sexual selection on females with a variable representing the extent of social polyandry. We sourced scores for both of these from Delhey *et al.* (2023) and noted that both variables represent social and not genetic definitions of breeding systems as they are based on social breeding system descriptions.

As many bird species engage in signaling to establish and defend territorial boundaries, the extent of territoriality also represents a dimension of avian social selection regimes (Tobias *et al.* 2016). To represent this dimension of social selection, we included the extent of territorial behavior as a predictor variable in analyses, following the scoring approach of Tobias *et al.* (2016), with 3 levels corresponding to non-territoriality, weak or seasonal territoriality, and year-round territoriality. As for habitat openness, we scaled this variable and then treated it as a numerical variable, such that its estimated coefficients in models can be directly compared to those of the other numerical variables.

Other

As general controls, we included measures of body size (log body mass) and migration behavior in our models. Some work has shown that smaller birds are more likely to have flash plumage patches than large birds (Baker and Parker 1979, Billerman *et al.* 2023). Migration is known to covary with sexual dichromatism and could affect estimates of winter flocking (Dale *et al.* 2015). We compiled body mass data from avian body mass compendia (Dunning 2008). We scored migration behavior from range maps (BirdLife International and NatureServe 2014). For any species where range maps indicated migratory behavior at any level (partial migration, facultative migration, or obligate migration), the species was scored as migratory.

Scoring frequencies for categorical predictor variables described above can be found in [Supplementary Material Table 1](#). The entire dataset used in analyses is found in [Supplementary Material Dataset 1](#).

Analyses

We compiled descriptive statistics about the presence or absence and color of each static and flash plumage patch scored across our focal group of species, separated by sex. We then matched compiled data for each species to a large, species-level phylogenetic tree for birds (Burleigh *et al.* 2015). Ultimately, we were able to match 294 species with comprehensive data for predictor variables and plumage patches in phylogenetic generalized linear models. We estimated phylogenetic signal for each plumage patch by calculating the scaled Fritz-Purvis *D* statistic (Fritz and Purvis 2010) for each sex separately. We report *P*-values based on the distribution of *D* from 1000 simulations of trait evolution without phylogenetic signal, and with phylogenetic signal as seen if the binary trait is a function of an underlying continuous trait evolving by Brownian motion. To examine evolutionary associations between other traits and the presence of the different plumage patches, we fit phylogenetic generalized linear models as phylogenetic logistic regressions (Ives and Garland 2010) using the R package *phylolm* (Ho and Ane 2014), with the presence or absence of plumage patches as the binary response variable. We used a model selection framework (Burnham and Anderson 2004) to ask whether presence of each plumage patch is predicted by body size (log-transformed), migration, habitat openness, winter flocking, ground foraging frequency, mixed-species flocking, polygyny, polyandry, territoriality, flush-pursuit foraging, and diet. We fitted a full model with all these predictors and all simpler subset models. We performed model selection for each of our 5 scored color patches as a response variable; static wing bar and tail tip signals, and flash wing, tail, and rump patches, using AIC as a criterion. We report the top model by AIC for each of the response variables. We then visualize variable coefficients for all predictor variables for the set of models with $\Delta\text{AIC} < 10$, for each combination of patch trait as response variable and sex as a way to account for model uncertainty and to demonstrate levels of consistency in the magnitudes and signs of variable coefficients across models. Ives and Garland (2010) suggest caution in employing model selection with large numbers of predictor variables in these analyses. However, we preferred to employ model selection over hypothesis testing with individual variables given that 2 of our hypotheses are represented by multiple predictor variables. Furthermore, our analyses are necessarily exploratory to some degree in that there is rela-

tively limited literature on the evolution of flash signaling in passerine birds, and very limited prior evidence on their evolution employing phylogenetic comparative methods. Thus, we focus on positive evidence for the presented hypotheses recovered via model selection in this study. In doing so, we rely on the relatively large sample of species in analyses ($n = 294$) and consistency in coefficient estimates across models to allay concern regarding potential inflation of coefficient estimates in phylogenetic logistic regression (Ives and Garland 2010).

RESULTS

In total, we scored static and flash plumage patch presence for 326 passerine species with ranges in North America. One-hundred-and-seventy-nine (54%) of these species had at least one flash plumage signal, while 180 (54%) had at least one of the static plumage signals we scored. Forty-three species (13%) had both static and flash plumage patches, often on different parts of their body. Wing bars (static) were the most common visual color patches that we scored, occurring in 123 species (Figure 2). The most frequently scored flash patches were tail edges, occurring in 117 species (Figure 2), with fewer species exhibiting wing ($n = 48$) and rump ($n = 69$) flash signal coloration. Static tail tip patches were the least frequently observed color patches (Figure 2). Wing and tail patches were predominantly white in coloration, while the majority of rump patches were colors other than white (Figure 2).

Phylogenetic Signal in Plumage Patches

Estimates of Fritz-Purvis *D* for plumage patch traits are found in [Table 1](#). A value of 0 corresponds to the level of phylogenetic signal expected under Brownian motion of a continuous trait (underlying a binary trait via a threshold value calibrated to yield observed prevalences), and a value of 1 corresponds to a trait randomly distributed across the phylogenetic tree. Negative values indicate that the phylogenetic signal is stronger than expected under Brownian motion of an underlying continuous trait, and values greater than 1 indicate traits that are overdispersed on the phylogeny (less phylogenetically clustered than random). Values for our plumage contrast traits varied from -0.092 to 0.502 (Table 1). Our analyses of the plumage patches that we scored rejected the null hypothesis of random distribution on the phylogenetic tree for all traits in both sexes, indicative of phylogenetic structure for all traits. Phylogenetic signal was broadly similar for each trait in females and males, with rump contrast showing the largest difference in Fritz-Purvis *D* between sexes.

Evolutionary Associations with Other Traits

To test our hypotheses about the function and evolution of flash color patches in birds, we ran phylogenetically controlled models to examine associations between color patch presence and multiple avian traits relating to flocking social/sexual selection, and foraging strategy. We further controlled for body mass and migratory behavior in these analyses. We present the results for each fitted model in the [Supplementary Material](#), including α (the measure of phylogenetic signal in our phylogenetic logistic regressions; Ives and Garland 2010), AIC, ΔAIC , coefficient estimates, and standard errors in [Supplementary Material Results 1](#). [Figures 3–5](#) show coefficient estimates for all models with $\Delta\text{AIC} < 10$. In these figures, larger points correspond to coefficient estimates from

TABLE 1. Phylogenetic signal, estimated as Fritz-Purvis D , for the presence of “static” plumage patches visible both in flight and at rest, and “flash” patches visible in flight. The 2 P -values represent the probability of finding the estimated D under random positioning across tips (no structure) or under Brownian motion for a thresholded continuous value underlying the binary trait.

Trait	Sex	D	P (no structure)	P (Brownian motion)
Static patches				
Tail tip contrast	F	0.152	0	0.392
Tail tip contrast	M	0.103	0	0.448
Wing bar	F	-0.031	0	0.587
Wing bar	M	-0.002	0	0.502
Flash patches				
Tail edge contrast	F	-0.092	0	0.671
Tail edge contrast	M	-0.092	0	0.692
Wing contrast	F	0.426	0	0.111
Wing contrast	M	0.429	0	0.048
Rump contrast	F	0.502	0	0.014
Rump contrast	M	0.36	0	0.046

better models. Positive values indicate greater probabilities of gaining the relevant color patch, and negative values indicate greater probabilities of losing the appropriate color patches in conjunction with the relevant predictor. Model coefficients for each variable indicate the change in the log odds of the presence of each signal. Coefficient estimates from the best model by AIC are shown in black, with bars indicating standard errors. Large error estimates resulted from uneven trait distributions across the dataset; in particular, flush-pursuit foraging results have high standard error because only 9 species in the dataset were reported to use this foraging strategy.

We report the phylogenetic signal parameter α and 2 different pseudo- R^2 values for the best model by AIC for each trait/sex combination in the figure legends. To assess the explanatory power of the models, we calculated 2 versions of (Ives 2019), which compare the likelihood of a full model (in this case the best model by AIC) to that of an intercept-only model. We report ρ , that reflects both what is explained by the predictors and what is explained by phylogenetic effects, and ρ_{rel} , which reflects what is explained by the predictors relative to an intercept-only model that accounts for phylogenetic effects. We emphasize that log body mass, ground foraging activity, habitat openness, social polygyny, social polyandry, and territoriality were continuous variables scaled so that their magnitudes can be directly compared as a measure of effect size, whereas the remaining variables were categorical. Interpretation of reference group vs. other states is explained in the captions of Figures 3–5.

Model results differed across plumage patches and to a limited degree between sexes. We present coefficient estimates across all models in Figures 3–5, such that the consistency of the magnitudes and signs of variable coefficients can be compared across fitted models. Generally, this consistency was high, in that coefficients with more substantial magnitudes were highly consistent in sign across models. We proceed to evaluate the evidence from the best model in the context of the coefficient comparisons across candidate models (those models with a delta AIC < 10).

Flash Patch Models

Across sexes, wing patch flash models were predicted to occur at a greater frequency in larger birds with plant-based diets

(seeds, fruits, and/or nectar), and at lower frequency in smaller birds with invertebrate diets. Evidence for an association with flush-pursuit foraging, was strong in females (in which flush-pursuit foraging was a variable in the best model by AIC), and modest in males when examining the candidate model set, where the coefficient estimate was universally positive (although variable) when present, across models (Figure 3). This sex difference resulted from a higher background rate of flash patch presence among males. Additionally, there was evidence for a positive association of wing patch flashes with mixed flocking in males, whereas this coefficient varied between negative and positive values in the candidate model set for females.

Tail edge flash models showed support for an association with flush-pursuit foraging in both females and males (Figure 4), with large coefficients but also large standard errors. No other variables entered the best models for tail flashes in either sex, though migration was positively associated with, and invertebrate diets negatively associated with, tail edge flashes whenever included in male models.

Across both sexes, rump flash patches were positively associated with plant-based diets, smaller mass, migratory movement, and winter flocking (Figure 5). All these variables were present in the best model by AIC for each sex and were consistent in sign as coefficients across models in the candidate model set. Rump contrast patches were negatively associated with an invertebrate diet and flush-pursuit foraging.

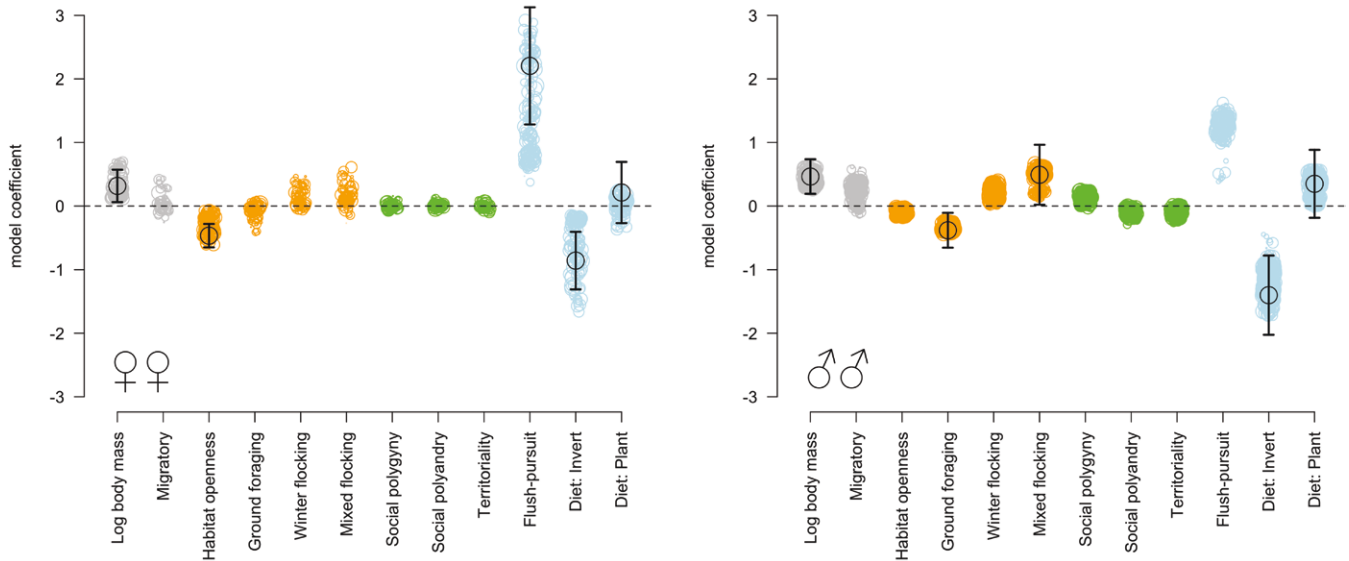
Static Patch Models

Models for tail tip patches did not reveal strong candidates for evolutionary drivers. The intercept-only model was the preferred model by AIC for both sexes. In the other candidate models, flush-pursuit foraging was negatively associated with tail tip patches while the other variables had coefficients generally near zero. Across both sexes, wing bars were positively associated with migration and plant-based diets, and negatively associated with increasing mass, social polygyny, and flush-pursuit foraging.

DISCUSSION

More than half of all North American passerine species have flash plumage signals, with wing flash patches occurring in

Flash - Wing patch



Static - Wing bar

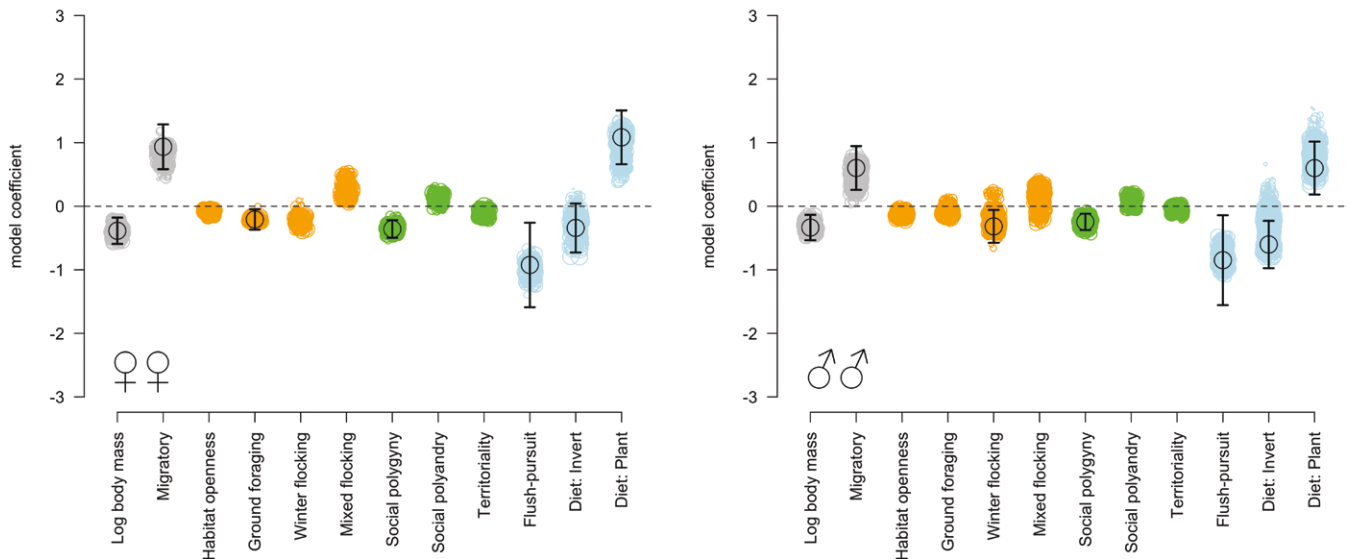


FIGURE 3. Model coefficients from phylogenetic logistic regression model sets testing for evolutionary associations between wing color patch presence and other traits. Point color relates to functional hypotheses for flash patches as indicated in the text: flocking (orange) variables include habitat openness, ground foraging, winter & mixed flocking, social/sexual selection (green) variables include polygyny, polyandry, territoriality, and foraging strategy (blue) variables include flush-pursuit foraging, diet. Coefficients are shown for all models with $\Delta AIC < 10$. Coefficient estimates from the best model by AIC are shown in black, with bars indicating standard errors. Point size is scaled by model fit, such that the best models have the largest points. For categorical predictor variables, coefficients indicate the change in log odds associated with being migratory, engaging in winter flocking, using flush-pursuit foraging, and having either an invertebrate or plant diet versus an omnivorous diet. The remaining variables (log body mass, habitat openness, ground foraging activity, and territoriality) were treated as numerical variables and were scaled such that their coefficient magnitudes can be compared. α , $R^2_{lik_full}$, and $R^2_{lik_pred}$ for the best models for each sex/patch combination were as follows: Female wing patch: $\alpha = 0.023$, $R^2_{lik_full} = 0.260$, $R^2_{lik_pred} = 0.229$. Male wing patch: $\alpha = 0.071$, $R^2_{lik_full} = 0.232$, $R^2_{lik_pred} = 0.162$. Female wing bar: $\alpha = 0.029$, $R^2_{lik_full} = 0.460$, $R^2_{lik_pred} = 0.176$. Male wing bar: $\alpha = 0.033$, $R^2_{lik_full} = 0.424$, $R^2_{lik_pred} = 0.116$.

15% of species, rump patches in 21% of species, and tail flash patches in 35% of species. On wings, flash patches are less common than the static signal that we measured, wing bars, suggesting wing flash patches are not widely favored by selection as a signal. Tail flash patches, in contrast, are much more abundant than static tail tip coloration, suggesting that flash

coloration on a bird's hind end might be favored by selective advantages in many biological circumstances. The high rate of tail flash patches matches what is often seen in mammals, where tails have contrasting color patches known to be important flash signals (Caro *et al.* 2020). It also fits with work demonstrating that birds display tail flash patches in multiple

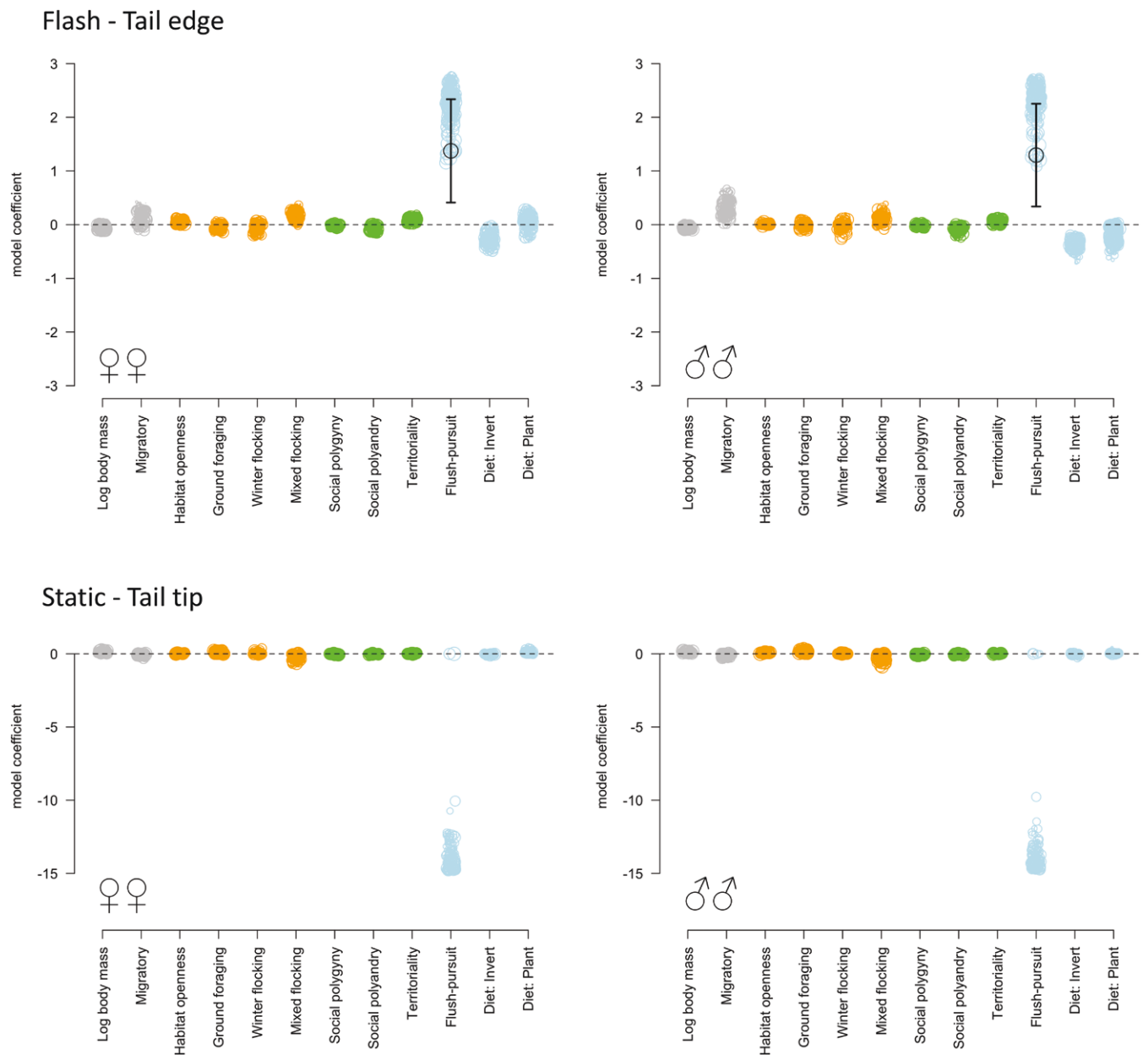


FIGURE 4. Model coefficients from phylogenetic logistic regression model sets testing for evolutionary associations between tail color patch presence and other traits. Point color relates to functional hypotheses for flash patches as indicated in the text: flocking (orange) include habitat openness, ground foraging, winter & mixed flocking, social/sexual selection (green) variables include polygyny, polyandry, territoriality, and foraging strategy (blue) variables include flush-pursuit foraging, diet. Coefficients are shown for all models with $\Delta AIC < 10$. Coefficient estimates from the best model by AIC are shown in black, with bars indicating standard errors. Tail tip point size is scaled by model fit, such that the best models have the largest points. For categorical predictor variables, coefficients indicate the change in log odds associated with being migratory, engaging in winter flocking, engaging in mixed flocking, using flush-pursuit foraging, and having either an invertebrate or plant diet vs. an omnivorous diet. The remaining variables (log body mass, habitat openness, ground foraging activity, and territoriality) were treated as numerical variables, and were scaled such that their coefficient magnitudes can be compared. α , $R_{lik_full}^2$, and $R_{lik_pred}^2$ for the best models for each sex/patch combination were as follows: female tail edge: $\alpha = 0.026$, $R_{lik}^2 = 0.458$, $R_{lik_pred}^2 = 0.040$. Male tail edge: $\alpha = 0.026$, $R_{lik}^2 = .458$, $R_{lik_pred}^2 = 0.037$. Female tail tip: $\alpha = 0.038$, $R_{lik}^2 = 0.239$, $R_{lik_pred}^2 = 0$. Male tail tip: $\alpha = 0.038$, $R_{lik}^2 = 0.245$, $R_{lik_pred}^2 = 0$.

contexts, including as anti-predator signals, mating displays, and when foraging (Baird 1967, Ramesh and Lima 2019, Randler and Kalb 2020).

The majority of wing and tail flash patches in North American passerines are white, while rump patches are typically other colors (Figure 2). Avian plumage has the potential to occupy a range of color space, suggesting that the predominance of white plumage in flash signals is convergent and likely functional (Brooke 2010, Stoddard and Prum 2011).

White coloration provides contrast with all other body colors, and is expected to be visible to a range of signal receivers across diverse lighting conditions (Beauchamp and Heeb 2001, Penteriani and Delgado 2017). The predominance of contrasting rump colors other than white was surprising to us but matches patterns documented in other groups of birds, notably Australian land birds (Delhey 2015). In multiple avian species, rump color is known to be a functional signal (Doucet 2002, Siefferman et al. 2005). Future work could

Flash - Rump

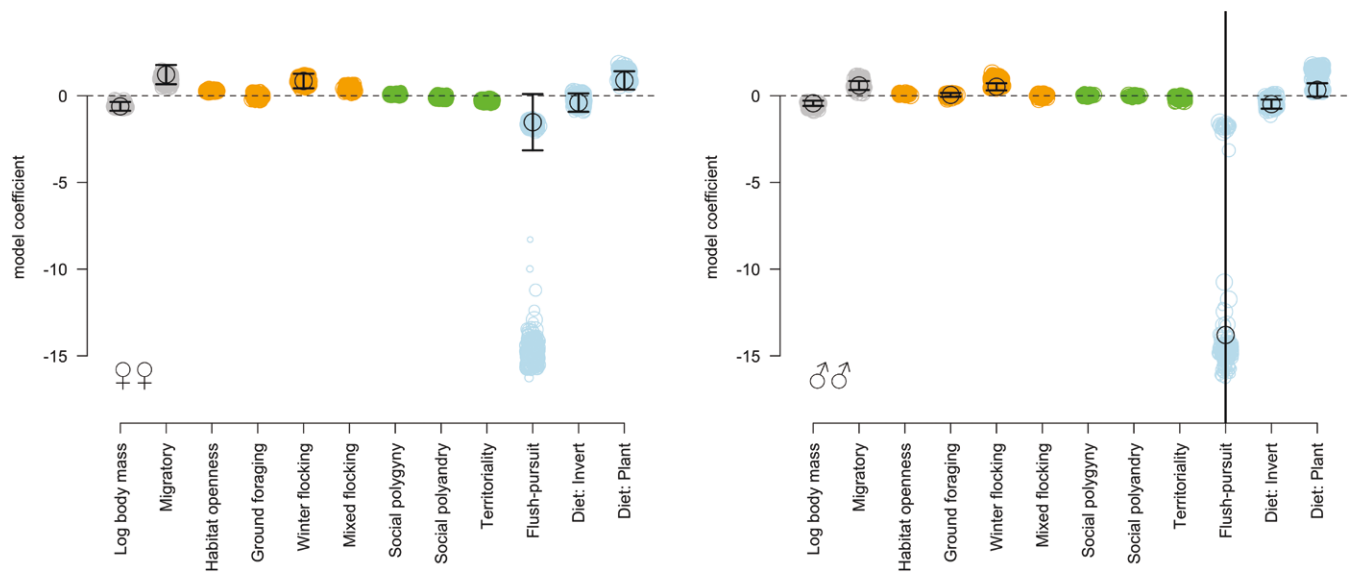


FIGURE 5. Model coefficients from phylogenetic logistic regression model set testing for evolutionary associations between rump color patch presence and other traits. Point color relates to functional hypotheses for flash patches as indicated in the text: flocking (orange) include habitat openness, ground foraging, winter & mixed flocking, social/sexual selection (green) variables include polygyny, polyandry, territoriality, and foraging strategy (blue) variables include flush-pursuit foraging, diet. Coefficients are shown for all models with $\Delta AIC < 10$. Coefficient estimates from the best model by AIC are shown in black, with bars indicating standard errors. Point size is scaled by model fit, such that the best models have the largest points. For categorical predictor variables, coefficients indicate the change in log odds associated with being migratory, engaging in winter flocking, engaging in mixed flocking, using flush-pursuit foraging, and having either an invertebrate or plant diet vs. an omnivorous diet. The remaining variables (log body mass, habitat openness, ground foraging activity, and territoriality) were treated as continuous numerical variables, and were scaled such that their coefficient magnitudes can be compared. α , $R^2_{lik_full}$, and $R^2_{lik_pred}$ for the best models for each sex/trait combination were as follows: Female rump: $\alpha = 0.184$, $R^2_{lik} = 0.232$, $R^2_{lik_pred} = 0.187$. Male rump: $\alpha = 0.006$, $R^2_{lik} = 0.328$, $R^2_{lik_pred} = 0.204$.

examine the effectiveness of differently colored avian flash patches in multiple communication contexts.

We found evidence for phylogenetic signals in all static and flash patches that we examined, indicating a fair degree of evolutionary conservatism of feather patch presence in both static and flash signals. Males and females exhibited similar levels of phylogenetic signal across traits, with the possible exception of the rump patch, in which females exhibited less phylogenetic signal ($D_{female} = 0.50$, $D_{male} = 0.36$). It is possible that this difference could indicate stronger among-lineage variation in selective environments for rump contrast in females vs. males, potentially due to life-history or behavioral sex-differences. Across species, the substantial level of evolutionary conservatism in feather patch presence could suggest either that closely related lineages experience similar selective environments on such patches, that selection is not especially strong, or that limited genetic variation occurs in the genes underlying these patches. We examined the first possibility by examining evolutionary correlations with other traits or proxies for selective environments. We tested 3 hypotheses for the evolution of flash signaling, and found evidence to support 2: (1) that flash signals are driven by flocking behaviors, and (2) that flash signals co-evolve with flush-pursuit foraging. We discuss these results below.

Hypothesis Group 1: Flash Signals Evolve to Promote Flocking Behaviors

We recovered evidence that contrasting rumps specifically are associated with flocking behaviors and additional movement-associated variables (migration and plant-based diets) across

phylogeny in North American passerines, while not recovering similar evidence for an association with such behaviors for wing and tail flash signals, or static signals. These results are consistent with Brooke (1998), who found correlations between dorsal flash signals and flocking behavior in shorebirds of the order Charadriiformes, though the strongest correlations among shorebirds were for back and wing patches instead of rumps. Further, our results are consistent with those of Stang and McRae (2009), who found an association between flocking and high-contrast white undertail coverts in the rails, family Rallidae. While not specified as flash signals by Stang and McRae (2009), rail undertail coverts are hidden in some postures, including when rails are at rest. Thus, there is evidence for correlated evolution of flocking behavior and flash patches visible from the rear across 3 major lineages of birds, suggestive of a broad evolutionary pattern.

Winter flocking, migration, and plant-based diets (fruits, seeds, and nectar) were positively associated with contrasting rumps in our best models for both sexes and across the candidate model sets. It can be reasonably argued that all 3 of these variables connect to aspects of group cohesion. The association of rump contrast patches with winter flocking provides the strongest support for a role for flock cohesion; however, there may be benefits of cohesion during migratory movements even for species that do not form winter flocks. Moreover, as plant resources tend to be patchily distributed, species with plant-based diets may be especially well poised to benefit from cohesion during group movements. Thus, we provide some evidence here that the evolution of contrasting rump patches is related to flocking behavior, and we find the most compelling potential functionality to be the

facilitation of flock cohesion, although anti-predator functionality (Palleroni *et al.* 2005) may also be present. Finally, we emphasize that we scored rump patches as occurring where rump colors contrasted with mantle plumage. In some cases, such contrast is subtle (to human observers). Future analyses could incorporate particular colors or forms of contrast, or examine the degree of contrast while incorporating bird color perception with an avian visual model, to examine this question in a more detailed fashion.

We hypothesized that signaling species identity would be important in contexts where species are intermingled, and therefore tested for the coevolution of flash plumage patches and mixed-species flocking. We found limited evidence that flash signals are disproportionately abundant in mixed-species flocks. In males, wing flash patches were weakly positively associated with mixed flocking. Color patches can be important signals of species identity in diverse animal lineages (Couldridge and Alexander 2002, Cuthill *et al.* 2017, Mason and Bowie 2020, Qvarnström *et al.* 2010, Svensson and Friberg 2007). Alternatively, these results suggest a possible convergent evolution of signals that maintain flock cohesion in mixed-species flocks, which can confer the same benefits as conspecific flocking for species that occur in them (Goodale *et al.* 2020). Most of the examples of possible convergent plumage evolution in Kimball *et al.* (2023) deal with static plumage patches or even outright mimicry involving may different static traits. Our results extend this result to include flash signals, which could help keep these flocks together when they move between patches. It would be interesting to determine if many of the hypothesized mimetic species that share similar static traits in the Asian flocks studied by Kimball *et al.* (2023) also share flash signals and if these traits vary within species that flock with different species across their ranges.

Hypothesis Group 2: Flash Signals Evolve via Social and/or Sexual Selection

We tested the hypothesis that avian flash signals result from variation in social or sexual selection environments by looking for evolutionary correlations between flash plumage patches and polygyny, polyandry, and territoriality. We ran analyses for both sexes and found no evidence that flash signaling coevolved with socially selected traits in males or females. Prior research shows that members of individual bird species (including some in our sample) use wing and tail flash patches in mate choice (Griggio *et al.* 2011, J. A. Hill *et al.* 1999, Török *et al.* 2003) and intrasexual competition (Cline *et al.* 2016, Järvistö *et al.* 2013, Morales *et al.* 2014). Despite this, flash signals do not appear to be more widespread among polygamous and territorial lineages. The same is true for some static plumage patches; although wing bars can carry information content in mate choice situations, they do not appear to coevolve with social traits more broadly (Moreno-Rueda and Hoi 2012, Senar *et al.* 2005).

As our subjects were North American species, many of them are dichromatic and show differentiated sex roles associated with mating, territoriality, social, and ecological conditions that can drive sex differences. For example, nest concealment pressures might be different for males and females in species where only females incubate. Flash signals appear to be more common among species with more concealed nests, but sex differences have not been tested (Baker and Parker 1979).

Flash signal presence can vary with parental care by each sex, confirming that sex roles and social variables can affect flash signaling (Baker and Parker 1979). Coverable plumage patches have also been implicated in maintaining dominance hierarchies in a dichromatic, polyandrous species (Hansen and Rohwer 1986). Thus, evidence suggests that differentiated sex roles might relate to mating behaviors, and flash signaling, but not in entirely consistent ways across species.

Hypothesis Group 3: Flash Signals Evolve in Conjunction with Diet and Foraging Strategy

Our results showed that the general diet (plant-based, insect-based, or omnivorous) did not strongly covary with flash signaling in North American passerines, but that diet in combination with other traits supported the flock cohesion hypothesis as discussed above. Additionally, a specific foraging technique predicted the evolution of wing and tail flash patches: flush-pursuit foraging. This foraging technique was relatively rare in the dataset but consistently co-occurred with flash patch evolution. The low sample size of flush-pursuit foragers led to large model error estimates relative to other traits, so we encourage future studies to include a robust, global sampling of foraging techniques among many more species, both with and without flash plumage signals. Our own observations suggest that this tactic is used by more species than the dataset reflected (S.K.R. personal observation), as our analyzed evidence of flush-pursuit foraging was restricted to those species for which it was reported in the *Birds of The World* (Billerman *et al.* 2023).

Interestingly, most of the flush-pursuit foragers in our dataset were insectivorous, so the observed association of flash signals with flush-pursuit foraging appears to be driven by foraging behavior, rather than prey item identity. Behavioral studies have confirmed that multiple avian species use flash patches specifically on the wing and tail during flush-pursuit foraging, and that tail flash patches are maintained by stabilizing selection (Mumme 2002, 2014, 2023, Mumme *et al.* 2006, Peltier *et al.* 2019). In accordance with this research, we found that a flush-pursuit foraging strategy was positively associated with wing and tail flash patches in our sample. We also supported our prediction that flush-pursuit foraging would not (or would negatively) correlate with rump flash patches because rumps are typically not visible to flushed prey. Our models linked wing flash patches to flush-pursuit foraging more strongly among females than males. Although minor, these sex differences raise questions about sex role differences that might drive dichromatism.

In contrast to the patterns seen in wing and tail flash coloration, we found that static color patches on tail tips and rump flash patches were negatively or not associated with flush pursuit foraging in a phylogenetic context. A flush-pursuit foraging strategy might be selected against white tail tips to prevent prey from recognizing the predator by the presence of continuously visible white coloration. Contrasting color is critical to the success of flush-pursuit foraging, and birds might benefit from limiting their contrasting signals to those used in flash displays (Jabłoński and Strausfeld 2009). The negative-trending correlation between flush-pursuit foraging and rump flash patches is less obviously functional but highlights that different flash patches can evolve independently in conjunction with other avian traits.

Conclusions

Researchers have called for more studies of dynamic color communication among animals (Hutton *et al.* 2015, Schön 2009). Here we contributed to that field by examining avian flash color patch presence within a phylogenetic context. Our analyses documented rates of flash color patch occurrence among North American passerines, demonstrated that most of these patches are white in color, and supported the hypotheses that flocking behaviors and a flush-pursuit foraging strategy can correspond with selective regimes that increase the probability of evolving avian flash signaling patches. We did not find evidence that flash signals coevolve with mating or territorial systems and thus did not support hypotheses relating to social selection. It is clear from other research that flash signals can evolve subject to social selection in individual species, but our proxies for dimensions of social selection were not predictive of widespread flash signal evolution. Overall, our results underscore the role that natural selection can play in the evolution of conspicuous avian plumage. Our analyses did not, however, test all possible flash signal functions or trait correlations, leaving room for future studies.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

The authors followed ethical scientific practices in collecting, analyzing, and reporting data. This study did not use live animals or specimens, so was not subject to animal welfare oversight.

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

L.B., J.M., and S.R. conceived and designed the research and methods. L.B., J.M., and H.J. conducted the research. J.M. led the data analysis. L.B. wrote the manuscript with assistance from all authors.

Data availability

Dataset and results are provided in the Supplementary Material. Scripts and the data files necessary to perform analyses are available at Benedict *et al.* (2024).

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