New Idea

The paradox of the Birds-of-Paradise: persistent hybridization as a signature of historical reinforcement

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Abstract

The birds-of-paradise (Paradisaeidae) exhibit some of the most diverse color patterns and courtship displays among species. Paradoxically, birds-of-paradise hybridize more frequently than other birds, even hybridizing across species and genera with remarkably divergent color patterns. Hybridization among such distinctly colored species might suggest that reinforcement was unimportant for color pattern divergence because reinforcement favors trait divergence that reduces the likelihood of hybridization over time, and is expected to eliminate hybridization between species. Here I present an alternative view: that persistent but infrequent hybridization among species that differ markedly in prezygotic isolating traits, such as color pattern in birds, represents the signature of historical reinforcement, and occurs when (i) divergence in single traits can reduce, but not prevent, hybridization, (ii) trade-offs constrain the divergence of prezygotic isolating traits, and (iii) selection against hybrids is weak when hybrids are rare. Considering these factors, the paradox of the birds-of-paradise—where species with distinct prezygotic isolating traits are more likely to hybridize at low frequencies—is the expected outcome of reinforcement. Sexual selection by female choice could further intensify the effects of reinforcement, particularly if reinforcement directs sexual selection to different traits in hybridizing populations. This latter process could potentially explain the exceptional diversity of extravagant ornaments in the birds-of-paradise.

Keywords: speciation, sexual character displacement, sexual selection, mate choice, color pattern, reproductive isolation

Male birds-of-paradise (Passeriformes: Paradisaeidae) represent the pinnacle of color pattern evolution, with exaggerated feather structures and diverse plumage and bare part coloration that are used in eccentric and complex courtship displays (Wallace 1869, Darwin 1871, Mayr 1945, Frith and Beehler 1998, Frith and Frith 2009, Laman and Scholes 2012). Sexual selection has been important in the evolution of such diversity—most species display singly or in leks, with few males obtaining most copulations and females of most species raising offspring without male help (Pruett-Jones and Pruett-Jones 1990, Frith and Beehler 1998, Frith and Frith 2009). Species differences in color pattern have also been thought to allow females to avoid mating with another species (Wallace 1889, Mayr 1963: 96–98), and thus represent a prezygotic isolating trait common to many species of birds (Dobzhansky 1970). Intensive studies of birds-of-paradise, however, revealed what appears to be a paradox. While male color patterns are often dramatically different among species, hybridization among birds-of-paradise is common at low frequencies, even among some of the most divergent of species and genera (Mayr and Gilliard 1952, Frith and Beehler 1998). For example, Mayr (1945, 1963) suggested that one in every 20,000 museum specimens of birds-of-paradise was a hybrid, contrasting with one in every 60,000 specimens for birds in general. In addition, 13 different intergeneric, and 7 different intrageneric hybrid cross combinations have been described from the wild (Frith and Beehler 1998, Frith and Frith 2009), despite only 40 species in the family and deep divergences between most of the hybridizing species (Irestedt et al. 2009). While sampling bias could

potentially explain part of the pattern (i.e., hybridization in the birds-of-paradise is reported more often than in other bird families because their hybrids look strikingly different), other groups with much less divergence in color pattern among species show virtually no hybridization despite close scrutiny and broad regions of sympatry (McCarthy 2006). These apparent differences in the tendency to hybridize beg the question: why do species of birds with such distinct coloration continue to hybridize?

Recurrent hybridization among the birds-of-paradise, and in other groups of distinctly colored birds, might suggest that reinforcement did not play an important role in the divergence of color patterns in birds. If reinforcement was important in the evolution of color patterns, we might expect distinctly colored species of birds to hybridize less frequently than similarly colored species because reinforcement favors trait divergence that reduces the likelihood of hybridization over time, and is expected to eliminate hybridization between species (Coyne and Orr 2004: 66). Alternatively, reinforcement could be important in birds, but instead act on female discrimination rather than male color pattern (Price 2008), leaving male color pattern divergence uncorrelated with the likelihood of hybridization among species. These relationships between hybridization, trait divergence, and reinforcement have broader implications beyond birds: if reinforcement underlies major phenotypic differences among closely related species, then the species with large phenotypic differences should have lost their tendency to hybridize.

Here I propose an alternative hypothesis that, to my knowledge, has not been considered. The occurrence of hybridization should be more common among species with greater divergence of traits involved in prezygotic isolation if they have evolved these traits due to reinforcement. In other words, the persistent hybridization among phenotypically divergent species is a signature of historical reinforcement rather than evidence against it. I first illustrate the predicted relationships between hybridization and color pattern divergence for within species patterns of selection versus among species patterns of evolution using a well-known, unrelated example of nestling begging and nest predation. I use this parallel example of nest predation and nestling begging because it is well documented and exhibits broadly similar patterns of trade-offs, selection, and evolution to the case of hybridization, reinforcement and color pattern evolution. I follow with evidence to support the mechanisms underlying the predicted patterns in the case of hybridization, reinforcement, and the divergence of color pattern and other prezygotic isolating traits.

A parallel example: nest predation and nestling begging loudness

Patterns of selection on a trait within species are often opposite to patterns of evolution among species for the same trait. For example, within a population, nestling birds that beg loudly are more likely to be found by predators and eaten (Figure 1a, McDonald et al. 2009, Haff and Magrath 2011). Selection due to predation thus favors quieter nestlings within a population. The evolutionary relationship between predation and begging among species, however, is the opposite pattern: species of birds with the highest nest predation rates, like thrushes (Turdidae), have quiet nestlings, while species with safer nest sites, like woodpeckers (Picidae), have nestlings that beg very loudly (Figure 1b, Briskie et al. 1999). Two factors cause the opposing slopes between selection and evolution. (i) Nestling begging influences, but does not control nest predation rates. Instead, many factors influence the likelihood of predation (e.g., Thompson 2007), and thus thrushes have higher nest predation rates than woodpeckers, even in the absence of nestling begging (Martin and Li 1992, Martin et al. 2000). (ii) The evolution of begging in response to nest predation involves constraints and trade-offs. Nestling begging has a benefit of eliciting more food from parents (Budden and Wright 2001), and thus in the absence of nest predation as a constraint, nestlings should beg very loudly, as they do in many woodpeckers (Briskie et al. 1999). These two factors cause the evolution of loud nestlings in species with safe nest sites, and quiet nestlings in species whose nests are more likely to be depredated (Figure 1b, Briskie et al. 1999). The opposing slopes for patterns of selection versus evolution is a common pattern, characterizing many diverse traits in nature (e.g., plant defense and rates of herbivory, Coley and Aide 1991, immune function and rates of infection, Møller 1998).

Reinforcement and the divergent evolution of species

Similarly, reinforcement is thought to favor individuals with color patterns that are more divergent from closely related species because these individuals are less likely to mate with the wrong species, which is costly (Figure 1c, Servedio and Noor 2003). Across species, however, we should again expect the opposite relationship, where species with the most divergent color patterns are more likely to hybridize (at low levels), reflecting historical reinforcement for the divergence of color patterns among species (Figure 1d). We expect the opposing slopes between patterns of within species selection versus among species evolution for the same reasons as

Figure 1. A parallel example of opposing slopes between patterns of selection within populations (a), and patterns of evolution among species (b), using the established relationships between nestling begging loudness and nest predation in birds (Briskie et al. 1999, McDonald et al. 2009, Haff and Magrath 2011). Within a population, louder nestlings are more likely to be found by a predator and eaten (a), but across species, the species with the highest nest predation rates have the quietest nestlings (b). The patterns within populations versus among species are opposite because (i) nestling begging loudness does not control nest predation — the evolution of quieter nestlings reduces, but not prevent, nest predation, and (ii) trade-offs constrain the evolution of nestling begging — begging provides benefits (increased food) to nestlings and thus in the absence of nest predation, nestlings should beg loudly. We expect similar relationships between color differences among closely related species and the probability of hybridization, where patterns of selection within populations (c) should be opposite to patterns of evolution among species (d). We expect these opposite patterns for within population patterns of selection versus among species patterns of evolution because (i) divergence in color patterns can reduce, but not prevent, hybridization, and (ii) trade-offs constrain the divergence of color patterns due to reinforcement, and in the absence of hybridization [e.g., in geographically isolated (allopatric) species], many species will show little divergence in color pattern and no current hybridization. In the case of color pattern divergence and hybridization, we also expect opposing patterns of within population selection versus among species evolution because (iii) selection against hybrid mating is weak when hybridization is rare, hindering the complete elimination of hybridization by reinforcement.

the nestling begging example. (i) Color pattern divergence influences, but does not control the propensity to hybridize. Instead, the tendency to be rare, displays, display sites, songs and mechanical sounds, imprinting, habitat choice, lack of paternal help in rearing young, and other factors can cause hybridization, even when color patterns are divergent (Sibley 1950, Randler 2002, Frith and Beehler 1998, Price 2008). (ii) The evolution of color pattern involves constraints and trade-offs. Color patterns are important for mate attraction (Hill 2006), especially in the birds-of-paradise (Frith and

Beehler 1998), and divergent evolution of color pattern in response to reinforcement could make males less attractive to females. Color pattern evolution may also be constrained by other factors, such as developmental pathways, signaling efficacy, the need for crypticity to reduce predation, or resistance to wear and feather parasitism (Wallace 1889, Hill and McGraw 2006). These other factors may similarly constrain the divergent evolution of color patterns due to reinforcement, and in the absence of hybridization as a selective pressure [e.g., in geographically isolated (allopatric) species that

have never hybridized and did not diverge in color due to reinforcement], we should find species with little color pattern divergence and no present day hybridization. One other factor also helps to create a positive relationship between color pattern divergence across species and the tendency to form hybrids: (iii) selection against hybridization becomes weak when hybrids are rare, making the complete elimination of hybrids by reinforcement unlikely (Moore 1957: 336, Spencer et al. 1986, Coyne and Orr 2004: 371-372, Price 2008). Thus, species that evolved divergent color patterns, or other prezygotic isolating traits, in response to reinforcement should continue to hybridize at low frequencies (Figure 1d), consistent with the patterns of hybridization in the birds-of-paradise.

Whether the relationships between trait divergence and hybridization show opposite slopes within populations versus among species (Figure 1) depends on the time frame for comparisons. In the case of species in the process of diverging by reinforcement, we should expect to find species pairs at any stage of divergent evolution, and thus the patterns among species are more likely to reflect the patterns of selection (Figure 1c). At the opposite extreme, diverging lineages should eventually cease hybridizing altogether, as traits involved in reproductive isolation continue to diverge and accumulate (Coyne and Orr 2004). In birds, natural hybrids are common within genera, rare between genera, and virtually unknown between taxonomic families (McCarthy 2006).

Within the broad time frame after reinforcement has occurred, but before complete isolation has evolved, however, a greater incidence of hybridization among phenotypically distinct species (Figure 1d) should be a common pattern among organisms that have diverged by reinforcement, not just birds. We should expect this relationship for the same reasons: (i) the likelihood of hybridizing is unlikely to be controlled by one trait, (ii) prezygotic traits should frequently encounter trade-offs and constraints, and (iii) reinforcement should reduce, but not eliminate, hybridization because selection against hybrids is weak when hybrids are rare. One or more of these conditions should be met in most diverging lineages.

Sexual selection by female choice, hybridization, and reinforcement

Sexual selection has played a significant role in the evolution of color patterns and courtship displays in the birds-of-paradise (Frith and Beehler 1998), and could also help to intensify the effects of reinforcement on prezygotic isolating traits through several different mechanisms (e.g., Liou and Price 1994, Price 2008). For example, the lack of male parental care in groups with strong sexual selection, such as the birds-of-paradise,

Figure 2. Sexual selection could increase the likelihood and rate of hybridization among populations, increasing the potential for reinforcement. For example, allopatric populations within species may differ in the degree to which they develop sexually selected traits (e.g., due to differences in mutations, sexual selection, or drift). Once sympatric, females, regardless of their population of origin, may prefer males with the most extravagant traits, leading to higher rates of hybridization. In this example, females from both populations prefer males from population B because B males are most extravagant for all traits (crown and throat). Female preference for extravagant traits would thus increase rates of hybridization and the potential for reinforcement, provided that gene flow is not excessive.

may increase the likelihood of errors in mating (thus increasing rates of hybridization) because females are raised without the opportunity to imprint on their fathers (Mayr 1942, Sibley 1950). Similarly, if females prefer the most extravagant expression of a trait, and diverging populations differ in their extravagance, then females of two populations may favor the more extravagant males of one population, increasing rates of hybridization (Randler 2002, Figure 2). In both of these examples, if hybrids are unfit, the increased hybridization could increase the potential for reinforcement, provided gene flow is not excessive (Servedio and Noor 2003). In the latter case (Figure 2), reinforcement may focus on the population whose females are most prone to hybridization, and would favor both female discrimination and male traits that can draw females away from males of the opposite population.

We might also expect isolated populations to show differential divergence of traits due to sexual selection, where some traits are more extravagant in one

population, and other traits more extravagant in the other population (e.g., Endler and Houde 1995, Figure 3). If females prefer the most extravagant expression of a trait, then females that prioritize the trait that is most extravagant in another population may be more likely to hybridize, as compared with females that prioritize the trait that is most extravagant in their own population (Figure 3). If hybrids are unfit, then reinforcement would favor females that prioritize different ornaments—specifically the ornament most extravagant in their own populations—directing sexual selection to distinct ornaments in different populations (Figure 3). This direction of sexual selection by reinforcement would intensify divergence by sexual selection in different ornaments, creating diverse ornamentation across species. Such a process could potentially explain another mystery of the birds-of-paradise: why species show such diverse sexual ornamentation across species, with different traits elaborated in different species (including extravagant breast, tail, crown, scapular, and other feathers, legs, bills, eyes, skin patches, mechanical sounds, vocalizations, courtship displays, and other behaviors; Frith and Beehler 1998, Laman and Scholes 2012).

Persistent hybridization as a signature of historical reinforcement

Why do species of birds with such distinct coloration continue to hybridize? I suggest here that they continue to hybridize because they historically hybridized at high levels, but reinforcement caused the divergence of color pattern that reduced, but could not eliminate, their tendency to hybridize. If true, we might expect other evidence of reinforcement in the birds-of-paradise, such as greater divergence of color patterns with increased sympatry among lineages. A recent test of this prediction found some support—color pattern of male birds-of-paradise differed more as levels of sympatry among lineages increased (Giglio 2012)—but the effect of sympatry could not be adequately distinguished from the correlated effect of divergence over evolutionary time, once phylogeny was controlled (P.R. Martin, unpublished data). We have little information on selection against hybrids in nature; however, the prolonged time required for taxa to achieve sympatry (following initial divergence in allopatry; minimum time to 50% sympatry = 6.2 million years; Giglio 2012), and the lack of evidence for introgression among the majority of hybrid combinations (Frith and Beehler 1998: 502), suggests that hybrids in the birds-of-paradise are often unfit, particularly among hybridizing genera. These patterns are also consistent with a lack of evidence for hybrid origins of species in the birds-of-paradise (Frith and Beehler 1998: 75-76) that suggest that hybridization has not been an important creative

Figure 3. Reinforcement may direct sexual selection to different traits, resulting in the elaboration of different traits in different species. For example, populations within species may differ in the degree to which they develop different sexually selected traits in allopatry. Once sympatric, females may differ in how they rank the importance of different traits in mate selection. In this example, females that rank crowns over throats or red over blue will favor males from population A, while females that rank throats over crowns or blue over red will favor males from population B. In this example, selection against hybrids will direct sexual selection to different traits in different populations (females preferring crowns or red in population A, females preferring throats or blue in population B), intensifying sexual selection on different traits in different populations. Thus, reinforcement can lead to the evolution of diverse, extravagant traits, by favoring differences in the intensity of sexual selection on different traits among sympatric populations. These diverse traits may include completely different characters, such as sounds, colors, plumes, or courtship displays, or similar characters that differ in their patterns of expression, such as different color or sound preferences or regions of coloration.

force in this group, in contrast to some recently diverged radiations of birds (e.g., *Geospiza*; Grant and Grant 1992). We should also expect similar patterns of

persistent hybridization among other groups that show marked differences in prezygotic isolating traits, besides the birds-of-paradise. Ducks (Anatidae), pheasants and grouse (Phasianidae), and hummingbirds (Trochilidae) provide other possible examples in birds (Grant and Grant 1992, McCarthy 2006).

Alternative hypotheses could also explain the paradox of the birds-of-paradise, and I have not rejected any of these alternatives here. For example, intense sexual selection may predispose species to persistent hybridization, such as in cases where females prefer novel traits (Christidis and Schodde 1993), or where females prefer the most extravagant traits, and these traits are more extravagant in one species relative to another (Randler 2002, Figure 2). Alternatively, polygyny may increase rates of hybridization due to selection for indiscriminate mating in males, or increased errors in mate choice resulting from young females raised without male parental care (Mayr 1945, Sibley 1950, Frith and Beehler 1998: 501–503, Frith and Frith 2009).

Nonetheless, from an evolutionary perspective, the paradox of the birds-of-paradise—where hybridization persists at low frequencies among remarkably divergent species—is perhaps not really a paradox at all, nor is it evidence that color pattern differences are unimportant for species recognition during mate choice, or that historical reinforcement did not contribute to the divergent color patterns among species. Instead, hybridization among species with divergent prezygotic isolating traits is the pattern that we should expect if these traits diverged due to reinforcement—a signature of historical reinforcement. Viewing persistent hybridization as an expected consequence of reinforcement, rather than evidence against it, changes our perspectives on the potential importance of reinforcement in speciation and in creating the diversity of traits in nature.

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Response to referee

Hill (2015) contrasts three broad selective pressures on signals or ornaments that can arise during mate choice: species recognition (incorporating evolution by reinforcement), mate quality, and runaway selection. The contrast between selective pressures is clear and helpful, and I agree with much of what he writes. Hill goes on to suggest that the proposal in my essay, that reinforcement may have favored the divergence of ornaments in the birds-of-paradise, is unlikely because (1) reinforcement, as I describe it, would require that many or complex traits be involved in premating isolation, (2) reinforcement (or selection for premating isolation) will rarely act on male signals, and (3) the complexity of selective pressures acting on ornaments will negate a role for reinforcement in their evolution. I disagree with all of these points, and I address each in turn below.

(1) Reinforcement, the elaboration of ornaments, and traits involved in premating isolation

Hill suggests that an implicit prediction in my essay is that "stronger selection for premating isolation leads to the evolution of more elaborate ornamentation" and as a consequence, will require complex female recognition systems that are increasingly prone to error. To be clear, in the essay above I discuss how reinforcement could direct sexual selection to different traits in different populations (Figure 3), potentially causing the elaboration of distinct traits in different populations or species. The elaboration of different ornaments, however, does not require multiple or complex traits for reproductive isolation, as Hill suggests. Instead, we might expect selection to favor the divergence of just one trait—the ranking of trait preference by females. This idea is consistent with a simple basis to species recognition because only one trait is involved. By acting on female trait preference, reinforcement could influence how sexual selection acts on male signals and ornaments, regardless of whether the traits involved are variable signals of quality, or are complex ornaments favored by runaway selection.

I suggest that the directing of sexual selection by reinforcement could help to explain why different species of birds-of-paradise show different elaborated ornaments, such as elaborate head plumes in some species, and elongated tail plumes in others. I don't

suggest that such an interaction would explain diverse ornamentation within populations (although it could). Indeed, the example in Figure 3 shows a reduction in ornamentation in population B after reinforcement, with the loss of crown coloration over time.

(2) Reinforcement rarely acts on male signals

Reinforcement is expected to favor females that prefer males of their own population or species (Noor 1999, Coyne and Orr 2004). In birds, a contentious issue is whether females should simply evolve to better discriminate, or whether females will also favor variant male signals that differ more from co-occurring populations or species, leading to the divergent evolution of male signals by reinforcement (Price 2008, Hudson and Price 2014). Hill (2015) states "selection for premating isolation will act primarily on the recognition systems of females, not male ornaments (Hudson and Price 2014)," implying that male ornaments or signals in birds will rarely diverge in response to reinforcement. What evidence supports this statement? For evidence, Hudson and Price (2014) point out that some species of birds with very different colors or songs hybridize, while some species with similar colors and songs do not. As I discuss in the paper, hybridization between species with divergent signals is entirely consistent with reinforcement acting on these signals (Figure 1). Hudson and Price (2014) also point to the absence of a correlation between song and male color divergence and estimates of assortative mating in a comparative analysis across 17 hybridizing species pairs of birds. These 17 pairs include gulls, quail, woodpeckers, and warblers—groups that differ in the traits that diverge during species formation. To expect a significant correlation in their analysis is overly optimistic, and the lack of correlation provides weak evidence that male signals in birds rarely evolve by reinforcement. In contrast, detailed work on *Ficedula* flycatchers provides excellent evidence for the divergence of both female preferences and male signals in sympatry, and a role for reinforcement in this divergence (Sætre et al. 1997, Sæther et al. 2007, Qvarnström et al. 2010, Sætre and Sæther 2010, Laaksonen et al. 2015). Clearly reinforcement has caused male signals to diverge in some birds. How widespread is this pattern?

If male signals are important for species recognition and evolve by reinforcement, then we expect greater divergence of signals among closely related species that live together in sympatry, relative to allopatry (Coyne and Orr 2004). Previous comparative work found greater divergence in color patterns among sympatric, closely related birds in a test involving 7 diverse families of New World birds (Martin et al. 2010). Hudson and Price (2014) suggest that this relationship reflects a statistical artifact; however, the greater divergence of color pattern as closely related species

move into sympatry persists in a global study involving 246 species and 39 families of birds, using different methods that obviate their concerns (Martin et al. 2015). Importantly, the greater divergence of color patterns among closely related, sympatric birds need not reflect evolution by reinforcement; other selective pressures such as interspecific aggression and ecological interactions that secondarily influence signal evolution could also explain the pattern (Martin et al. 2010, 2015). But evidence to date is certainly consistent with reinforcement driving male signal evolution in birds. The mounting evidence for signal evolution by reinforcement in insects, plants, amphibians, and other groups (e.g., Higgie et al. 2000, Pfennig 2003, Coyne and Orr 2004, Lukhtanov et al. 2005, Lemmon 2009, Ortiz-Barrientos et al. 2009, Hopkins and Rausher 2012, Bacquet et al. 2015, Norton et al. 2015) further begs the question: why should birds be different?

(3) Complexity and conflict among selective pressures acting on ornaments

Hill closes by highlighting the conflict between signals that evolve by sexual selection (mate quality, runaway selection) and those predicted to evolve for species identification, suggesting that the conflict among selective pressures makes signal evolution by reinforcement, as I describe it, unlikely. Not only do I recognize the potential for conflict between sexual selection and reinforcement, I invoke this conflict as a key mechanism for why hybridization might persist following evolution by reinforcement (Figure 1), and for how reinforcement should act in organisms subject to strong sexual selection (Figures 2, 3). For example, I expect hybridization to persist after traits such as color or song have diverged by reinforcement (Figure 1) because many other factors influence the propensity for species to hybridize. These factors include traits associated with strong sexual selection, such as a lack of male parental care and the potential for indiscriminate mating within lekking systems. Thus, hybridization could persist in species that have diverged by reinforcement, in part, because of strong runaway selection.

There is little doubt that the ornaments in the birds-of-paradise evolved in response to sexual selection; we do not expect reinforcement to create elaborate ornaments. However, we should expect sexual selection and reinforcement to interact, in part because sexual selection can increase the risk of hybridization among divergent populations that become sympatric (e.g., Figure 2). If costs of hybridization occur and gene flow is not excessive, how might selection reduce the likelihood of hybridization over time? Some have argued that we should see only greater female discrimination and little change in male signals over time (Hudson and Price 2014). Instead, empirical examples

suggest that both preferences and signals often evolve together to reduce the risk of hybridization (e.g., Sætre et al. 1997, Lemmon 2009). Such dynamic interactions may help to explain broad patterns of signal variation across species, including groups subject to strong sexual selection like the birds-of-paradise.

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